IX. *The Development of the Skull of the Shrew.*

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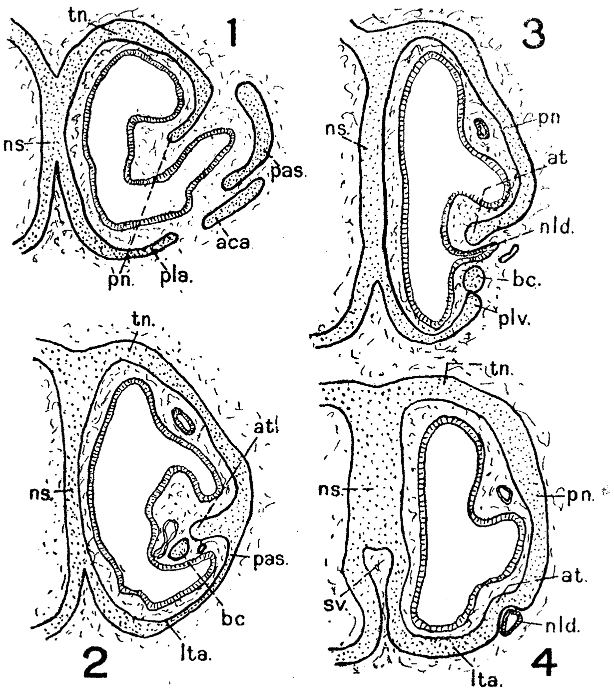
§ I. INTRODUCTION.

THE student of the mammalian chondrocranium, the existing knowledge of which has recently so excellently been summed up by MATTHES (1921*b*, 1922), cannot but be surprised at the fact that a mammal so interesting and easily available as the shrew has not yet been thoroughly studied by modern methods. Of PARKER's magnificent pioneer work (1885) it is unnecessary to speak; the only other investigator who has turned his attention to the shrew is LEVI (1909), who did not, however, make a model of it, and ÄRNBÄCK CHRISTIE-LINDE (1907), who studied certain special points only.

The present work was done in the Department of Zoology and Comparative Anatomy of the Oxford University Museum, on a number of embryos of *Sorex araneus*, which I owe to the generosity of my friend Mr. C. S. ELTON, to whom my thanks are here extended. These embryos were cut into series of sections, and one of these, of an embryo 11 mm. in length, was reconstructed into a blotting-paper—wax model, at a magnification of 80 diameters. In the construction of this model I enjoyed the assistance of Mr. J. H. BEAL, which help is hereby gratefully acknowledged. To my wife I am greatly indebted for the preparation of the Plates illustrating the model for publication. Lastly, I take great pleasure in recording my debt to Prof. GOODRICH for his constant interest and encouragement in this and kindred work.

§ II. DESCRIPTION OF THE CHONDROCRANIUM.

The general form of the chondrocranium of a mammalian embryo is now, fortunately, sufficiently well known and familiar to render unnecessary an exhaustive description of that of the shrew. The various structures will therefore be described and their relations given in as brief a manner as possible, consistent with inclusion of only that detail which is necessary to bring out points of comparison and interpretation. There are two chief methods of describing the chondrocranium. One, which is favoured by most German investigators, consists in dividing the skull transversely into a number of regions, such as occipital, otic, sphenoid and ethmoid, each of which can be treated separately. The other method, which was devised by FAWCETT (1917), consists of a subdivision of the chondrocranium into: 1, the central stem; 2, its appendages; 3, the lateral structures; 4, the commissures interconnecting these; and 5, structures forming the roof. While the former method is undoubtedly convenient for purposes of description and consulting descriptions, the latter has the advantage of conveying a better impression of the developmental relationships of the parts to one another, and will largely be followed here.



FIGS. 1.—Section 1–2–3. 2.—Section 1–2–9. 3.—Section 1–3–5. 4.—Section 1–4–7.

A.—*The Central Stem.*

The central stem is divisible into a posterior or parachordal region (also called the basal plate), and an anterior trabecular region, which is continued forwards as the nasal septum. Except for the nasal septum, the central stem is a flat horizontal plate which forms the floor of the brain-case; the nasal septum, on the other hand, is a flat vertical plate dividing the two halves of the nasal capsule. The passage from one region to another is gradual, and, at the stages studied, the cartilages composing these regions are directly continuous. They lie in a gentle curve, concave ventrally, but not nearly so markedly as in many other forms. There is no dorsum sellæ (crista transversa or clivus), nor tuberculum sellæ, and consequently the depression which lodges the pituitary body (the fossa hypophyseos) is barely visible.

The nasal septum is thin; the trabecular region is narrow in front and broader behind; the parachordal region or basal plate is also narrower in front than behind because of the cochlear portions of the auditory capsule which constrict it and form prominences on each side. The notochord has quite disappeared.

On each side of the central stem in the trabecular region is a projection, the processus alaris, by means of which the ala temporalis is attached to the central stem.

1. *Foramina in the Central Stem.*—The *fenestra hypophyseos*, in the middle line, marks the region of the original division between the trabecular and parachordal portions of the central stem. Through it passes the vestige of the hypophysial stalk.

The *carotid foramina* serve for the entry into the cranial cavity of the internal carotid arteries. They are situated on a level with the fenestra hypophyseos, and each carotid foramen is bounded: medially by the main body of the central stem; posteriorly by the front of the cochlear portion of the auditory capsule; laterally by a bar of cartilage which represents the hindmost part of the trabecula cranii of lower vertebrates, and which in mammals stretches from the processus alaris to the cochlear capsule and is called the alicochlear commissure; anteriorly by the region of the central stem which lies at the root of the processus alaris.

The *basicranial fenestra* is absent in 11 mm. embryos of Sorex, but in younger embryos (8·3 mm. long) remnants of it are perhaps found in two perforations of the basal plate in the middle line, one behind the other.

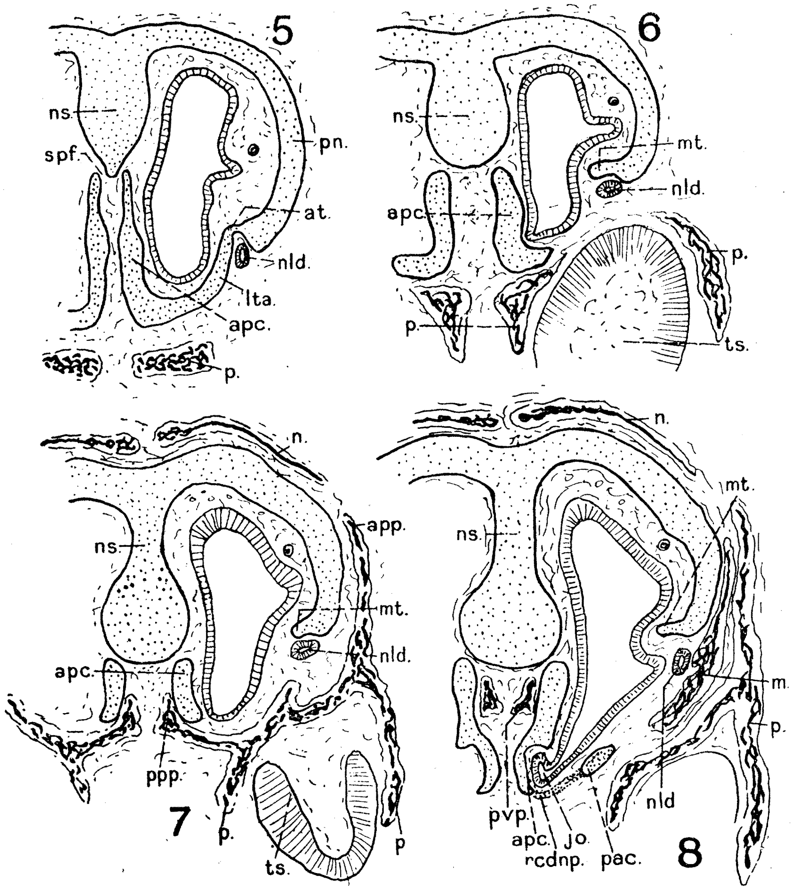
2. *Foramina enclosed between the Central Stem and neighbouring Structures.*—A number of structures are attached to the lateral edges of the central stem, many of them thereby enclosing foramina and fissures. These structures are the following: occipital arch, auditory capsule, ala temporalis, postoptic and preoptic roots of the ala orbitalis, planum antorbitale, and tectum nasi. The suprafacial commissure is morphologically a lateral appendage of the central stem, but in mammals it is closely associated with the auditory capsule and will be dealt with in connexion with that structure.

The *foramen magnum* is enclosed between the hindmost edge of the basal plate, the two occipital arches, and the tectum posterius of the supraoccipital cartilages. Through it the spinal cord and the basilar artery pass out of the skull.

The *condylar foramen* is situated between the root of the occipital arch and the basal plate, and is a comparatively small hole through which the hypoglossal nerve emerges from the cranial cavity. No trace was found of additional foramina.

The *fissura metotica* is a slit-like aperture between the basal plate medially, the occipital arch posteriorly, and the auditory capsule laterally. The fissura metotica is closed anteriorly by the fusion of the medial wall of the auditory capsule with the edge of the basal plate. By the approximation of the medial wall of the auditory capsule to the lateral edge of the basal plate, the fissura metotica is divided into two apertures. The hindmost of these is the foramen jugulare, through which the glossopharyngeal, vagus, and spinal accessory nerves, and the internal jugular vein, leave the cranial cavity. The anterior subdivision of the fissura metotica is the *apertura medialis* of the recessus scalæ tympani, which contributes to the formation of the *aquæductus cochleæ*, through which the ductus perilymphaticus enters the cranial cavity. Further description of these structures is reserved for the discussion.

The *sphenoparietal fontanelle* is the very large opening in the side of the chondrocranium, which is bounded :—medially by the central stem (and the ala temporalis) ; posteriorly by the auditory capsule ; dorsally by the orbitoparietal commissure (tænia marginalis) ; and anteriorly by the ala orbitalis. Through it the oculomotor, trochlear, trigeminal, and abducens nerves leave the cranial cavity.



FIGS. 5.—Section 2-1-4. 6.—Section 2-2-7. 7.—Section 3-1-1. 8.—Section 3-1-6.

The *optic foramen* is enclosed between the postoptic and preoptic roots of the ala orbitalis, and serves for the exit of the optic nerve.

The *orbitonasal fissure* is an opening bounded :—posteriorly by the ala orbitalis ; dorsally by the commissura sphenethmoidalis ; anteriorly and ventrally by the planum antorbitale. Through it the first or profundus branch of the trigeminal nerve (also termed the ethmoid nerve) leaves the orbit and passes into the supracribrous recess, beneath the dura mater and over the cribriform plate, to reach the dorsal surface of the nasal capsule.

The *fenestra olfactoria* is bounded :—medially by the dorsal edge of the septum nasi (crista galli) ; anteriorly by the hinder edge of the tectum nasi ; laterally and posteriorly by the commissura sphenethmoidalis and ala orbitalis. The fenestra olfactoria is closed by the dura mater, which is stretched over it, but which is pierced by the strands of the olfactory nerve, which thereby leave the cranial cavity and enter the supracribrous recess.

The *fenestra cribrosa* (which must be distinguished from the fenestra olfactoria) is subdivided into a number of smaller apertures by the cartilages of the cribriform plate but its general relations are as follows. It is bounded :—medially by the dorsal edge of the septum nasi ; anteriorly by the hind edge of the tectum nasi ; laterally by the dorsal edge of the planum antorbitale ; and posteriorly by the front edge of the tectum nasi posterius. The fenestra cribrosa is thus wholely outside the true cranial cavity, and it serves to admit the olfactory nerve from the supracribrous recess into the nasal capsule. The supracribrous recess is the space comprised between the fenestra olfactoria and the fenestra cribrosa.

The *fenestra basalis* and the *fenestra narina* are described below with the nasal capsule.

3. *Ossifications in the Central Stem.*—Two cartilage-bones are to be found ossifying in the central stem. The more anterior of these is the basisphenoid which surrounds the fenestra hypophyseos. The more posterior is the basioccipital which contributes to the border of the foramen magnum.

B. *The Lateral Structures Appended to the Central Stem.*

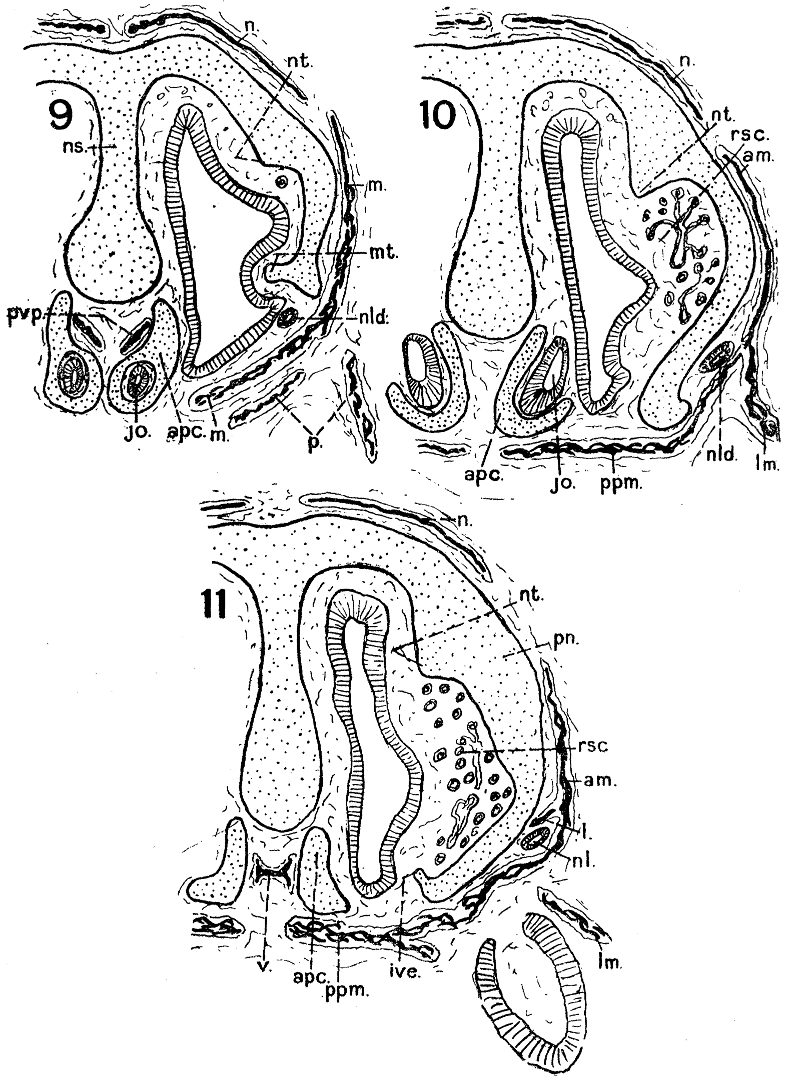
1. The *occipital arches* are curved plates of cartilage, attached to the postero-lateral corners of the basal plate. The posterior edge of each occipital arch forms a side of the foramen magnum. The greater part of the anterior edge (which forms the so-called lamina alaris) is fused with the posterior wall of the auditory capsule, for the fissura occipito-capsularis inferior of other forms is obliterated in Sorex. Its position is indicated by the recessus supra-alaris, which lodges the lateral venous sinus. Ventrally, the recessus supra-alaris runs into the foramen jugulare. Seen from the outside, the processus paracondyloideus (formed from the ventral part of the lamina alaris) is not at all prominent. Dorsally, the occipital arch is fused with the supraoccipital cartilage.

The exoccipital bones are ossifying in the cartilage of the occipital arches.

2. The *auditory capsule* is divisible into two portions. One is postero-dorsal in position and lodges the utricle and the semicircular canals, forming the canalicular part of the auditory capsule. The other is antero-ventral in position, and accommodates the ductus cochlearis of the saccule, forming the cochlear capsule. The shape and relations of the auditory capsule are difficult to describe, and this difficulty is increased by the fact that the roof of the cochlear capsule appears to replace a part of the basal plate, because it carries the suprafacial commissure and is attached to the alicochlear commissure.

The medial and posterior relations of the auditory capsule have already been dealt with, viz., the fusion with the basal plate medially and with the occipital arch posteriorly, leaving the fissura metotica which is subdivided into foramen jugulare and apertura medialis of the recessus scalæ tympani.

Dorsally, the auditory capsule is surmounted by the *lamina parietalis*, or parietal plate, which is attached to it. This is a plate of cartilage which stands in the sagittal plane, fused beneath with the auditory capsule, behind with the supraoccipital cartilage, and in front with the orbitoparietal commissure. An aperture is left between the auditory capsule and the supraoccipital cartilage, behind the attachment of the parietal plate to the auditory capsule ; this is the *fissura occipito-capsularis superior* (which is



FIGS. 9.—Section 3–2–3. 10.—Section 3–3–5. 11.—Section 4–1–1.

also called the *foramen jugulare spurium*), through which the lateral jugular vein (emissarium temporale, SHINDO, 1915) leaves the cranial cavity.

From the antero-lateral edge of the canalicular part of the auditory capsule springs the tegmen tympani, or processus perioticus superior. This is a cartilaginous structure which projects forwards over the fossa incudis, in which the incus and stapes are lodged. The root of the tegmen tympani forms part of the roof of the sulcus facialis. Ventrally, the tegmen tympani is continuous with the crista parotica, and forms part of the side wall of the sulcus facialis. The crista parotica, in its turn, is continuous with the styloid process, which projects downwards, inwards, and forwards. The hinder edge of the root of the styloid process forms the anterior wall of the lateral opening of the sulcus facialis, or primary stylomastoid foramen, through which the facial nerve emerges. The side wall of the auditory capsule in this region corresponds to that which gives rise to the mastoid process of other forms, but this process is not evident in Sorex. The sulcus facialis is continued backwards as the sulcus for the stapedial muscle.

Median to the tegmen tympani, a bar of cartilage stretches like a bridge from the antero-medial edge of the canalicular capsule to the lateral edge of the cochlear capsule, thus enclosing an aperture which is the *foramen faciale secundarium.* Through this the main branch of the facial nerve leaves the cavum supracochleare and enters the sulcus facialis.

The anterior leg of the suprafacial commissure rests on the cochlear capsule, and arches upwards and backwards to the antero-medial edge of the canalicular capsule, thus enclosing the *primary facial foramen.* Between the primary and secondary facial foramina lies the hindmost part of the space known as the cavum supracochleare, into which the facial nerve runs, passing through the primary facial foramen. The gap in between the primary and the secondary facial foramina is also called the *hiatus spurius*, and through it the greater superficial petrosal (or palatine) nerve runs forwards. The suprafacial commissure appears to lie in direct ventral prolongation of the root of the orbitoparietal commissure. The front of the cochlear capsule is attached to the alicochlear commissure, which encloses the carotid foramen.

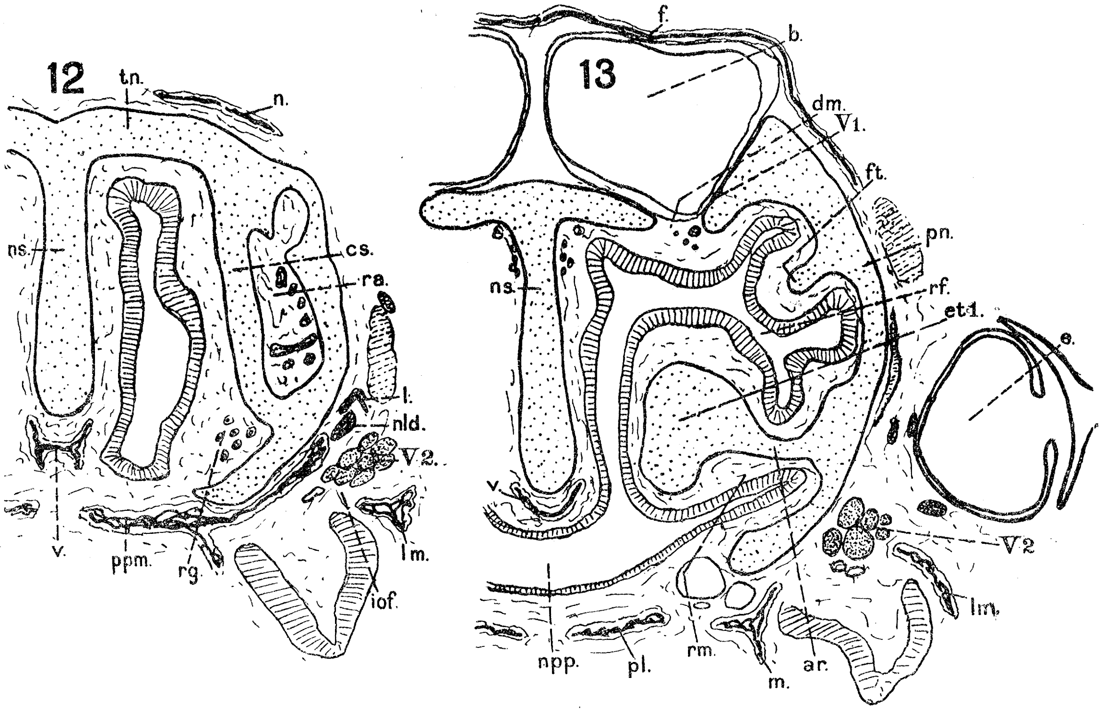
Attached to the dorsal side of the root of the tegmen tympani, and to the side wall of the canalicular capsule immediately behind the latter, is a large plate of cartilage called the processus opercularis. This structure lies in the sagittal plane, and extends upwards and forwards, lateral to the line of the true wall of the skull. The latter is represented by the root of the orbitoparietal commissure and the parietal plate, and between it and the processus opercularis is a space, through which the lateral jugular vein runs down from the foramen jugulare spurium, and the arteria meningea media runs up from the stapedial artery. The anterior and dorsal edges of the processus opercularis are free. A small fissure between the ventral edge of the processus opercularis and the side wall of the canalicular capsule shows that this edge was probably also originally free, and that its fusion with the wall of the auditory capsule is secondary.

The median wall of the canalicular part of the capsule has a depression (*fossa sub-*

arcuata interna) facing the cranial cavity. This depression is more accentuated in younger than in older embryos.

3. *Foramina in the wall of the auditory capsule.*—Immediately behind the suprafacial commissure, the median wall of the auditory capsule shows a small depression known as the internal auditory meatus. The anterior part of this depression runs into the already-mentioned primary facial foramen: the posterior part runs into the cavity of the auditory capsule through the foramina acustica.

The *foramen acusticum* is divided into two by a horizontal bar of cartilage forming the crista falciformis. The foramen acusticum superius transmits those branches of the auditory nerve which supply the utricle, the anterior and lateral ampullæ, and the dorsal and posterior regions of the saccule. The foramen acusticum inferius serves for the passage of the branches of the auditory nerve which supply the ductus cochlearis, the anterior and ventral regions of the saccule, and the posterior ampulla. The latter branch is in Sorex not (or not yet) enclosed in a special foramen singulare.



FIGS. 12.—Section 4–1–7. 13.—Section 4–3–5.

The *foramen endolymphaticum* is an elongated slit in the medial wall of the canalicular part of the auditory capsule. It runs obliquely backwards and upwards, beneath the fossa subarcuata interna, and serves for the emergence of the ductus endolymphaticus out of the auditory capsule into the cranial cavity.

The *aquæductus cochleæ* is a tunnel in the medio-posterior corner of the cochlear part of the auditory capsule. The inner opening of the tunnel is the apertura medialis of the recessus scalæ tympani (anterior portion of the fissura metotica), enclosed between the edge of the basal plate beneath and the ventral edge of the medial wall of the auditory capsule above.

The floor of the aquæductus cochleæ is formed by the processus recessus (which makes the cartilaginous floor of the recessus scalæ tympani). The roof of the aquæductus cochleæ is formed by the floor of the canalicular part of the auditory capsule. This floor is at a higher level than that of the cochlear part of the capsule, and it projects forwards into the cavity of the latter like a shelf. The edge of this shelf is an important structure, for it is morphologically the posterior boundary of the original foramen perilymphaticum of the reptile. The anterior boundary of the latter foramen is not so easy to determine, because of the backward projection of the floor of the cochlear capsule to form the processus recessus. The morphological position of the anterior boundary of the foramen perilymphaticum is in the floor of the cochlear capsule, along a line in the same transverse plane as the anterior border of the fenestra rotunda.

Through the aquæductus cochleæ the ductus perilymphaticus leaves the auditory capsule and enters the cranial cavity.

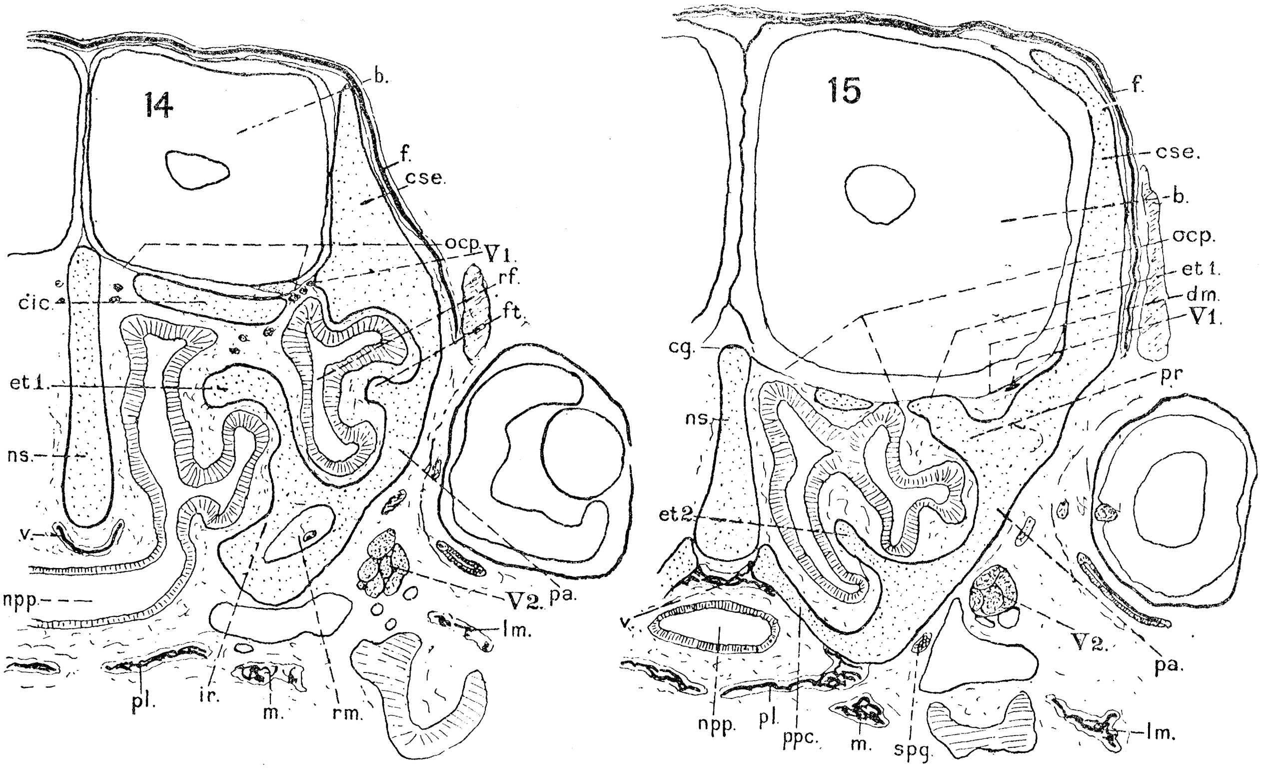
The *fenestra rotunda* is an aperture in the postero-lateral wall of the cochlear part of the auditory capsule. Its medial border is formed by the processus recessus, or cartilaginous floor of the recessus scalæ tympani. Its anterior border is the hind edge of the floor of the cochlear capsule (the promontorium); and its posterior border is formed by the underside of the floor of the hindmost part of canalicular capsule (the prominentia utriculo-ampullaris inferior). Its lateral border is formed by the cartilage which connects the outer walls of the canalicular and cochlear capsules. The fenestra rotunda faces downwards, outwards, and backwards, and is covered over by the secondary tympanic membrane.

The *fenestra ovalis* is an aperture in the side wall of the cochlear capsule, looking out into the sulcus facialis, opposite the root of the styloid process. Into the fenestra ovalis fits the foot of the stapes.

Immediately behind the aquæductus cochleæ is an aperture in the wall of the canalicular capsule, facing the foramen jugulare. It is a deficiency in the wall, perhaps due to pressure, and which is obliterated at later stages.

4. *The interior of the auditory capsule.*—The auditory capsule contains a complicated system of inter-connecting spaces in which the various parts of the membranous labyrinth are lodged. Like the auditory capsule itself the cavity can be subdivided into canalicular and cochlear portions, and for the sake of convenience the latter can be further separated into cochlear and vestibular segments. These subdivisions are, however, very indefinite, and it is almost impossible to define their limits. The cavum vestibulare occupies the postero-dorsal part of the cochlear capsule. It lodges the saccule and the proximal portion of the ductus cochlearis; its outer wall is perforated by the fenestra ovalis, and its medial wall by the foramina acustica. The cavum vestibulare is directly continuous anteriorly and ventrally with the cavum cochleare,

which lodges the distal, coiled, part of the ductus cochlearis. Posteriorly, the cavum cochleare becomes the cavum perilymphaticum and the recessus scalæ tympani, the walls of which are pierced by the aquæductus cochleæ and the fenestra rotunda. This hindmost part of the cavum cochleare is at a lower level than the cavum vestibulare, and is slightly marked off from it by a ridge projecting from the median wall which is continued backwards into the floor of the hindmost part of the canalicular capsule and which forms the roof of the aquæductus cochleæ. Anteriorly, the cavum cochleare is partly obstructed by a spiral septum. This septum is attached to the foremost point of the crista falciformis, and sweeps downwards, outwards and forwards to the floor of the cochlear capsule. The septum separates the first turn of the ductus cochlearis from the second, and it also marks the division between the front of the cavum vestibulare (which lies above it) and the cavum cochleare (which lies median and anterior to it).



FIGS. 14.—Section 5-1-7. 15.—Section 5-2-9.

The cavum canaliculare is freely continuous with the cavum vestibulare in front; in fact the anterior part of the cavum canaliculare may be said to have no floor. This part is expanded to form the recessus utriculo-ampullaris anterior and lateralis, into which open the anterior and lateral semicircular canals respectively. The floor of the posterior part of the cavum canaliculare has already been mentioned as forming a shelf which projects forwards over the cavum perilymphaticum and the aquæductus cochleæ, and its under surface (which forms the prominentia utriculo-ampullaris inferior) makes the hind border of the fenestra rotunda. The cavum canaliculare contains the utricle and the semicircular canals, the loops of which are separated from the utricle by the septa semicircularia. The posterior part of the cavum canaliculare gives off the sinus superior (through which the crus commune of the anterior and posterior semicircular canals connects with the utricle), and expands into the recessus utriculo-ampullaris posterior. This recess receives the lower opening of the posterior semicircular canal, and the posterior opening of the lateral canal. Just before opening into the recess, these canals communicate with one another by a perforation in the septum semicirculare posterius. Owing to the fact that the fossæ subarcuatæ (interna and externa) are shallow, the massa angularis (between the posterior and lateral canals) is thick. The median wall of the cavum canaliculare is perforated by the foramen endolymphaticum, and by the pressure-deficiency mentioned above.

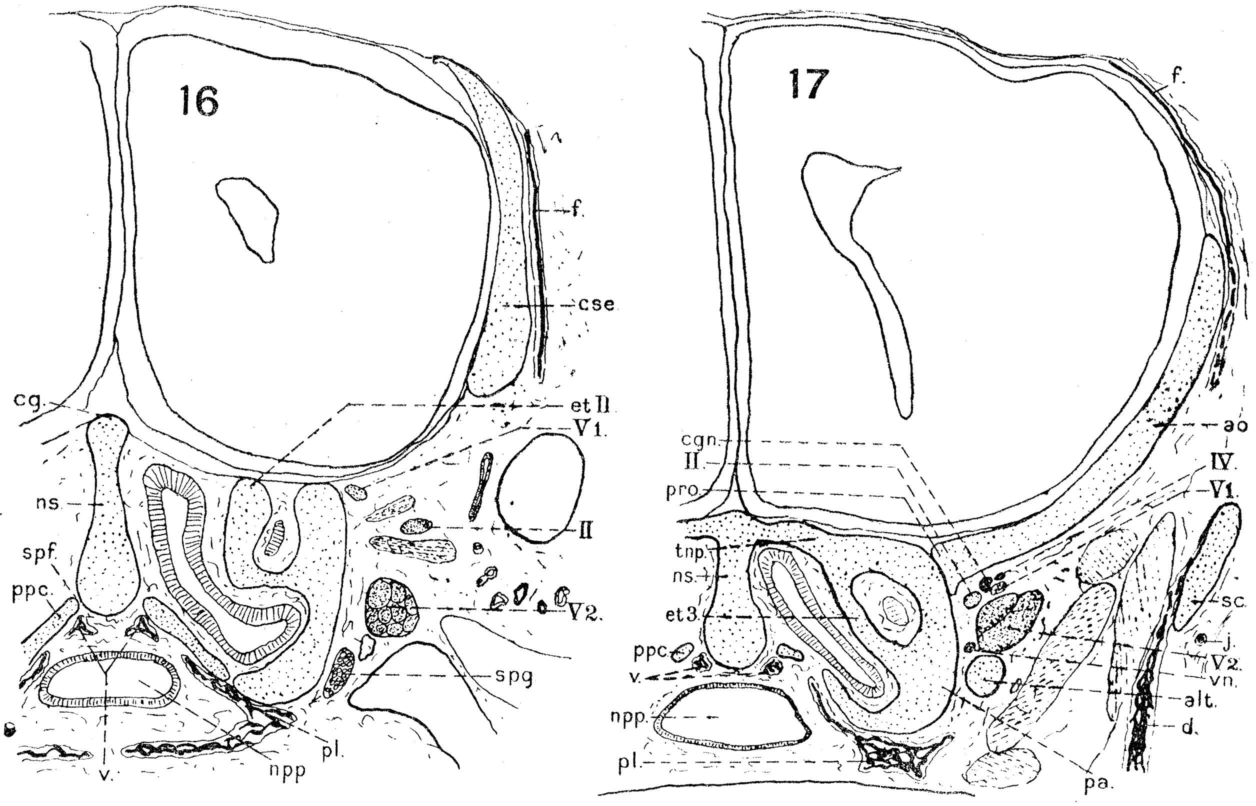
5. *The ala temporalis.*—The ala temporalis is a plate of cartilage attached to the central stem by the processus alaris. The outer border of the ala temporalis is slightly raised, and protects the ganglion of the trigeminal nerve from the side. A notch in this raised edge serves for the passage of the mandibular branch of the trigeminal nerve. The front of the ala temporalis reaches as far as the anterior (preoptic) root of the ala orbitalis. On its median side, anterior to the processus alaris, the ala temporalis gives off the pterygoid process, which is here of exceptional interest because it is in direct cartilaginous continuity with the pterygoid cartilage. The general shape of the ala temporalis in Sorex is flat, and not upstanding. It is therefore difficult to speak of a " lamina ascendens." The ala temporalis forms a large part of the floor of the cavum epiptericum. At the stages studied, the ala temporalis, processus alaris, and central stem, are all in direct cartilaginous continuity, without evidence of sutures.

6. *The ala orbitalis.*—The ala orbitalis is a large triangular plate of cartilage, with the apex directed towards the central stem. The anterior corner of the base of this triangle is continued into the commissura sphenethmoidalis ; the posterior corner is continued into the commissura orbitoparietalis. The apex is divided and forms the preoptic and postoptic roots of the ala orbitalis. These roots do not rest directly on the central stem but on the planum antorbitale, and they are not even fused on to that but are separated by a suture, which can be regarded as evidence of originally separate chondrification of the ala orbitalis. The postoptic root is continued backwards as a projecting point of cartilage, which forms the anterior clinoid process.

7. *The nasal capsule.*—On each side of the central stem (which in this region is the septum nasi) is a large curved cartilage which forms the roof, hind wall, and part of the side wall and floor of the hindmost portion of the nasal capsule. That part which forms the roof is the *tectum nasi posterius* ; where it forms the hind wall the cartilage is known as the *cupula posterior* ; that part which forms the floor is the *lamina transversalis posterior* ; and where it forms the side wall it is known as the *planum antorbitale.* The tectum nasi posterius is fused medially with the nasal septum, but this

fusion is secondary. The cupula posterior and the lamina transversalis posterior are separated from the nasal septum by a narrow fissure. The lamina transversalis posterior is assisted in the formation of the floor by the paired *posterior paraseptal cartilages*. These are triangular in shape, and each is separated from the ventral edge of the nasal septum by the septoparaseptal fissure. Each is also attached in two places to the lamina transversalis posterior, leaving a fissure between these points of attachment.

The front edge of the tectum nasi posterius and the upper edge of the planum antorbitale form respectively the hind and lateral borders of the fenestra cribrosa, which is subdivided by strips of cartilage to form the cribriform plate. The dorsal edge of the nasal septum is free between the two fenestræ cribrosæ, where it forms a low crista galli. Immediately in front of this, the nasal septum is fused with the *tectum nasi* on each side.



FIGS. 16.—Section 5–3–8. 17.—Section 6–2–5.

The tectum nasi posterius forms the floor of the hinder part of the supracribrous recess (*i.e.* the space between the fenestra olfactoria and the fenestra cribrosa), and it may also be termed the lamina infracribrosa. The planum antorbitale is continuous above with the commissura sphenethmoidalis, and in front with the side wall of the nasal capsule, or *paries nasi*. The paries nasi is continuous with the roof of the nasal capsule (or tectum nasi) in front of the fenestra olfactoria, and the tectum nasi is continuous with the nasal septum. The middle portion of the nasal capsule has no floor (the space which it would occupy is the *fenestra basalis*, through which the naso-pharyngeal passage leaves the nasal capsule and enters the buccal cavity), and consequently the lower edges of the paries nasi and of the nasal septum end freely in this region. Further forwards, a floor is present, formed by the *lamina transversalis anterior*. This cartilage is continuous with the lower edge of the nasal septum on the inside, and with the lower edge of the paries nasi on the outside, with the result that the nasal cavity is in this region surrounded on four sides by cartilage, forming the zona annularis. The lamina transversalis anterior is at a lower level than the ventral edge of the nasal septum, which has the result that a deep sulcus ventralis is formed beneath the nasal septum and between the median portions of the lamina transversalis anterior which rise up to fuse with it. These uprising median portions of the lamina transversalis anterior are continued backwards as the *anterior paraseptal cartilages*. The latter for a considerable part of their length are hollow cylinders lodging the organs of JACOBSON. The anterior paraseptal cartilages, like the posterior paraseptal cartilages, are separated from the nasal septum by the septoparaseptal fissure.

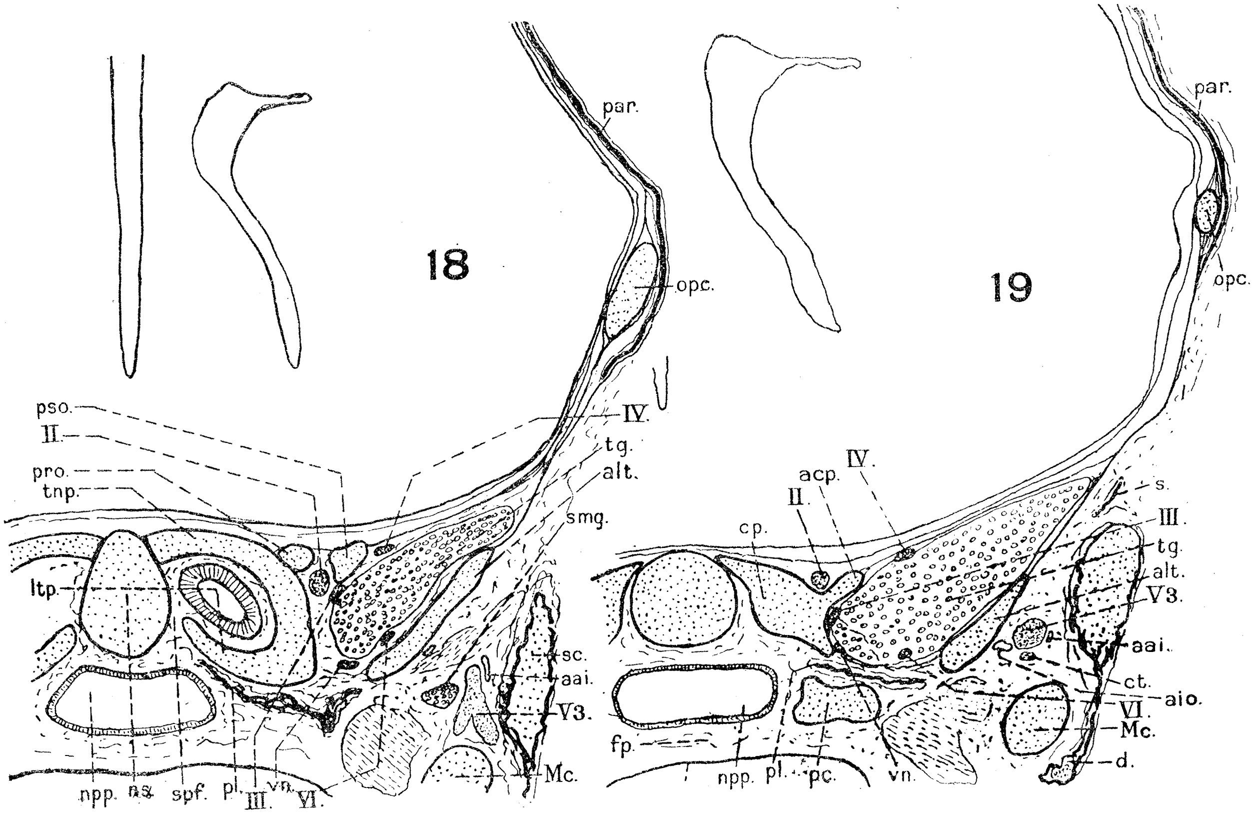
Continuous with the antero-ventral edge of the anterior paraseptal cartilage on each side is a mass of dense tissue which represents the rudiment of the cartilago ductus nasopalatini of other forms. This dense tissue extends laterally, passing in front of the ductus nasopalatinus, and is then continuous with a small *palatine cartilage*. The latter, which is quite small, lies on the lateral side of the ductus nasopalatinus, and on the medial side of the palatine process of the maxilla, beneath the mucosa of the nasal sac.

The postero-lateral corner of each lamina transversalis anterior projects very slightly, forming a rudimentary processus transversalis, which lies ventral to the nasolachrymal duct. Further back, facing the processus transversalis, the ventral edge of the paries nasi projects slightly to form the processus maxillaris anterior. Anteriorly, the floor of the lamina transversalis anterior drops suddenly, forming what may be called a prominentia subtransversalis, the sides of which give rise to the processus laterales ventrales, from the antero-lateral portion of which the processus alaris superior springs. The latter rises up at the side of the paries nasi, to which it is fused for a short distance. Median to the processus alaris superior, there is another little bar of cartilage which runs from the antero-lateral corner of the processus lateralis ventralis to the antero-ventral corner of the paries nasi. This little bar of cartilage forms the anterior boundary to the foramen pretransversale through which the nasolachrymal duct leaves the nasal cavity.

The *fenestra narina* is bounded on the inside by the front of the nasal septum ; above by the front of the tectum nasi ; below by the processus lateralis anterior. The lateral boundary of the fenestra narina is very irregular ; it is formed partly by the small accessory cartilage detached from the distal end of the processus lateralis anterior, and partly by the anterior edge of the processus alaris superior.

There is no foramen epiphaniale, nor a foramen dorsale, and the ramus lateralis nasi of the ethmoid or profundus branch of the trigeminal nerve appears to reach the dorsal surface of the nasal capsule by passing forwards dorsal to the cribriform plate and ventral to the dura mater and frontal bone. (*Cf.* crocodile, Shiino, 1914.) The fenestra cribrosa is converted into the cribriform plate by a number of cartilages, chief of which is the crista intercribrosa, which is continuous with the first ethmoturbinal.

8. *The turbinals and recesses of the nasal capsule.*—The cavity of the nasal capsule is divided up into a number of recesses by projections from its walls. In order, commencing from the anterior end, the following structures are met with :—The atrioturbinal is a slight projection formed by an inrolling of the cartilage of the paries nasi forming the hind border of the foramen pretransversale. The posterior prolongation of the atrioturbinal, as the internal counterpart to the sulcus nasolachrymalis (which as its name implies lodges the nasolachrymal duct) is very ill-defined.



FIGS. 18.—Section 6-3-5. 19.—Section 7-1-4.

The maxilloturbinal is formed by the inrolling of the lower (free) edge of the paries nasi. It is more or less in posterior prolongation of the atrioturbinal. Posteriorly, the maxilloturbinal ceases to form the ventral edge of the paries nasi, for that edge is now lateral and ventral to it : in other words the maxilloturbinal is now well within the nasal cavity, and it ends as a small free projection. The nasoturbinal projects from the paries nasi, dorsal to the maxilloturbinal (between which two, the recessus supraconchalis is delimited), and becomes more accentuated as it runs backwards and fuses with the crista semicircularis.

The crista semicircularis is (as its name implies) a curved crest which projects inwards and backwards, whose inner edge is free, and whose lateral edge is fused to the paries nasi and to the side of the tectum nasi. Between the crista semicircularis and the paries nasi is a recess which ends blindly in front : the recessus anterior. The recessus glandularis is on the inner side of the foot of the crista semicircularis.

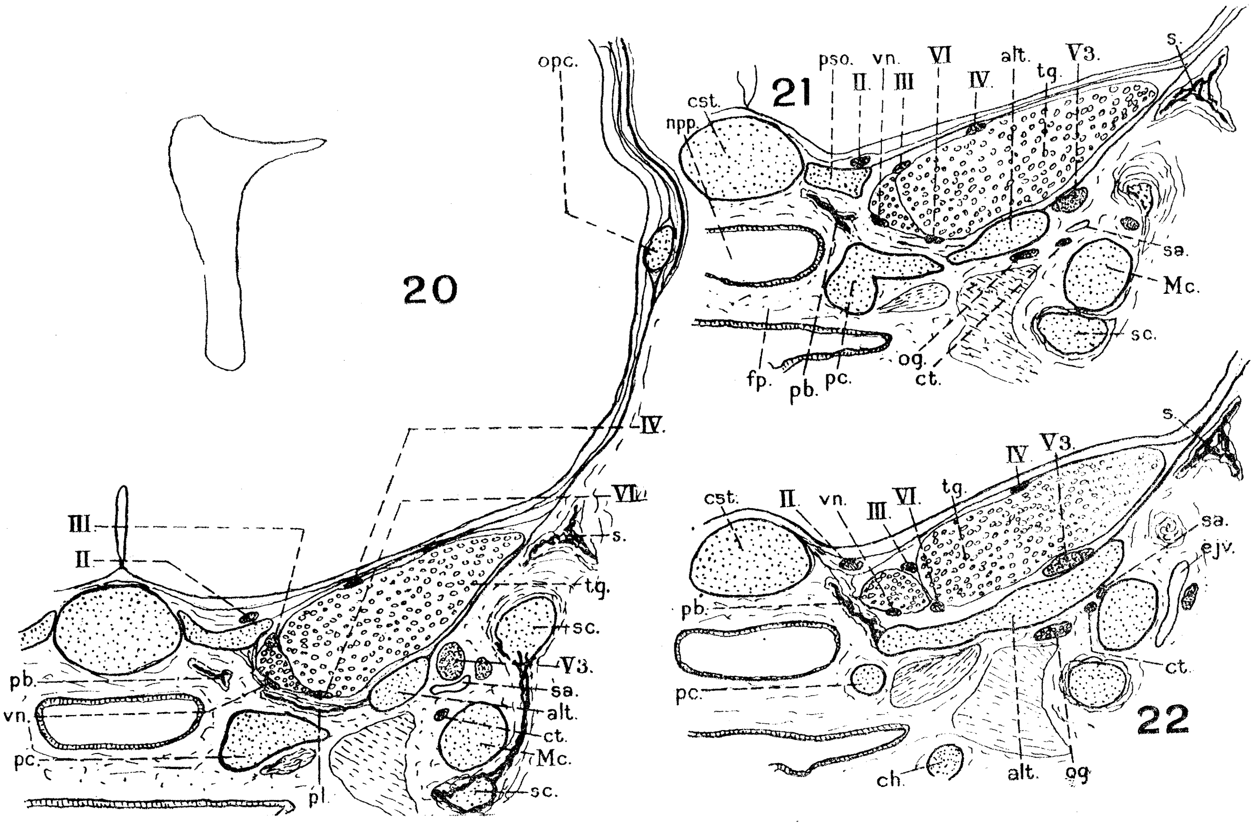
The 1st ethmoturbinal is a large plate of cartilage which is situated behind the crista semicircularis. The 1st ethmoturbinal projects forwards and inwards from the inner side of the planum antorbitale, its attachment to which forms its posterior root. It is also attached to the middle of the paries nasi along a line sloping forwards and downwards, forming the anterior root. From this attachment, another branches off, and runs downwards to the ventral edge of the paries nasi, forming the inferior root of the ethmoturbinal. The dorsal edge of the ethmoturbinal is continuous with the crista intercribrosa. The anterior root of the ethmoturbinal presents a horizontal free edge which separates a recessus maxillaris beneath from a recessus frontalis above. The hind wall of the recessus maxillaris is formed by the inferior root of the 1st ethmoturbinal. The recessus frontalis is subdivided into three by the two frontoturbinals which project into it from the paries nasi. The 2nd ethmoturbinal is situated posterior and medial to the 1st, and is considerably smaller than the 1st. Its attachments are similar and parallel to the posterior and inferior roots of the 1st ethmoturbinal.

The 3rd ethmoturbinal is a miniature replica of the 2nd, and is situated median and posterior to it. Between the 1st and 2nd, and between the 2nd and 3rd ethmoturbinals, there are deep recesses which are bounded below by the lamina transversalis posterior and the posterior paraseptal cartilage, behind by the cupula posterior, and above by the tectum nasi posterius. The ethmoturbinals which have just been described are all primary ethmoturbinals ; the secondary ethmoturbinals have not yet appeared.

The space enclosed behind the 1st ethmoturbinal between the cupula posterior and the lamina transversalis posterior is the recessus cupularis, and, as VAN GILSE (1927) has shown, it corresponds to the palæosinus or anterior part of the sphenoidal sinus of those mammals in which the sphenoid bone is invaded and pneumatised.

C. *The Commissures and Dorsal Structures.*

Mention has already been made of the orbitoparietal and sphenethmoid commissures, and it suffices here to repeat that the sphenethmoid commissure connects the planum antorbitale with the ala orbitalis, lying dorsal to the profundus branch of the trigeminal nerve, and enclosing the orbitonasal fissure from above. The orbitoparietal commissure (or tænia marginalis) connects the ala orbitalis with the parietal plate, and encloses the sphenoparietal fontanelle from above. The parietal plate is attached to the roof of the auditory capsule, and is attached to the supraoccipital cartilage behind. The latter is separated from the auditory capsule by the fissura occipito-capsularis superior (or foramen jugulare spurium), and is fused behind with the upper end of the occipital arch. The supraoccipital cartilages of each side are interconnected by a narrow cartilaginous bridge, called the tectum posterius, which forms all that there is of the roof of the chondrocranium, and in which the supraoccipital bone ossifies.



FIGS. 20.—Section 7-1-8. 21.—Section 7-2-8. 22.—Section 7-2-6.

D. *The Splanchnocranium.*

The ala temporalis, which has already been mentioned as an appendage of the central stem, is really part of the splanchnocranium, for it is partially homologous with the processus ascendens of the pterygo-quadrate of lower vertebrates. Of the remainder of the splanchnocranium, little need be said. Meckel's cartilage, the hind portion of which forms the malleus; the incus (quadrate) which articulates with it and with the stapes; the stapes which is perforated in the usual way by the stapedial artery, are all typical.

The styloid process, which is attached by its dorsal posterior end to the crista parotica of the auditory capsule, has already been mentioned. It runs forwards, and slightly downwards and inwards, as the tympanohyal and stylohyal cartilage to a point beneath the processus alaris, where it makes a sutural connexion with another cartilage, the ceratohyal. The ceratohyal is a slender cartilage, like the stylohyal, but it is much shorter, and its anterior end is sutured on to the hypohyal. The hypohyal is a stumpy cartilage which is connected to its fellow of the opposite side by the basihyal, forming a transverse bar ventral to the larynx. The hyoid bone is undergoing ossification in the basihyal cartilage. Touching the basihyal cartilage, ventrally, and running up on the side of the larynx, is the thyrohyal cartilage, which represents the skeletal element of the 1st branchial arch. Dorsally, the thyrohyal cartilage bears a horn which projects backwards and is fused to the dorsal end of the thyroid cartilage. The thyroid cartilage is fused with its fellow of the opposite side in the middle line beneath the larynx, and represents the skeletal element of the 2nd branchial arch. In Monotremes and Marsupials, the thyroid cartilage consists of the skeletons of the 2nd and 3rd branchial arches, but in the Placental mammals the skeletal elements of the 3rd branchial arch seem to have disappeared (EDGEWORTH, 1916). In regard to this matter, therefore, Sorex presents nothing unusual. A cartilaginous horn projects backwards from the dorsal end of the thyroid cartilage, lateral to the arytenoid and cricoid cartilages.

The arytenoid cartilages are situated medially to the thyroid cartilages. The cricoid cartilage forms a complete ring round the larynx, and surrounds it more closely than do the thyrohyal or thyroid cartilages. There can be little doubt that the arytenoid and cricoid cartilages form morphologically no part of the skeleton of branchial arches, but are to be regarded as enlarged and modified tracheal rings.

E. *The Relations of the Cartilages to Certain Nerves and Blood-vessels.*

Some of the relations of the cartilages to the neighbouring nerves and blood-vessels will come up for discussion in the later part of this paper. For the sake of convenience a few of the more important relations may be summarised here. (See Text-fig. 38.)

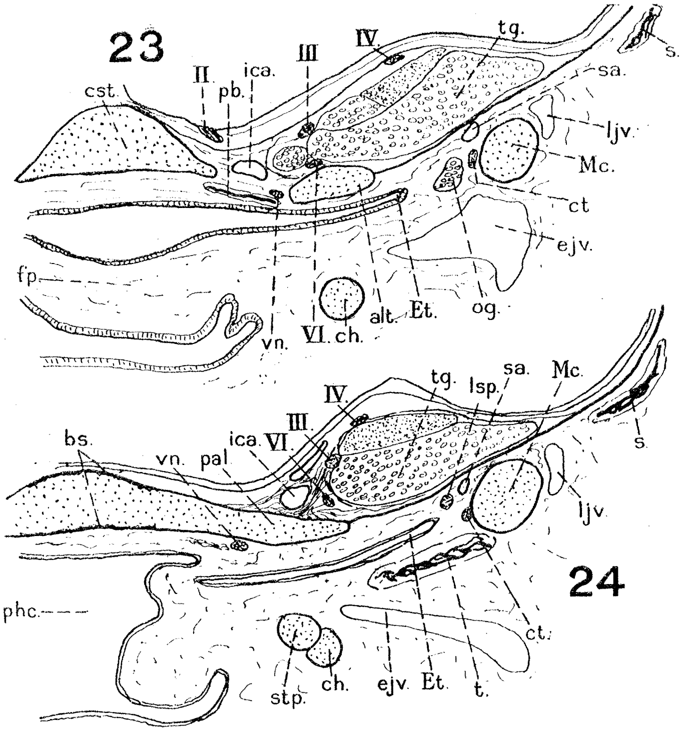
Facial nerve.—Through primary facial foramen (under suprafacial commissure) out of cranial cavity into cavum supracochleare. Out of latter through secondary facial foramen into sulcus facialis, in which it runs back, lying dorsal to lesser superficial petrosal, stapes, stapedial muscle, and stapedial artery; median to arteria meningea media and styloid process. Runs out behind styloid process.

Chorda tympani.—Given off by facial nerve on emergence behind styloid process. Runs forwards, its position being lateral to styloid process, and to the dorsal extension of the tympanic cavity, median to manubrium of malleus, ventral to tensor tympani muscle, between Meckel's cartilage and processus Folii, dorsal to tympanic bone, lateral to otic ganglion, median to mandibular branch of trigeminal. Runs to submaxillary ganglion.

Greater superficial petrosal, or palatine nerve.—Given off by facial in cavum supracochleare. Does not enter secondary facial foramen but emerges through hiatus spurius and runs downwards and forwards on roof of cochlear capsule, passes lateral to alicochlear commissure, and joins deep petrosal, or internal carotid nerve, lateral to internal carotid artery. Continues forwards as Vidian nerve.

Vidian nerve.—From junction of greater superficial petrosal with deep petrosal the joint nerve lying ventral to processus alaris, dorsal to pterygoid bone and cartilage, dorsal to palatine bone, ventral to abducens, median to maxillary branch of trigeminal nerve, to sphenopalatine ganglion.

Lesser superficial petrosal.—Given off by glossopharyngeal on emergence from jugular foramen. Runs forward close to wall of auditory capsule, being dorsal to fenestra rotunda, median to styloid process, median to dorsal extension of tympanic cavity, lateral to stapedial artery, where latter rises to pierce stapes, median to chorda tympani, to otic ganglion.



FIGS. 23.—Section 7–3–7. 24.—Section 8–1–3.

Stapedial artery.—Given off by internal carotid, runs up median to lesser superficial petrosal, pierces stapes, and gives off the arteria meningea media, which continues upwards, lateral to facial nerve, median to lateral jugular vein and processus opercularis, and then runs forwards beneath ventral edge of orbitoparietal commissure. The stapedial artery runs forwards, median to malleus, dorsal to tensor tympani muscle, median to Meckel's cartilage, and divides behind the mandibular branch of trigeminal into two. One branch, the arteria alveolaris inferior accompanies the mandibular branch through the inferior dental foramen of the mandible; the other, the arteria infra-orbitalis continues forwards median to the mandibular nerve.

III. The Bones of the Skull of an 11 mm. Embryo.

A. *The Cartilage-Bones.*

At this stage, the skull of the shrew contains 6 centres of perichondral ossification. They are :—basisphenoid, basioccipital, supraoccipital, paired exoccipitals, and the hyoid.

The *basisphenoid* arises in the dorsal and ventral surface of the cartilage of the central stem, in the vicinity of the foramen hypophyseos, which it lines. The bone is at this stage a single whole, but the denser nature of the bone at two points immediately on either side of the foramen hypophyseos suggests that it originally arose from two centres in those situations.

The *basioccipital* arises on both surfaces of the cartilage of the posterior region of the basal plate, in the middle line. The ossification spreads a short distance to each side, and posteriorly it reaches the centre of the lower border of the foramen magnum.

The *supraoccipital* is, likewise, unpaired, and arises on both surfaces of the cartilage of the tectum posterius. The supraoccipital is partly covered over by a dermal bone—the interparietal (or postparietal, dermosupraoccipital).

The *exoccipitals* are paired ossifications which arise on both surfaces of the cartilage of the occipital arches. They just reach the hind surface of the occipital arches.

In spite of careful search, no ossification was found in the auditory capsule at the stages studied.

The *hyoid* is an unpaired ossification in the transverse bar formed by the basihyal cartilage. It appears to be the most advanced of all the cartilage-bones of the skull, but its horns are not yet ossified.

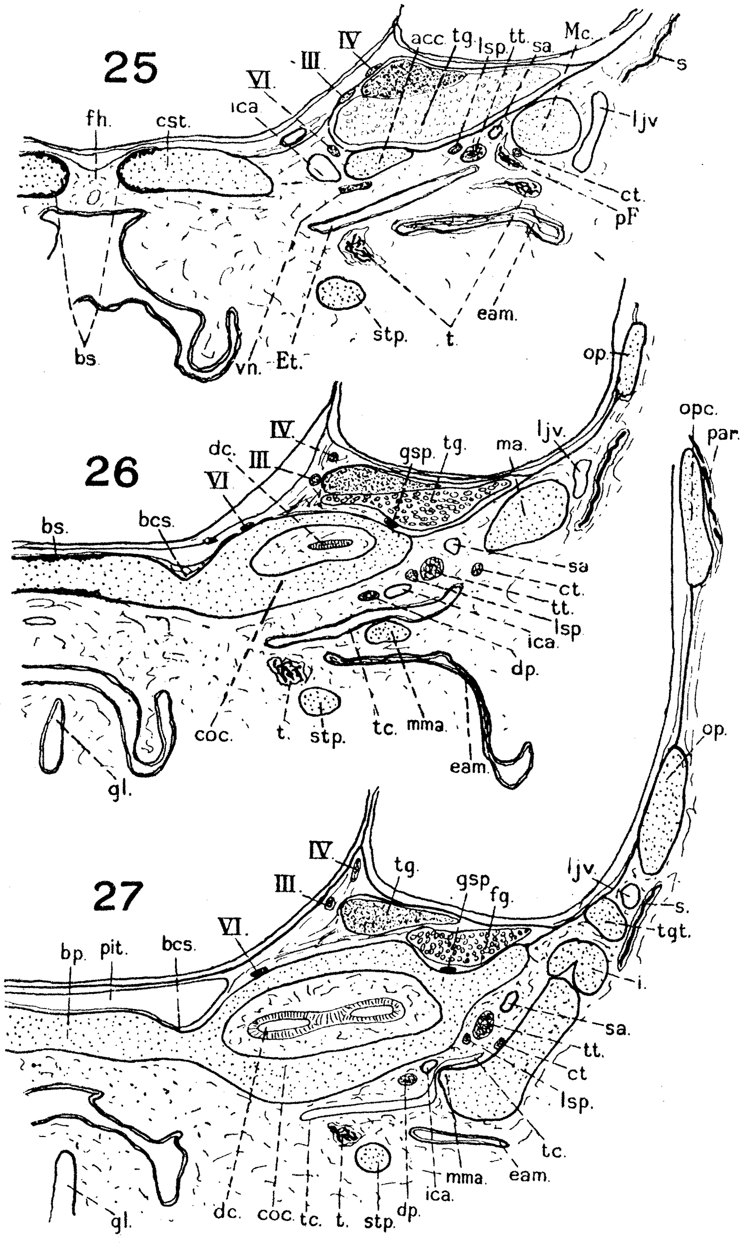
B. *The Dermal Bones.*

The 11 mm. shrew has 28 centres of dermal ossification, of which 2 are unpaired and median, and the remaining 26 represent 13 pairs of paired bones.

The paired dermal bones are :—premaxilla, maxilla, lachrymal, palatine, pterygoid, nasal, frontal, parietal, squamosal, jugal, tympanic, processus Folii, and dentary. The unpaired bones are the vomer and interparietal.

The *premaxilla* begins some distance behind the extremity of the snout. It is composed of a main portion which contains sockets in which the incisor teeth are lodged, an ascending portion which covers the lower portion of the paries nasi, and a so-called palatine process.

The latter runs medially from the main portion, and turns back ventral to the anterior paraseptal cartilage, close to the middle line and its partner of the opposite side. It extends still further back as a spur, which lies dorsal to the bulge of the paraseptal cartilage in which Jacobson's organ is lodged, and ventral to the ventral edge of the nasal septum. Between this palatine process of the premaxilla and the palatine process of the maxilla, the foramen incisivum is enclosed, through which the primary choana and Stenson's duct from Jacobson's organ communicates with the mouth. Reasons will be given in the discussion for regarding the palatine process of the premaxilla as a composite structure, of which the anterior portion is a true part of the premaxilla, while the posterior portion represents the prevomer of reptiles and the dumb-bell-shaped bone of Ornithorhynchus.



FIGS. 25.—Section 8–2–1. 26.—Section 8–2–9. 27.—Section 8–3–8.

The *maxilla* consists of an ascending portion which covers the lower part of the side wall of the nasal capsule ; a lateral alveolar portion which forms the outer boundaries of the tooth-sockets; and a median portion which extends as a shelf ventral to the anterior paraseptal cartilage, forms a floor to the fenestra basalis of the nasal capsule, and contributes to the formation of the hard false palate. This last portion is the palatal process of the maxilla. From the hindmost extremity of the lateral alveolar portion, a very small zygomatic process projects laterally and backwards, but does not touch the jugal. The palatine process of the maxilla contains a nodule of secondary cartilage.

The *lachrymal* is a small bone situated at the antero-internal angle of the orbit. It is pierced by a foramen, through which the nasolachrymal duct passes, and a considerable portion of the bone is exposed freely on the side of the skull. The anterior portion of the lachrymal is concealed beneath the ascending portion of the maxilla. The posterior portion of the lachrymal rests on the lateral alveolar portion of the maxilla, and so comes to form the roof of the infraorbital foramen, through which the maxillary branch of the trigeminal leaves the orbit and runs out on to the side of the snout.

The *palatine* forms a posterior continuation of the palatine process of the maxilla. Posteriorly, the bone leaves the false palate, and forms a plate which passes beneath the lamina transversalis posterior dorsally, and above the pterygoid cartilage ventrally, to end in the anterior region of the floor of the cavum epiptericum. Laterally, this hindmost part of the palatine comes close to the ala temporalis; medially, there is a gap between it and the dermal pterygoid ossification.

The *pterygoid*, at this stage, is composed of two elements. One is the pterygoid cartilage, which, as already described, fuses with the pterygoid process of the ala temporalis. The other is a small more or less horizontal plate of dermal bone, which starts just ventral to the posterior root of the ala orbitalis and its anterior clinoid process, and reaches back as far as the anterior edge of the processus alaris, where it forms the roof of the cavity lodging the Eustachian tube. The pterygoid bone forms the floor of a small Vidian canal, through which the Vidian nerve passes forwards. Laterally, this little bone is connected with the ossification which is beginning to set in in the pterygoid cartilage at the point of fusion of the latter with the pterygoid process of the ala temporalis. The bulk of the pterygoid cartilage shows no sign of ossification. Reasons will be shown in the discussion for regarding the plate of dermal bone here described as the homologue of the basitemporal, or detached lateral wing of the parasphenoid; while the ossification to which the pterygoid cartilage (which is secondary cartilage) gives rise represents the pterygoid bone of reptiles.

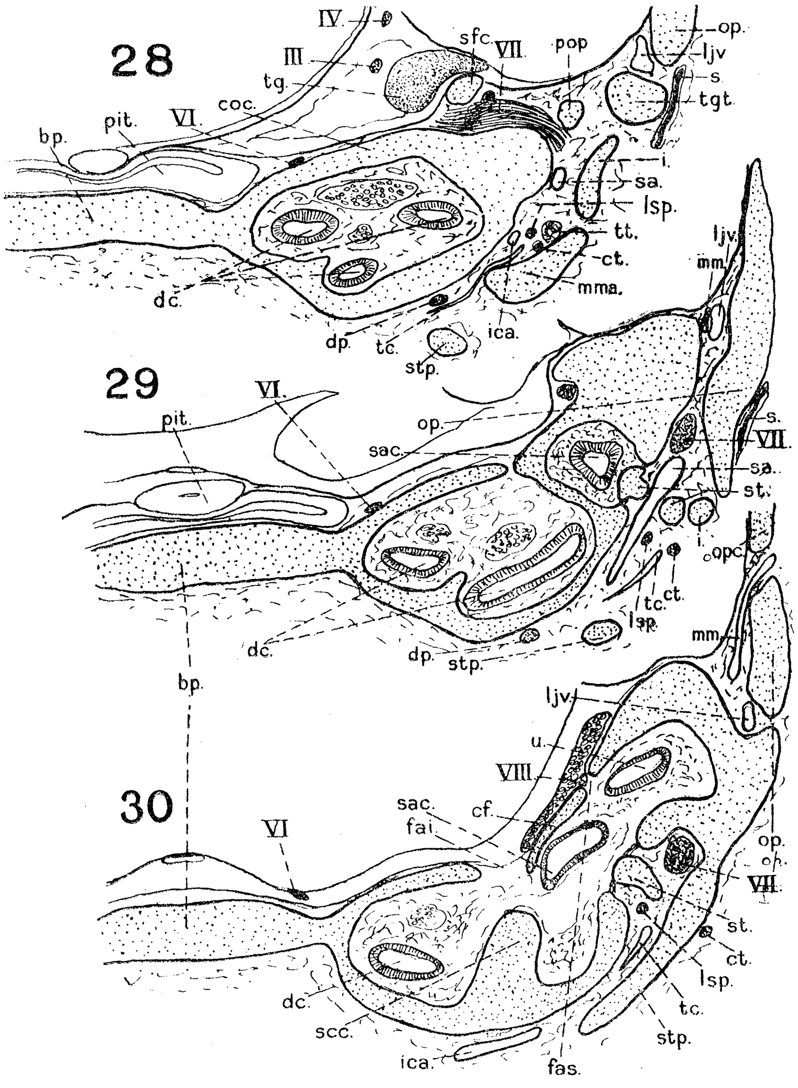
The *nasal* lies over the roof of the nasal capsule, and presents little of particular interest.

The *frontal* extends from the hindmost part of the roof of the nasal capsule laterally, and overlies the commissura sphenethmoidalis, and the major part of the ala orbitalis.

The *parietal* forms a posterior prolongation of the frontal, and lies lateral to the commissura orbitoparietalis.

The *squamosal* has a large zygomatic process, which stretches freely forwards dorsal to the ascending ramus of the mandible, and does not touch the jugal. The posterior portion of the squamosal forms a plate which covers over the tegmen tympani and the base of the processus opercularis from the side.

The *jugal* is a completely unattached, minute spicule of bone, lying horizontally, lateral to the ascending ramus of the mandible, and not touching either the maxilla in front, or the squamosal behind. The jugal is about 0·02 mm. in diameter, and 0·3 mm. long.



FIGS. 28.—Section 9–1–6. 29.—Section 9–2–3. 30.—Section 9–3–1.

The *tympanic* forms a semicircle stretched round the median side of the tympanic membrane.

The *processus Folii* (or goniale) is a little spicule of bone lying close to the ventral surface of Meckel's cartilage, dorsal and posterior to the anterior horn of the tympanic. The chorda tympani passes between the processus Folii and Meckel's cartilage.

The *dentary* extends laterally and ventrally to Meckel's cartilage, and contains sockets for the teeth of the lower jaw. The dentary contains three distinct nodules of secondary cartilage, which are situated in the coronoid process, anterior to the sigmoid notch; in the condylar process, behind the sigmoid notch; and in the postero-ventral angle. The inferior dental and the mental foramina are large gaping apertures.

The *vomer* extends underneath the ventral edge of the nasal septum from a point just anterior to the hind end of the anterior paraseptal cartilages, to a point level with the anterior extremity of the ala temporalis. The vomer is median and unpaired for the anterior three-quarters of its length; its hindmost quarter is formed of paired struts.

The *interparietal* is a median bone, overlying the tectum posterius, and partially covering the supraoccipital bone, which ossifies in that cartilage.

IV.—Discussion.

A. *The Palatine Process of the Premaxilla and the Prevomer.*

An account has already been given in the descriptive part of this paper of the palatine process of the premaxilla. Its relations to the neighbouring structures are important, and especially those to the paraseptal cartilages and the nasal septum. Anteriorly, where the palatine process joins the main body of the premaxilla, the bone is ventral to the paraseptal cartilage, in which Jacobson's organ is lodged, and forms a little plate beneath it. Further posteriorly, however, the bone passes up on the median side of the paraseptal cartilage, and extends backwards as a spur. This spur lies just above the shelf formed by the bulging of the paraseptal cartilage to accommodate Jacobson's organ, and just beneath the nasal septum. The palatine processes of each side remain separate, but their median edges are close to one another anteriorly, where they lie beneath the paraseptal cartilages. Supposing that they were to fuse at this point, and that their connexions with the main body of the premaxillæ were to disappear, the palatine processes of Sorex would be identical with the os paradoxum, or dumb-bell-shaped bone in Ornithorhynchus, which has been described by Wilson and Martin (1893) and Wilson (1894). In both cases, the anterior parts form a plate beneath the paraseptal cartilages, and posteriorly there are spurs stretching back at a more dorsal level, beneath the nasal septum, and ceasing some distance in front of the anterior extremity of the (mammalian) vomer.

Now, in his paper published in 1894, Wilson held that the then prevalent view, that the dumb-bell-shaped bone was homologous with the palatine process of the premaxilla, was improbable; for the palatine plates of the premaxillæ "join the maxillary palate, completing the secondary palate in front" (*loc. cit.*, p. 140). He proposed, therefore, to homologise the dumb-bell-shaped bone of Ornithorhynchus with the "'anterior vomer,' formed, of course, by the fusion of two symmetrical halves." In 1901, Wilson published his discovery that in the early young of Ornithorhynchus, the premaxillaries not only meet in the middle line but send back palatine processes, and that these processes end some distance in front of the splints of the developing dumb-bell-shaped bone. There is then no doubt that the dumb-bell-shaped bone is homologous with the "anterior paired vomers" of non-mammalian vertebrates, to which BROOM (1895*a*) gave the name "prevomers." The question remains as to whether the prevomer is homologous with the palatine process of the premaxilla of higher mammals.

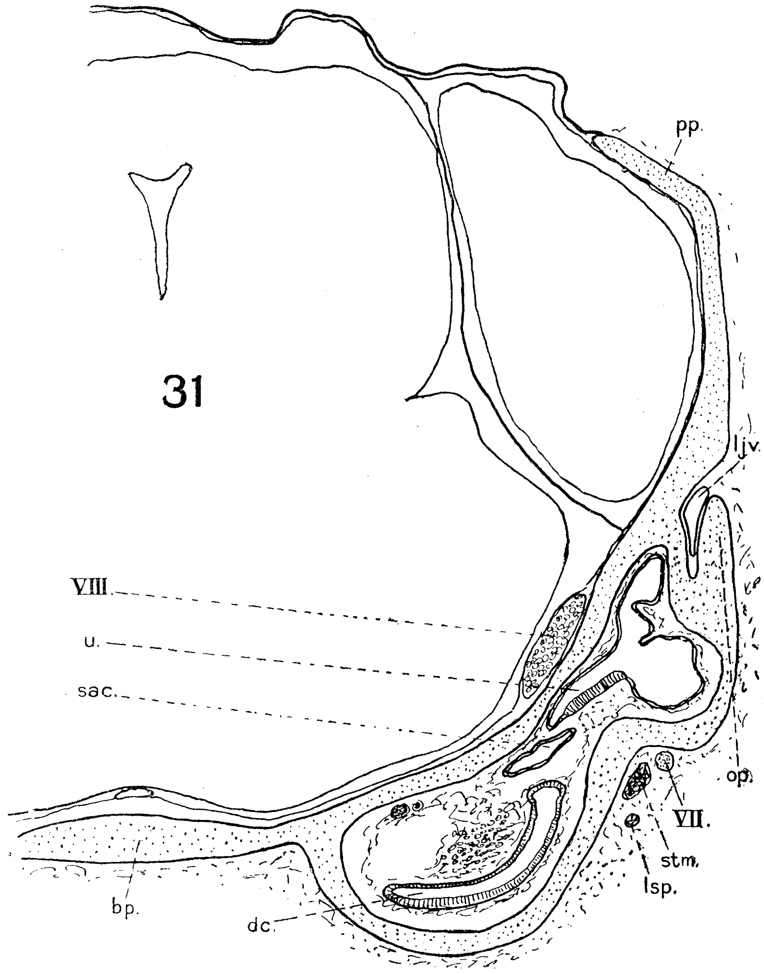


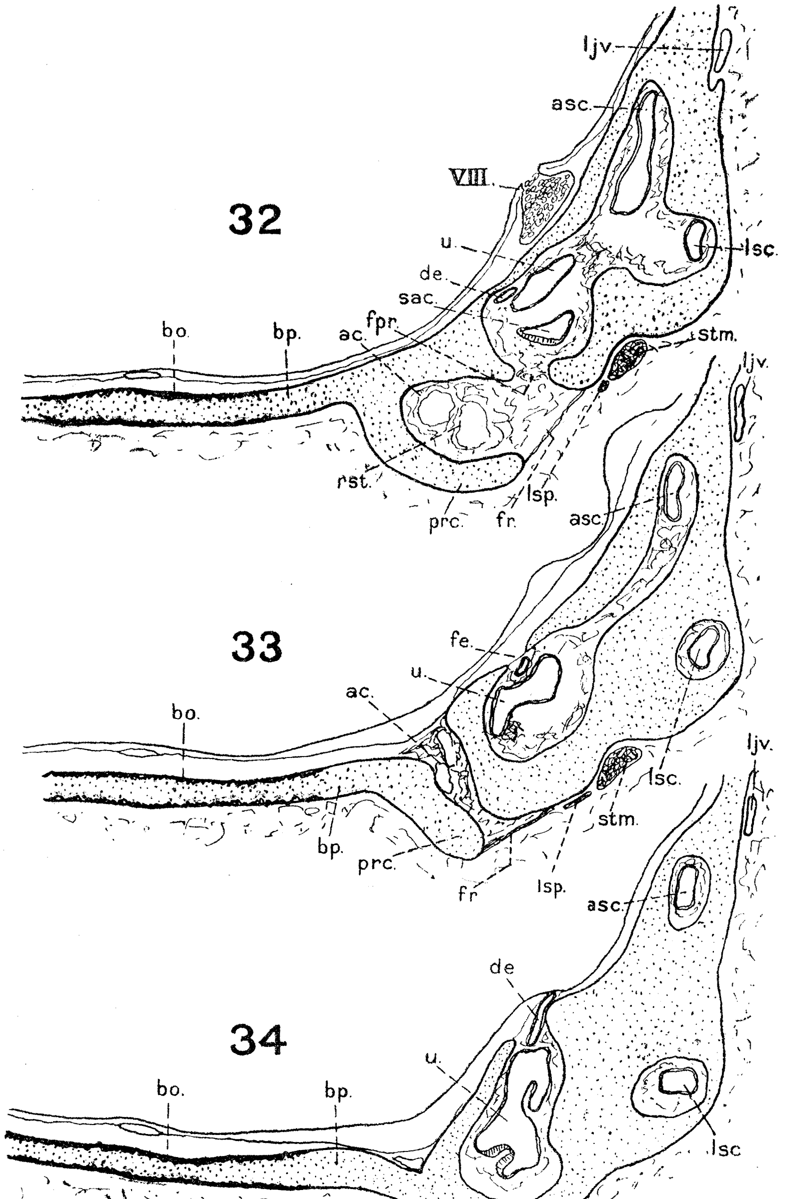
FIG. 31.—Section 10-1-1.

BLAND SUTTON (1884) held that the palatine process of the premaxilla was a distinct morphological element, and that it was homologous with what are now known as the prevomers. This was also the view of BROOM in 1895, who showed that there was a distinct bone in Miniopterus occupying the position of the dumb-bell-shaped bone of Ornithorhynchus. In 1885, PARKER had described "anterior vomers" as ossifying separately in Tatusia and in Erinaceus and becoming subsequently attached to the hind end of a process directed backwards near the middle line from the premaxilla of its own side. The separate ossification of the "anterior vomer" in Tatusia has been confirmed by FAWCETT (1921), who calls it the "paraseptal process (BROOM's 'Prevomer')." FAWCETT has also described (1911) the independent ossification of the palatine process of the premaxilla in Man. In the rabbit, the palatine process is stated to be distinct from the premaxilla, as discovered by BURNE and quoted from HOWES by BROOM (1895*a*). Further, separate "anterior vomers" were reported by PARKER (1885) in a number of Edentates, viz., Dasypus, Cholœpus, Manis, and Orycteropus. Lastly, GAUPP (1906, p. 850) refers to the discovery of palatine processes ossifying independently in man, sheep and pig.

Now, it would seem that WILSON's discovery that Ornithorhynchus has a palatine process of the premaxilla, in addition to the dumb-bell-shaped bone, led to a change in BROOM's views, when he stated (1902*a*, p. 551) "it seems much more satisfactory to regard it (*i.e.*, the palatine process of the premaxilla) as a true portion of the premaxilla which has replaced an anterior vomerine element, such as the dumb-bell bone of Ornithorhynchus, than to regard it itself as the homologue of that bone." However, it seems to me that there is a way in which these views can be reconciled.

On turning to Lacerta, it can be seen that the prevomers extend posteriorly parallel to one another, in front they taper to a point and die out behind the premaxilla, with which they do not fuse. Their relation to the paraseptal cartilages is such as to suggest very strongly that they are homologous with the palatine process of the premaxilla in mammals, and this resemblance is increased by the fact that in some lizards according to GAUPP (1906), the prevomers fuse with one another, like the dumb-bell-shaped bone of Ornithorhynchus. It is obvious that the efficiency of the prevomer as a structural support for the paraseptal cartilage and JACOBSON's organ will be increased if it becomes attached to some other firm bony element such as the premaxilla. The backgrowth of a process from the premaxilla, such as WILSON (1901) describes in Ornithorhynchus, is just what would be expected. It seems, therefore, that the coexistence of what WILSON called the palatine process of the premaxilla with the dumb-bell-shaped bone in Ornithorhnychus is not to be taken to mean that the bone which BLAND-SUTTON (1884) called the palatine process of the premaxilla (PARKER's "anterior vomer," 1885; FAWCETT's paraseptal process, 1921), in higher mammals, is not the homologue of the prevomer. The palatine process of the premaxilla in Ornithorhynchus is in an intermediate condition between the reptile where prevomer and premaxilla are separate, and higher mammal in which prevomer and premaxilla are fused. Further intermediate stages are to be found in the cases in which the "anterior vomers" ossify separately.

It seems advisable not to use the same term "palatine process" for the structure in Ornithorhynchus, which is definitely part of the premaxilla, and for the structure in the higher mammal, which may ossify separately, and which represents the prevomer. The structure in Ornithorhynchus has the better logical right to the term, and such a structure is also shown by Parker (1885) in a number of forms in which the "anterior vomer" subsequently becomes attached to it. He says (*loc. cit.*, p. 139), referring to the 2nd stage of Erinaceus :—" The premaxillaries are largely hollowed out for the teeth, and their palatine processes are, *at present*, short and small." Later, referring to the 5th stage (p. 149), he says :—" The premaxillaries have a large dentary part, and a small short palatine process ; over this, however, the anterior paired vomer is seen, which afterwards makes that process of the normal size."



FIGS. 32.—Section 10-2-1. 33.—Section 10-2-7. 34.—Section 10-3-3.

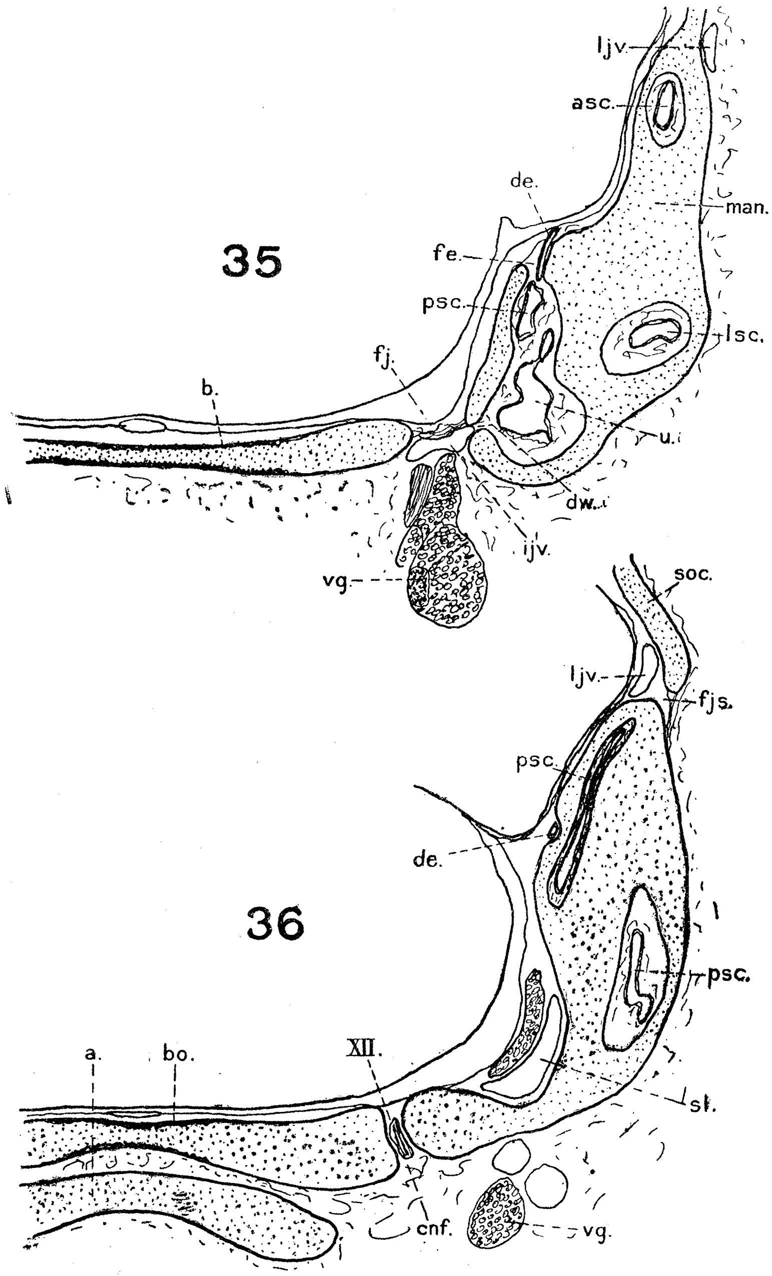
The complete process of bone which stretches back from the premaxilla in most higher mammals is a palatine process of the premaxilla *plus* prevomer, and for that part of it which is not premaxillary the term "prevomerine process" might be suggested.

The conclusions here arrived at are, therefore, in complete agreement with those of WILSON (1901, p. 726), who finds reason "for the belief that the anterior part of this process may originate as a direct backward extension from the body of the premaxilla, whilst the posterior part arises as a distinct prevomerine element." There is, therefore, good reason to believe that the prevomers of non-mammalian vertebrates are homologous with the dumb-bell-shaped bone of Ornithorhynchus, and with the prevomerine processes in those mammals in which the prevomers do not ossify independently. The attachment of the prevomerine process to the premaxilla becomes effected by the palatine process of the latter.

B. *The Nasal Capsule.*

The nasal capsule of Sorex is not very different from that of Erinaceus, which has been so admirably described by FAWCETT (1918*a*). There are present, an atrioturbinal, a maxilloturbinal, a nasoturbinal, two frontoturbinals, and three primary ethmoturbinals. The crista semicircularis, the numerous recesses, and the lamina transversalis anterior have the typical relations. The processus alaris superior, however, is directed more upwards than forwards, and the incisura pretransversalis of Erinaceus (through which the nasolachrymal duct passes) is in Sorex converted into a foramen pretransversale by a little cartilaginous bar which passes upwards and forwards from the antero-lateral corner of the processus lateralis ventralis to the atrioturbinal. The processus alaris superior itself, which also springs from the antero-lateral corner of the processus lateralis ventralis, is attached to the side wall of the fenestra narina a little higher up. Between the process and the bar of cartilage mentioned above, there is a little canal through which an arteriole passes. The distal pieces of the processus laterales anteriores are detached as accessory cartilages. A faint indication is present of the processus transversalis which FAWCETT discovered in Erinaceus. There is no epiphanial foramen in Sorex, which in this respect resembles FAWCETT'S (1918*a*) description of Erinaceus and differs from Talpa. However, MICHELSSON (1922) describes a foramen epiphaniale in Erinaceus.

The anterior paraseptal cartilages are continuous in front with the lamina transversalis anterior, but they have lost connexion with the posterior paraseptal cartilages. This seems to be the condition in most mammals so far known except in Halmaturus (SEYDEL, 1896), Dasyurus (FAWCETT, 1917), Trichosurus (BROOM, 1909), Lepus (VOIT, 1909), Microtus (FAWCETT, 1917), and Felis (ZUCKERKANDL, 1909, and TERRY, 1917), where they are at some time continuous. Sorex is, however, interesting in that the posterior paraseptal cartilage is almost independent of the lamina transversalis posterior. The posterior paraseptal cartilage is triangular, with the apex pointing backwards and the base forming the hind border of the fenestra basalis ; it is attached to the lamina transversalis posterior by thin cartilaginous connexions at the lateral corner of the base of the triangle, and at its apex. Between these two points of attachment there is a well-marked fissure, as there is between the medial margin of the posterior (and anterior) paraseptal cartilage and the nasal septum. FAWCETT (1921) found a separate posterior paraseptal cartilage in Tatusia.



FIGS. 35.—Section 10-3-7. 36.—Section 11-2-4.

The cribriform plate is beginning to form, and a crista intercribrosa is present, attached to the 1st ethmoturbinal. The original fenestra cribrosa is now divided on each side into three.

With regard to the general morphology of the nasal capsule, there is no doubt that GAUPP'S (1908) view is correct. He refers (*loc. cit.*, p. 713) to the lamina transversalis anterior as the primitive nasal floor, and it therefore corresponds to the lamina orbitonasalis of lower forms. But owing to the great backgrowth of the nasal sac, the planum antorbitale has also been pressed back. This is the case to some extent in the reptiles, and in all of them the planum antorbitale is free of the nasal septum. In the mammals the process has gone still further, and, presumably as a mechanical means of strengthening the posterior portion of the nasal capsule, that part of the planum antorbitale which forms the tectum nasi posterius has in the mammals effected a secondary fusion with the nasal septum.

The backgrowth of the planum antorbitale has resulted in an approximation of the fenestra cribrosa to the fenestra olfactoria. The effect of this has been that the space between these two fenestræ (the supracribrous recess, into which the profundus nerve enters from the orbit through the orbitonasal fissure) is very much compressed. The supracribrous recess being external to the dura mater is outside the true cranial cavity, but it comes to be included inside the cavity of a dry skull because of the close approximation of the planum antorbitale to the ala orbitalis, and the obliteration of the orbitonasal fissure by the maxilla and orbitosphenoid bones. For practical purposes the fenestra cribrosa and the fenestra olfactoria are then nearly coincident. The course of the profundus nerve, which appears to re-enter the skull, is to be explained in this way; but it must be remembered that the profundus nerve in the supracribrous recess is external to the dura mater.

The modifications of the nasal capsule which have taken place in the mammal are the opposite of those which are found in Teleost fish, such as Salmo. Here, the foramen olfactorium advehens (corresponding to the mammalian fenestra cribrosa) is separated by a wide gap from the foramen olfactorium evehens (corresponding to the mammalian fenestra olfactoria), with the result that the olfactory nerve appears to traverse the orbit (DE BEER, 1927).

The palatine cartilage in Sorex is as ÄRNBÄCK CHRISTIE-LINDE (1907) described it. This cartilage represents the cartilago ectochoanalis of Lacerta (GAUPP, 1900), and it is therefore a part of the primitive cartilaginous nasal floor. The palatine cartilage is present in :—

Echidna ..	PARKER (1894), BROOM (1895*b*), SEYDEL (1899), GAUPP (1908).
Ornithorhynchus	BROOM (1900).
Dasyurus ..	BROOM (1896).
Trichosurus ..	BROOM (1896).
Sorex	ÄRNBÄCK CHRISTIE-LINDE (1907 and 1914), DE BEER.

Crocidura	Ärnbäck Christie-Linde (1914).
Tupaja	Ärnbäck Christie-Linde (1914), Broom (1915).
Macroscelides	Broom (1902*b*).
Gymnura	Broom (1915).
Vesperugo	Grosser (1902).
Pteropus	Zuckerkandl (1909), Ärnbäck Christie-Linde (1914).
Vespertilio	Zuckerkandl (1909).
Miniopterus	Broom (1900), Fawcett (1919).
Chirogaleus	Ärnbäck Christie-Linde (1914).
Galago	Ärnbäck Christie-Linde (1914).
Cebus	Frets (1913).
Mycetes	Frets (1913).
Ateles	Frets (1913).
Chrysothrix	Frets (1913).
Lepus	Broom (1900), Voit (1909).
Felis	Zuckerkandl (1909), Broom (1900), Terry (1917).

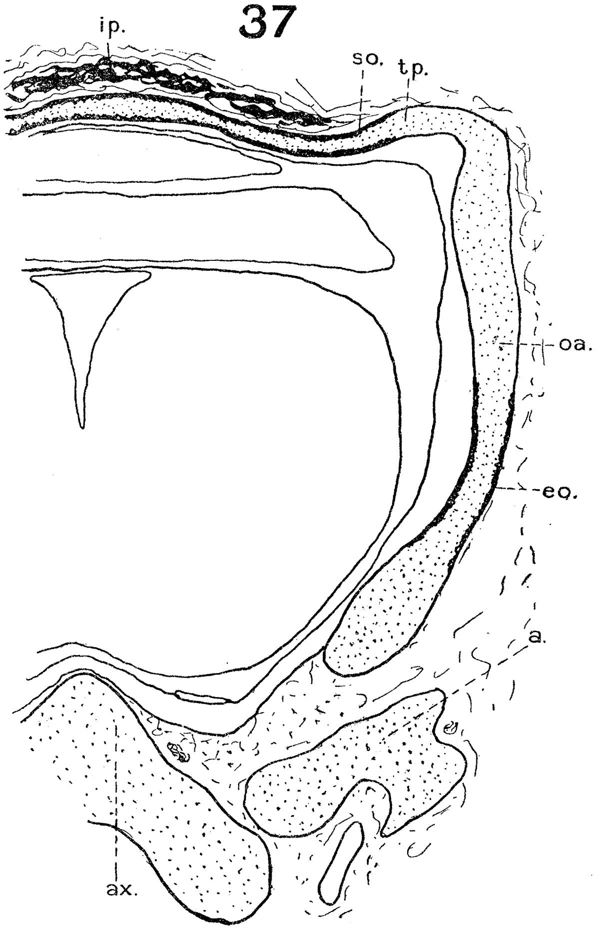


Fig. 37.—Section 12–2–4.

It is worth noticing that these animals belong to the most primitive mammalian orders. In most of these forms, the palatine cartilage ("outer nasal floor cartilage," processus posterior lateralis, of other authors) is attached to the anterior paraseptal cartilage by means of the cartilago ductus nasopalatini (or incisive cartilage) which lies just in front of the nasopalatine duct. This nasopalatine cartilage has not yet chondrified in the stages of Sorex studied, and it appears to be absent in Tupaja, Macroscelides and Lepus, with the result that the palatine cartilage is free in these forms (Ärnbäck Christie-Linde, 1914). The nasopalatine cartilage has been found in the calf by von Mihalkovics (1899), and in the horse, pig, deer, sheep, ox, and rabbit, by Spurgat (1896). It is not clear that by cartilago ductus nasopalatini some authors do not mean the element which other authors call the palatine cartilage. When the former is present, it is according to Ärnbäck Christie-Linde (1914) always in continuity with the anterior paraseptal cartilage, which fact raises doubts as to whether the cartilago ductus nasopalatini has a real independence. It deserves further study, and particularly in regard to the papillary cartilage which is present in some mammals.

Recently, Jacobson (1928) has tried to show that in Talpa the palatine cartilage is represented by the nodule of secondary cartilage in the palatine process of the maxilla. My studies on Sorex led me, however, to the conclusion that this view is erroneous. In Sorex the palatine cartilage is present, as is also the secondary cartilage in the palatine process of the maxilla. Histologically, these cartilages are quite distinct, and I can find no evidence for the view that the secondary cartilage of the maxilla represents the original primary palatine cartilage. On the contrary, it appears to me to be more probable that the palatine process of the maxilla effects a functional replacement of the primary palatine cartilage in the floor of the nasal capsule, but is not derived from the latter, and is in no way to be regarded as the ossified representative of the original cartilaginous nasal floor. The appearance of secondary cartilage in the palatine process of the maxilla must be due to the same factors which are responsible for its presence in a number of other dermal bones.

C. *The Ala Orbitalis.*

Both the anterior and posterior roots of the ala orbitalis in Sorex show a suture where they are attached to the central stem. This is consistent with the separate chondrification of the ala orbitalis, which has been observed in :—

Man ..	.. Levi (1900), Kernan (1916), Lewis (1920).
Felis ..	.. Terry (1917).
Talpa ..	.. Noordenbos (1905).
Crocidura	.. Levi (1909).
Echidna	.. Gaupp (1908).

It is also consistent with the homology of the ala orbitalis with the orbital cartilage, which appears to chondrify independently in all classes of vertebrates.

The posterior or postoptic root seems to be lacking in Monotremes and Marsupials.

In Sorex, the anterior or preoptic root abuts on the planum antorbitale on a level with the 3rd primary ethmoturbinal, and therefore well in front of the hind end of the nasal capsule. That the ala orbitalis should be attached to the lamina orbitonasalis must be due to the fact that the latter structure has been forced back by the backward extension of the nasal sac.

No structure was found in Sorex capable of identification with the ala hypochiasmatica of other forms (Tatusia, FAWCETT, 1921; Man, KERNAN, 1916).

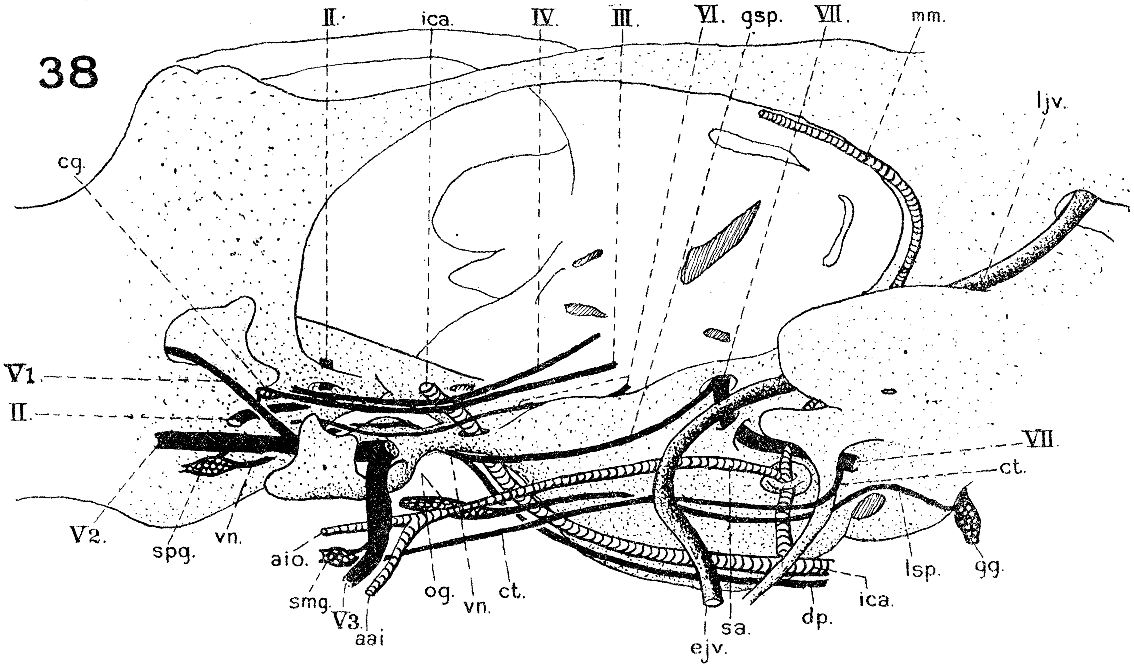


FIG. 38.—The orbitotemporal region of the skull of an 11-mm. embryo of *S. araneus* showing the relations of the cartilages to the chief blood-vessels and nerves.

D. *The Dorsum Sellæ.*

The dorsum sellæ is the ridge which forms the posterior border of the pit (sella turcica) which accommodates the pituitary body. In Sorex, however, it is absent, and the floor of the pituitary fossa (if it is permissible to speak of such a structure in Sorex) passes insensibly back into the basal plate. In this respect, Sorex resembles :

Erinaceus ..	FAWCETT (1918*a*).
Talpa	FISCHER (1901).
Tupaja	HENCKEL (1928*b*).
Halicore ..	MATTHES (1921*a*).
Bradypus ..	WEBER (1927).
Tatusia.. ..	FAWCETT (1921).
Didelphys ..	TERRY (1917).
Caluromys ..	TERRY (1917).
Perameles ..	ESDAILE (1916).
Echidna ..	GAUPP (1908).

On the other hand, a more or less well-marked dorsum sellæ is present in :—

Man	Gaupp (1906), Fawcett (1910), Kernan (1916), Macklin (1921).
Semnopithecus	Fischer (1903).
Macacus ..	Fischer (1903).
Chrysothrix ..	Henckel (1928*a*).
Tarsius	Henckel (1927).
Nycticebus ..	Henckel (1928*a*).
Equus	Limberger (1926), Arnold (1928).
Lepus	Voit (1909).
Felis	Terry (1917).
Poikilophoca ..	Fawcett (1918*b*).

The problem of the dorsum sellæ is complicated by the question of the age of the embryos studied, and by the fact that in some forms (Man, Semnopithecus, Macacus, Lepus, and Felis) there is an additional independently chondrifying structure, which co-operates with the anterior edge of the basal plate in its formation. Until further evidence is obtained, it is impossible to say which of these two elements corresponds to the crista sellaris of reptiles, the prootic bridge of fish, and the acrochordal of Selachians. At all events, the dorsum sellæ as a whole agrees well with the crista sellaris of the lizard, for example, in that its lateral extremities are continuous with the roots of the pilæ antoticæ, or their mammalian homologues the tæniæ clino-orbitales, and the posterior clinoid processes, which in Semnopithecus almost, and in Sus completely, enclose the abducens nerve in a cartilaginous canal. In Lacerta, a comparable canal is present at the root of the pila antotica.

E. *The Posterior Basicranial Fenestra.*

In the 11 mm. embryo of Sorex of which the model was reconstructed the basal plate is imperforate : indeed, the only median unpaired apertures in the whole skull are the foramen hypophyseos and the foramen magnum. In an embryo of the length of 8·3 mm., however, a small median perforation of the basal plate is visible, and shown in section in fig. 39. It is on a level with the fenestra rotunda. Further posteriorly, another median and even smaller gap is seen in the basal plate, between the jugular foramina. All traces of the notochord have vanished.

Noordenbos (1905) has shown how a posterior basicranial fenestra is formed in Talpa between the pole-plate and the parachordal plate, and the anterior of the two perforations in Sorex may correspond with that ; that the posterior one originally formed part of a larger opening which has since closed seems questionable because of its position. Perhaps it is to be referred to a perforation of the basal plate which Gaupp (1906) reports to exist in Man and Rat, Fawcett (1917) has found in Microtus, and Fischer (1903) describes in Semnopithecus. In Man, Semnopithecus and Microtus this gap serves for the exit of the notochord, which passes out on to the under surface of the skull. The question as to whether and in how far the posterior basicranial fenestra of mammals corresponds to the similarly-named aperture in the skulls of reptiles requires for its definite solution more evidence concerning Noordenbos' pole-plate, and the dorsum sellæ.

F. *The Pterygoid problem.*

One of the most interesting features of the chondrocranium of Sorex described in this paper is the fact that the pterygoid cartilage is in direct cartilaginous continuity with the cartilage of the ala temporalis, by the intermediary of the processus pterygoideus of the latter. That this is no mere fortuitous relation is shown by the fact that the continuity is present symmetrically on both sides in four embryos varying in length between 8·7 and 11 mm., of which I have studied complete serial sets of sections. It is interesting to compare these relations in Sorex with those which Terry (1917, p. 322) has described in the cat. In that animal, the pterygoid cartilage " presents a short cylindrical, transversely placed pedicle. . . ." " The pedicle consists of dense mesenchyma, continuous with the perichondrium of the margin of the pterygoid process of the lamina ascendens " of the ala temporalis. Were this

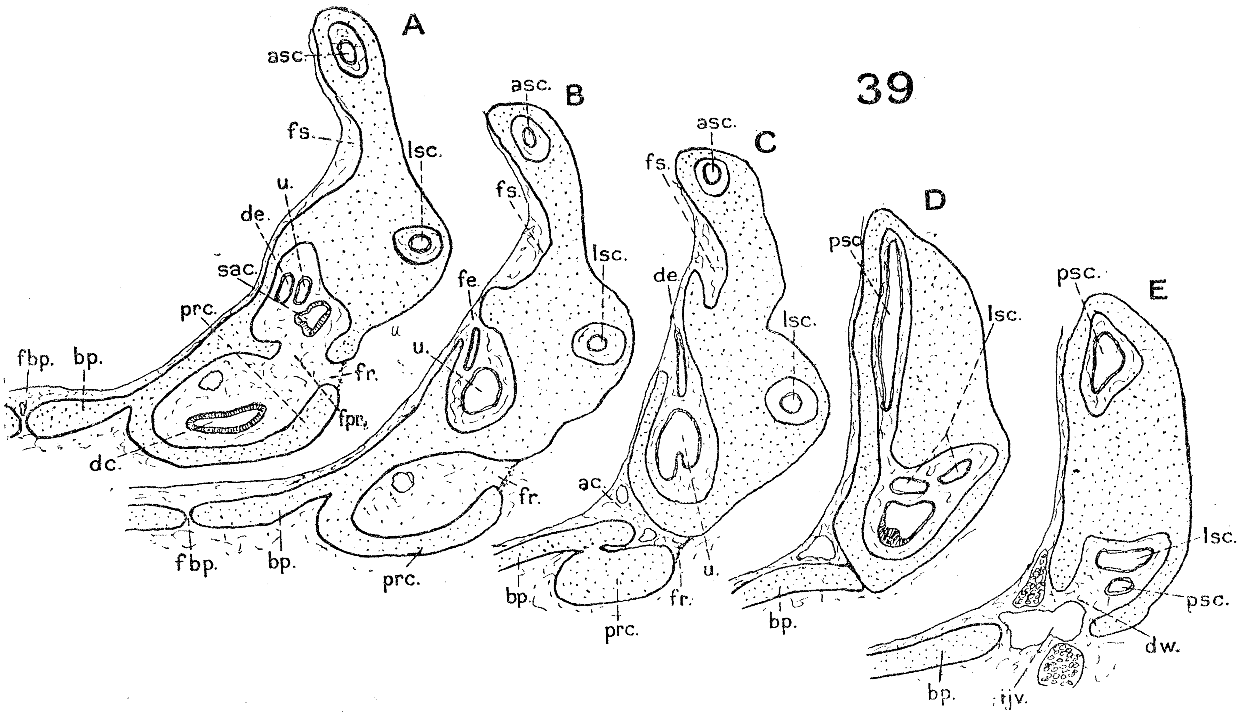


Fig. 39.—A series of transverse sections through an embryo of *S. araneus* 8·3-mm. in length, showing the relations of the fenestra rotunda and aquæductus cochleæ.

A. Section 5–3–3. B. Section 5–3–6. C. Section 5–3–9. D. Section 5–4–5. E. Section 5–4–8.

pedicle to chondrify, the conditions as present in Sorex would be reproduced. The only other case known to me in which the pterygoid cartilage comes into relation with other structures forming part of the neurocranium is an obscure one described by FISCHER (1901), in Talpa. On p. 515 he says :—" Erst später, wenn schon die Verknöcherung beginnt, verwachsen auch die Pterygoidknorpel mit der Schädelbasis," and the place of fusion is the " Unterseite der Orbitalflügelbasis." On the other hand, NOORDENBOS (1905), working also on Talpa, says on p. 405 :—" Nur habe ich sicher stellen können, dass der knorpelige Proc. pterygoideus beim Maulwurf nicht synchondrotisch mit der knorpeligen Schädelbasis sich verbindet, wie es ausdrücklich auch von FISCHER betont worden ist." It would seem, therefore, that in Talpa the connexion is bony, and it differs from my cases, not only in the place of attachment of the pterygoid cartilages, but also in the fact that the attachment in this case occurs late (" when ossification sets in "), whereas in my cases, the rudiments of the pterygoid cartilage and ala temporalis are already connected in procartilage.

The interpretation of the conditions in Sorex depends largely on the meaning attached to the pterygoid cartilage. FUCHS (1909) regards this cartilage as primitive, and as representing a remnant of the original palato-pterygoid cartilage of lower forms. Since the ala temporalis is certainly a visceral cartilage, and partly homologous with the processus ascendens of the pterygo-quadrate of lower forms, I do not doubt that FUCHS would see a support for his theory in the conditions in Sorex. However, the pterygoid cartilage is of a peculiar nature. The histological picture which it presents is quite different from that of undoubted primitive cartilage (such as that of the ala temporalis, for example), but is identical with that of the nodules of cartilage which are to be found in the angular and coronoid regions of the dentary bone of the mandible in several mammals. I therefore agree with GAUPP (1901) that this cartilage is of a secondary nature, and that it does not represent any primitive *cartilaginous* structure. FAWCETT (1905) came to the same conclusion. The question then arises as to what such secondary cartilage really represents. I think that there can be no doubt that it represents a preformation of a dermal ossification, and it may be noticed that, in the case of the dentary, as well as of the pterygoid, the dermal ossification is not plate-like, but thick, and is sunk at some little distance beneath the surface. Prof. WATSON has also kindly drawn my attention to the fact that the preformation of dermal ossification in secondary cartilage tends to occur at places where muscle-attachments are formed. There seems, then, every reason to believe that secondary cartilage is an embryonic adaptation of a functional nature, and that qua cartilage it is secondary, though the dermal bone which it precedes is a primitive structure, inherited from the reptiles.

Now, the relations of the secondary pterygoid cartilage to the ala temporalis in Sorex are very suggestive of those of the pterygoid bone to the processus ascendens of the pterygo-quadrate of a reptile such as Lacerta, and of which a drawing of a transverse section is given in text-fig. 42. I would draw attention not only to the relative topographical positions of the structures, including the palatine (or Vidian) nerve, but also to the thick, stumpy nature of both pterygoid cartilage (of Sorex) and pterygoid bone (of Lacerta). I therefore come to the conclusion that the pterygoid cartilage of the mammal and consequently the dermal bone which subsequently ossifies in this secondary cartilage, is homologous with the pterygoid bone of reptiles. This view is borne out further by the fact, emphasised by Fuchs (1910) that the pterygoid muscles have similar relations to these structures in reptiles and mammals.

This conclusion, which is now supported by tangible evidence, throws open the whole question of the homology of the pterygoids of monotremes, reptiles, and mammals, which has been thrown into utter confusion ever since Gaupp (1908) described two " pterygoid " bones on each side in Echidna. He observed that the more ventral of these bones in Echidna—the " Echidna-pterygoid "—bore the relations of the pterygoid of the reptile (which, in order to avoid confusion, I will refer to as the " rep. pterygoid "), while the more dorsal bone of Echidna, the " Säugerpterygoid," corresponded to the pterygoid of mammals (the " mam. pterygoid "). Consequently, Gaupp was driven to the conclusion that the pterygoids of reptiles and mammals were not homologous; that the rep. pterygoid was absent in the higher mammals unless possibly represented by the entotympanic; and that the mam. pterygoid, by a process of exclusion, could represent nothing else than the lateral wings of the parasphenoid, detached from their median rostral portion, as are the basitemporals in birds (Parker, 1869), crocodiles (Parker, 1883), and in some higher mammals. Of the latter, Parker (1885) says on p. 260 :—" I shall have to describe a pair of bones found *in membrane*, and added to the basisphenoid, when I come to other and higher kinds of Eutheria : these have long been known in Man as the ' lingulæ sphenoidales.' I strongly suspect that they are the ' basitemporals '—symmetrical remnants of the parasphenoid—so well seen in Birds and the Crocodilia." Unfortunately, Parker never came to describe these most interesting structures. It will be necessary, however,

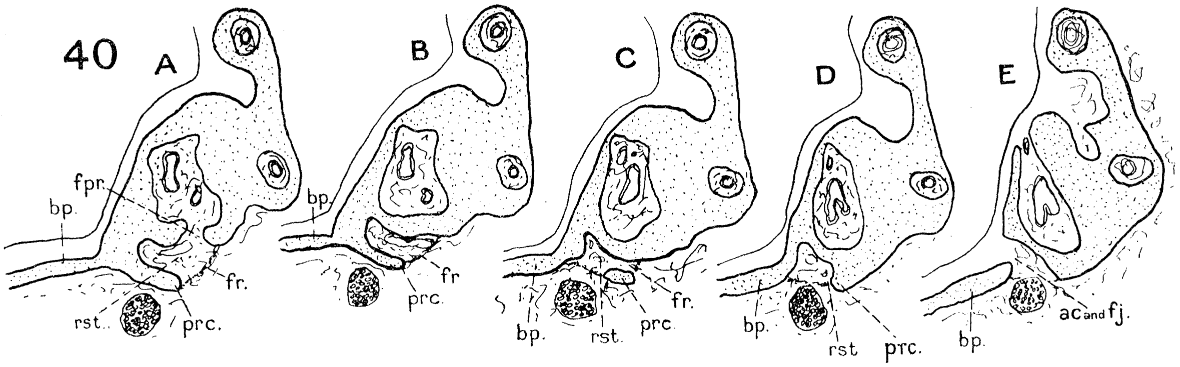


Fig. 40.—A series of transverse sections through an embryo mouse, stage S (from the collection of the late J. W. Jenkinson) showing the relations of the fenestra rotunda and aquæductus cochleæ A. Section 27–3–5. B. Section 28–1–1. C. Section 28–2–2. D. Section 28–2–4. E. Section 28–3–5.

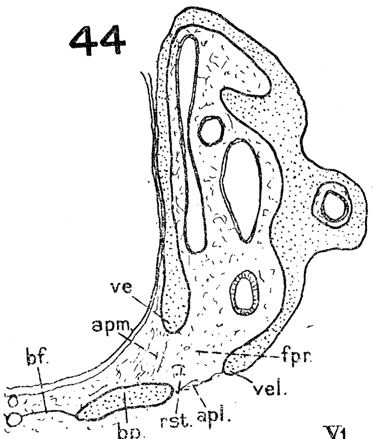
to refer to PARKER's work again below. Meanwhile, it may be mentioned that the lateral wings of the parasphenoid were found to ossify separately in Lacerta by GAUPP (1900).

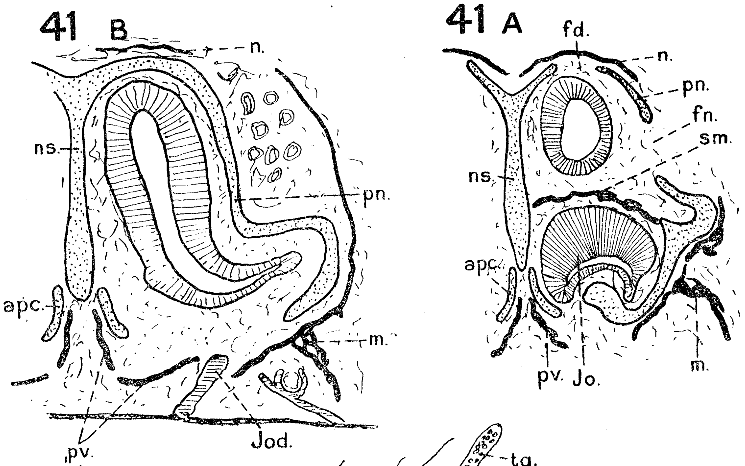
It will be noticed that, according to GAUPP's view, whereas the reptiles and the monotremes have two elements (pterygoid and parasphenoid : Echidna-pterygoid and Säugerpterygoid, respectively), the higher mammal only has one (leaving out of account the very problematical entotympanic). I imagine that GAUPP regarded the mammalian pterygoid as a single element, because both WINCZA (1896), in the hedgehog, and FISCHER (1901), in the mole, expressly state that they were unable to find any pterygoid dermal bone, in addition to the pterygoid cartilage. Now, on turning to Sorex, a description has already been given of a little pair of plate-like and flat dermal bones, which just touch the postero-dorsal corner of the pterygoid cartilage, and spread in the gap between the basisphenoid region of the central stem and the inner edge of the ala temporalis, lying ventral to the Vidian nerve. They extend almost to the anterior edge of the processus alaris, and their periosteum extends beneath that structure. There is, therefore, a small Vidian canal. Since the dermal bone is quite well formed, while most of the pterygoid cartilage is still unossified, I believe that they are really separate structures, as indeed, FUCHS (1909) found them to be in the rabbit. I therefore regard these flat plates of bone as homologous with the lateral wings of the parasphenoid, or basitemporals. It is interesting to note, further, that LUBOSCH (1907) found that the pterygoid was divided in young Cholœpus, and was led, as a result, to suggest, on p. 527 :—" der Befund von Choloepus hat mir den Gedanken nahe gelegt, in dem Pterygoid der erwähnten Edentaten eine Verschmelzung zwischen dem ' Parabasale ' und dem ' Echidna-pterygoid ' zu erblicken." Since the " parabasale " is the parasphenoid, and the " Echidna-pterygoid " is regarded by GAUPP as representing the rep. pterygoid, LUBOSCH has arrived, through considerations of morphology, at conclusions similar to those which I have been driven to as a result of embryological investigations. Further, in Man, FAWCETT (1905 and 1910 *a* and *b*) has described the internal pterygoid plate as ossifying early as a membrane-bone, with the hamular process chondrifying later, and then undergoing ossification in this chondrification. In the cat, TERRY (1917, p. 398) says " there is evidence of two ossific centres, and from these the medial pterygoid lamella and hamular process are formed." In Galeopithecus, PARKER (1885) describes and figures bones which he calls mesopterygoids which exist in addition to the pterygoids, and which he also shows in the pig (PARKER, 1874).

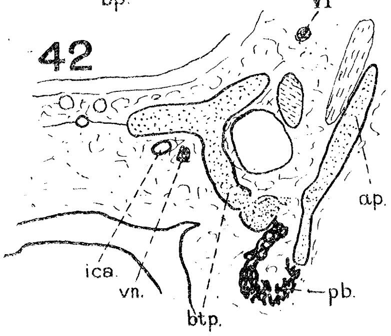
Further evidence for the composite nature of the mammalian pterygoid is supplied by VAN KAMPEN (1922). This author finds S-shaped bones in Cavia, which he regards as basitemporals, and he assigns the same value to the ossicula Bertini in Man. Further, he finds, in Erinaceus and in Talpa, certain dermal bony structures, which arise late, attached to the basisphenoid. These he calls the tympanic processes of the basisphenoid ; they are fused to the pterygoid in Erinaceus, but they are free of it in Talpa.

Broom (1914) reported the existence of elements distinct from the pterygoid in Petrogale, Tatusia, and Tamandua; and he regarded these elements as equivalent to the Echidna-pterygoid.

There is, therefore, considerable evidence that the mammalian pterygoid is a composite structure, and in this I agree with Lubosch and van Kampen. Whereas







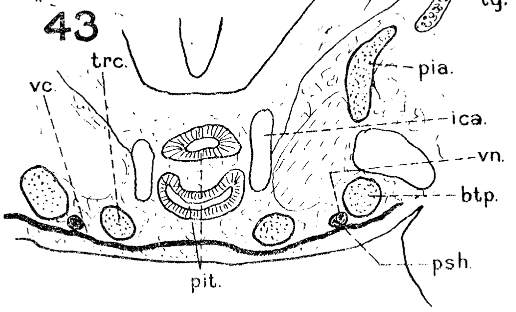


Fig. 41.—Transverse sections through the anterior (A) and the middle (B) regions of the nasal capsule of Lacerta, stage D, showing the relations of the anterior paraseptal cartilages and prevomers.

Fig. 42.—Transverse section through an embryo of Lacerta, showing the relations of the basitrabecular process to the Vidian nerve and pterygoid bone.

Fig. 43.—Transverse section through an embryo of Lacerta, showing the relations of the parasphenoid to the basitrabecular process and to the Vidian nerve.

Fig. 44.—Transverse section through an embryo of Lacerta, showing the relations of the recessus scalæ tympani, foramen perilymphaticum, and fissura metotica.

Lubosch regards one of these components as the parasphenoid, van Kampen prefers to regard it as a basitemporal, and declines to assert that basitemporals represent the lateral wings of the parasphenoid, although that is the sense in which Parker used the term. Instead (1922), he thinks it equally probable that the basitemporals were always distinct, and possibly equivalent to one of the pterygoid bones of the fish. He cites the instances of the existence of an unpaired parasphenoid (behind the vomer, which, following BLAND SUTTON (1884) is to be regarded as the rostrum of the parasphenoid) in Galeopithecus (PARKER, 1885) and Didelphys (FUCHS, 1908) in his support. But it would seem that the existence of these median unpaired vestiges of the parasphenoid does not exclude the possibility of the existence of paired vestiges of its lateral wings at the same time. Partly on the grounds of economy of hypotheses, and partly because of the difficulty of imagining any other homology for the basitemporals, I think that it is preferable to regard the basitemporals as the detached lateral wings of the parasphenoid, until both these elements can be shown to coexist in one animal at the same time.

The view adopted here has, I think, the merit of simplicity, and that of clarifying the confused state into which the pterygoid problem has fallen. If the mammalian pterygoid is composite and made up of the reptilian pterygoid plus the lateral wings of the parasphenoid, there is no need to look for the homologue of its dorsal constituent in the pars perpendicularis of the palatine, as FUCHS (1910) has done. Nor is it necessary to look for its ventral constituent in the alisphenoid (WATSON, 1916) or the ectopterygoid (BROOM, 1914), for both these authorities have been led on palæontological grounds to deny the homology of the Echidna-pterygoid with the reptilian pterygoid, and on this point they differ from all others. In this connexion, it may be mentioned that the pterygoid cartilages of Talpa stretch relatively far forwards. NOORDENBOS (1905, page 406) states :—" Es ist merkwürdig dass die Lamina medialis vom Pterygoid (the pterygoid cartilage) beim Maulwürfe so weit nach vorn reicht und rostral von der ala temporalis sich findet. Etwas derartiges fand VAN BEMMELEN (1901) am knöchernen Schädel von Ornithorhynchus." . . . " Das knöcherne Pterygoid (and by that he must mean Echidna-pterygoid, because the other pterygoid had then not yet been discovered) des erwachsenen Schädels von Ornithorhynchus verhält sich dann zum Palatinum, wie das knorpelige Pterygoid am foetalen Schädel bei Talpa." The pterygoid cartilage of Talpa can hardly fail to be homologous with the pterygoid cartilage of Sorex, and as the latter can be regarded as the representative of the rep. pterygoid, these considerations give additional reasons in favour of homologising the Echidna-pterygoid with the rep. pterygoid.

GAUPP'S (1911) chief objection to the homology of the rep. pterygoid with the mam. pterygoid is the fact that the former is related to the palato-pterygoid arch, whereas the latter enters into relations with the base of the skull. But Sorex shows that the pterygoid cartilage *is* related to the visceral cartilage of the palato-pterygoid arch (ala temporalis) by cartilaginous continuity, at the same time as the dermal bone behind it is related to the base of the neurocranium. It is only necessary to make this modification in GAUPP'S view (viz., to regard the pterygoid of higher mammals as composite) for it to fall perfectly into line with that which is advocated here : all his other arguments will then hold. It may be mentioned that the pterygoid cartilage does not exist in Echidna (GAUPP, 1905). This negative evidence, so far as it goes, supports the present view ; for if it could be demonstrated that the pterygoid cartilage coexisted with the Echidna-pterygoid and the Säugerpterygoid, this view would fall to the ground. It is also interesting to note that in Echidna, secondary cartilage is absent not only from the pterygoid but also from the dentary. It would seem, therefore, that Echidna lacks one of the factors necessary for the formation of secondary cartilage altogether, and the fact that in Echidna the Echidna-pterygoid is not performed in secondary cartilage is no evidence against the view that the Echnida-pterygoid is homologous with the pterygoid cartilage of those forms which possess it.

As to the pterygoid cartilage itself, although the nature of the secondary cartilage of which it is composed is problematical, its distribution is so universal among the higher mammals that it cannot be dismissed as a structure of transitory importance. I mention this because, although its preformation in secondary cartilage is surely a mammalian innovation, I regard the element which it represents as the reptilian pterygoid. The following table gives the forms in which the pterygoid cartilage has been found :—

Man	Fawcett (1905, 1910*a*), Hannover (1885), Noordenbos (1905).
Semnopithecus	Fischer (1903).
Macacus	Fischer (1903).
Chrysothrix	Henckel (1928*a*).
Tarsius	Henckel (1927).
Erinaceus	Parker (1885), Fawcett (1918*a*).
Talpa	Parker (1885), Fischer (1901), Noordenbos (1905).
Sorex	Parker (1885), de Beer.
Rhynchocyon	Parker (1885).
Centetes	Parker (1885).
Miniopterus	Fawcett (1919).
Bos	Fawcett (1918).
Sus	Noordenbos (1905).
Felis	Terry (1917).
Mustela	Fawcett (1916).
Poikilophoca	Fawcett (1918*b*).
Mus	Gaupp (1905).
Lepus	Voit (1909), Noordenbos (1905).
Microtus	Fawcett (1917).
Halicore	Matthes (1921*a*).
Dasypus	Parker (1885).
Bradypus	Parker (1885).
Cycloturus	Parker (1885).
Manis	Parker (1885).
Perameles	Cords (1915).
Didelphys	Töplitz (1917).

It may be noticed that these examples cover nearly all the orders of Eutherian mammals.

Lastly, it may be noticed that many authors have been driven to conclusions of homology by a process of exclusion, because there was no other bone left with which the one in question might correspond. The relations in Sorex, however, of the pterygoid cartilage to the ala temporalis and of the dermal basitemporal bone to the Vidian nerve, skull-base, and processus alaris, are positive.

I append the views of the various authors, as to the homologies of the pterygoid bones, in tabular form:—

Authority.	Reptile.	Monotreme.	Higher Mammal.
Gaupp	Parasphenoid	= Pterygoid	= Mam. pterygoid.
	Rep. pterygoid	= Echidna-pterygoid	
Fuchs		Pterygoid	= Pars perpendicularis palatini.
	Rep. pterygoid	= Echidna-pterygoid	= Mam. pterygoid.
Watson	Rep. pterygoid	= Pterygoid	= Mam. pterygoid.
	Epipterygoid	= Echidna-pterygoid	= Alisphenoid.
Broom	Rep. pterygoid	= Pterygoid	= Mam. pterygoid.
	Ectopterygoid	= Echidna-pterygoid	= Ectopterygoid of Tatu, etc.
Lubosch		Pterygoid	= Mam. pterygoid.
		Echidna-pterygoid	
van Kampen ..	Basitemporal	= Pterygoid	= Processus tympanici.
	Rep. pterygoid	= Echidna-pterygoid	= Mam. pterygoid.
Parker	Parasphenoid		= Basitemporal.
	Rep. pterygoid		= Mam. pterygoid.
de Beer	Parasphenoid	= Pterygoid	= Mam. pterygoid.
	Rep. pterygoid	= Echidna-pterygoid	

G. *The Cavum Epipericum, Carotid Artery, and the True Side Wall of the Skull.*

The *cavum epipericum* (GAUPP, 1902) is a space which is extracranial in lizards and reptiles generally, but which in the mammals has been incorporated in the skull. This space is particularly easy to study in Sorex, because of the definite nature of the membranes surrounding it. In a transverse section the cavum epipericum appears in the form of a pointed triangle with the apex turned outwards and the base towards the cranial cavity. It therefore has three surfaces: a ventro-lateral, a medial, and a dorsal surface. The ventro-lateral surface is formed for the most part by the ala temporalis, and by a membrane which is attached to the lateral edge of the ala temporalis, and extends sideways and upwards to the apex of the triangle described above (where it joins the membrane representing the true side wall of the cranial cavity: DÜRER's membrane). The hindmost part of the palatine bone just enters into the formation of the most anterior region of the ventro-lateral surface or floor of the cavum epipericum. Behind the place where the ala temporalis is attached to the processus alaris, the floor of the cavum epipericum is formed by the alicochlear commissure, which runs to the anterior pole of the cochlear part of the auditory capsule. Behind this again, the cavum epipericum passes insensibly into the cavum supracochleare (VOIT, 1909), which, as its name implies, rests on the upper and outer surface of the anterior region of the cochlear part of the auditory capsule. Broadly speaking, the cavum epipericum accommodates the huge trigeminal ganglion, while the cavum supracochleare lodges the facial ganglion. In addition, the cavum epipericum is traversed by the oculomotor, trochlear, and abducens nerves, while the cavum supracochleare is traversed by the greater superficial petrosal, or palatine nerve. These spaces, therefore, correspond as GAUPP showed, to the space which in the lizard is comprised medial to the processus ascendens of the pterygo-quadrate, dorsal to the basipterygoid process, and lateral to the true side wall of the skull as indicated by the position of the pila metotica, pila antotica (GAUPP's pila prootica), the supratrabecular bar, and the prefacial commissure.

It is now necessary to make certain of the mammalian equivalents of the reptilian structures enumerated above.

Processus ascendens.—GAUPP (1900) was of opinion that this structure was absent in mammals, and that it was functionally replaced by an upgrowth from the lateral edge of the basipterygoid process, which gave rise to the ala temporalis, and which passed in the mammalian manner between V 2 and V 3, instead of between V 1 and V 2, as does the reptilian processus ascendens. On the other hand, BROOM (1909) regarded the processus ascendens as homologous with the ala temporalis, as do FUCHS (1912), GREGORY and NOBLE (1924). In Trichosurus (and also in Perameles, as shown by CORDS, 1915, and ESDAILE, 1916) the cartilaginous ala temporalis is perforated by a foramen rotundum for V 2; the cartilage in front of this foramen can be regarded as processus ascendens, and that behind it as true ala temporalis. In further support of the view that the ala temporalis is the (slightly modified) processus ascendens, is the fact that in a great many mammals, it chondrifies separately from the processus alaris. The following is a list of the forms in which the ala temporalis has been seen to arise separately, or in which its attachment to the processus alaris shows a suture :—

Man ..	.. Levi (1900), Noordenbos (1905), Fawcett (1923), Lewis (1920).
Macacus	.. Fischer (1903).
Erinaceus	.. Wincza (1896) (not mentioned by Fawcett, 1918*a*).
Crocidura	.. Levi (1909).
Lepus ..	.. Noordenbos (1905), Voit (1909).
Cavia ..	.. Fawcett (1917).
Microtus	.. Fawcett (1917).
Equus ..	.. Noordenbos (1905).
Bos ..	.. Fawcett (1917).
Sus ..	.. Noordenbos (1905).
Felis ..	.. Wincza (1896), Fawcett (1917), Terry (1917).
Canis ..	.. Wincza (1896), Olmstead (1911).
Ursus ..	.. Wincza (1896).
Mustela..	.. de Beer (1926).
Poikilophoca	.. Fawcett (1918*b*).
Phocæna	.. de Burlet (1913*a*).
Balænoptera	.. de Burlet (1914*a*).
Megaptera	.. Honigman (1917).
Tatusia	.. Fawcett (1917).
Didelphys	.. Levi (1909).
Trichosurus	.. Broom (1909).

On the other hand, the ala temporalis seems to chondrify in continuity with the processus alaris in

Ovis ..	.. Wincza (1896).
Talpa ..	.. Noordenbos (1905).
Sorex ..	.. This paper.
Echidna	.. Gaupp (1908).

It is possible that this last list will shrink still further when some of its forms are better known.

Processus basipterygoideus.—Gaupp (1902) regarded the processus basipterygoideus as homologous with the processus alaris of the mammal *plus* the ala temporalis. But now that the ala temporalis is regarded as equivalent to the processus ascendens, the processus basipterygoideus may be regarded as homologous with the processus alaris.

The relations of the palatine nerve seem to make this conclusion irresistible. The term processus basitrabecularis is synonymous with processus basipterygoideus.

Pila metotica.—This structure is posterior to the optic nerve, and anterior to the oculomotor; it corresponds, therefore, exactly to the postoptic root of the ala orbitalis of the mammal.

Pila antotica.—This pillar is situated posterior to the oculomotor nerve and pituitary vein, and anterior to the trigeminal nerve. Its mammalian homologue is to be found in the tænia clino-orbitalis of Monotremes (GAUPP, 1908, WILSON, 1906, WATSON, 1916, DE BEER, 1926). In higher mammals this structure usually disappears, but remnants of it are found in the posterior clinoid process of a number of forms, especially Semnopithecus (FISCHER, 1903) and Sus (MEAD, 1909), and in the isolated nodules of cartilage which VOIT (1909) has found in Lepus; TERRY (1917), in Felis; HENCKEL (1927), in Tarsius; TÖPLITZ (1917), in Didelphys; and MATTHES (1921*a*), in Halicore.

Supratrabecular bar.—This structure, which GAUPP (1906) showed to be present in Lacerta, corresponds to the tænia interclinoidea of Semnopithecus, and of which remnants are found in the anterior clinoid processes of Man (MACKLIN, 1921), Poikilophoca (FAWCETT, 1918*b*), and of Sorex, as shown earlier in this paper.

The prefacial commissure.—This structure is easily recognisable in the mammalian chondrocranium, where it has usually received the name of suprafacial commissure It is mounted on the top of the cochlear part of the auditory capsule, which relation will be discussed in the section dealing with the auditory capsule. There is, however, no doubt that the suprafacial commissure is a part of the true cranial wall, because it is directly continuous above with the orbitoparietal commissure, which itself corresponds to the tænia marginalis of Lacerta (GAUPP, 1900) and Salmo (DE BEER, 1927). This relation of the suprafacial commissure has been observed by TERRY (1917) in Felis.

The result of this discussion shows, then, that there is good agreement between certain structures in reptiles and in mammals. Attention need now only be turned to two special regions of the cavum, viz., that portion of the cavum epiptericum which rests on the alicochlear commissure, and the hind part of the cavum supracochleare where the facial nerve enters the facial canal.

The alicochlear commissure is situated lateral to the internal carotid artery, median to the palatine (greater superficial petrosal) nerve, behind the processus alaris, and in front of the cochlear part of the auditory capsule. It therefore has the relation typical of the posterior part of the trabecula cranii of lower vertebrates (GAUPP, 1902), which, in mammals, are seen elsewhere only in the Monotremes. VOIT (1909), however, has opposed this view, because, in Lepus, he finds that the internal carotid, where it rises up through its foramen and comes to enter the cavum epiptericum, lies considerably laterally to the abducens nerve. In its further course, the artery runs towards the abducens nerve, beneath it and up on its medial side. VOIT concludes from the lateral position of the carotid relative to the abducens (at the point of entry of the former) that the carotid of Lepus is not the same vessel as that of similar name in other forms: that the carotid foramen of Lepus is likewise different; and that the alicochlear commissure is not the trabecula.

In answer to this, it may be said that the entry of the carotid artery into the cavum epiptericum as described by VOIT in Lepus is altogether exceptional. GAUPP (1911) draws attention to the fact that in Talpa and in Mus, the carotid enters directly into the cranial cavity. The same is true in Phocæna (DE BURLET, 1913*a*) and in Echidna (GAUPP, 1908). In the cat, TERRY (1917, p. 383) says that the alicochlear commissure "does not, in the cat, enter into the floor of the cavum epiptericum, nor does the carotid artery pass directly into the primary cranial cavity. The vessel first traverses that part of the membrana limitans which is fixed to the cranial floor, before passing into the original cavity of the skull." In Sorex, the lateral half of the alicochlear commissure does form the floor on which the limiting membrane of the cavum epiptericum rests. The carotid artery on rising through its foramen finds itself median to the inner membrane of the cavum epiptericum, and just beneath the dura mater, which it pierces to enter the cranial cavity. At its very point of entry through the carotid foramen, the carotid artery is median to the abducens nerve.

I have, therefore, no reason to doubt that the carotid artery and carotid foramen are in every way identical with the similarly named structures in other vertebrates, and that the alicochlear is the trabecula. In passing, I may mention that the courses of the carotid and abducens in Lepus as described by VOIT (1909) are quite typical as regards their *morphological* relations: the artery rises up passing median to the nerve. The fact that the carotid artery enters to the outside of the nerve, and yet runs in beneath it to rise up on its inner side, and thus preserve the typical relations, is additional proof that the carotid of Lepus is the true carotid, which has undergone a slight topographical displacement. That the trabecula (alicochlear commissure), or rather its lateral portion, should come to form the floor of an extra-cranial space (cavum epiptericum) is easy to understand. The cavum epiptericum itself is developed as an expanded space accommodating the large trigeminal ganglion. In its expansion, this space has extended laterally as far as the ala temporalis would allow, and since the skull-wall is membranous in this region, it has bulged medially as well. In so doing, it has pushed its way in over the trabecula, and may be said to rest upon it, much as in Selachians the innermost part of the orbit "rests" on the subocular shelf.

The hindmost region of the cavum supracochleare is interesting, because it comes into relation with the suprafacial commissure and the facial canal. The hindmost portion of the cavum supracochleare is lodged between the suprafacial commissure on the inside and the secondary facial foramen on the outside. That the suprafacial commissure represents the true side wall is shown not only by the membranes, but also by the fact that as soon as the facial nerve has emerged through it, its palatine branch (greater superficial petrosal) separates from the main trunk and runs forwards and downwards, o pass laterally to the alicochlear commissure. The main trunk of the facial then passes laterally through another arch of cartilage (the secondary facial foramen) and into the sulcus facialis. The palatine branch thus slips out as it were between the two tunnels, and this space between the suprafacial commissure and the secondary facial foramen is the hiatus of the future facial canal. It is interesting to compare this facial canal and the separation of palatine from main branches with the analogous conditions which are to be found in Selachians and other forms (DE BEER, 1926). The arch of cartilage which encloses the secondary facial foramen corresponds in position to a postpalatine commissure.

H.—*The Relations of the Auditory Capsule to the Base of the Skull.*

The auditory capsule of the mammalian chondrocranium is distinguished from that of all other vertebrates by the great development of the cochlear part, lodging the ductus cochlearis, as distinct from the canalicular part which accommodates the semicircular canals. The cochlear part is non-existent in the skulls of fish and amphibia and it is practically speaking absent from the skulls of reptiles also. The question, therefore, arises as to how the cochlear part has been formed, in answer to which there are two possible alternatives: 1st, that it is formed from cartilage really belonging to the basal plate, which has been invaded by the auditory vesicle, and so converted into an annex of the auditory capsule; 2nd, that it is formed from the original auditory capsule as an extension, and has no relation to the basal plate at all.

The first of these alternatives was put forward by GAUPP (1900), who upheld it for the following reasons. In the mammalian skull, the basal plate between the cochlear capsules is relatively narrower than it is further posteriorly; the foramen acusticum is at some little distance from this flat portion of the basal plate; and the facial foramen beneath its suprafacial commissure is mounted on the top of the cochlear capsule. In the amphibian skull, on the other hand, the basal plate is of the same width anteriorly as posteriorly; the foramen acusticum is formed at the lateral edge of the basal plate; and the facial foramen behind its prefacial commissure is at the edge of the flat basal plate, and in front of the (canalicular) part of the auditory capsule. In addition, in Echidna (GAUPP, 1908), before chondrification sets in, the tissue surrounding the ductus cochlearis is in direct continuity with that from which the basal plate is formed. These facts led GAUPP to the conclusion (1900, p. 583) that "Grob mechanisch ausgedrückt kann man sagen, dass bei den Amnioten der Ductus cochlearis in die Basalplatte hineingewachsen sei und einen Teil derselben zur Pars cochlearis umgestaltet habe." . . . "Die vordere Kuppel der Ohrkapsel bei den Säugern entspricht somit nicht der vorderen Kuppel bei den Amphibien oder den Sauriern, sondern entspricht dem vorderen lateralen Abschnitt der Basalplatte der genannten Formen."

This view was opposed, and the second alternative put forward, by NOORDENBOS (1905). He observed in Talpa that the cochlear part of the auditory capsule chondrified together with the canalicular part and separately from the basal plate, with which it became connected by four commissures (1st, basivestibular, in front of the jugular foramen; 2nd, basicochlear, separated from the 1st by the posterior basicochlear fissure; 3rd, medial sphenocochlear, separated from the 2nd by the anterior basicochlear fissure; 4th, lateral sphenocochlear (corresponding to the alicochlear commissure), separated from the 3rd by the carotid foramen). He therefore considered that phylogenetically the mammalian auditory capsule represents a single structure, derived *in toto* from the auditory capsule of Amphibia. This view is supported by de Burlet (1916). Now, the occurrence of a basicochlear fissure, or deep cleft between the cochlear capsule and basal plate, is a very common feature in the mammalian chondrocranium. It is found in :—

Chrysothrix	Henckel (1928*a*).
Mycetes	Henckel (1928*a*).
Hapale	Henckel (1928*a*).
Tarsius	Henckel (1927), Mead (1909).
Tupaia	Henckel (1928*b*).
Talpa	Fischer (1901), Noordenbos (1905), Fawcett (1918*a*).
Miniopterus	Fawcett (1919).
Mus	Shindo (1915).
Lepus	Noordenbos (1905), Voit (1909).
Microtus	Fawcett (1917).
Canis	Olmstead (1911).
Felis	Terry (1917), Fawcett (1918*b*), de Beer.
Mustela	Fawcett (1918*b*), de Beer.
Poikilophoca	Fawcett (1918*b*).
Equus	Arnold (1928), Limberger (1926).
Bos	Decker (1883), Levi (1909).
Sus	Mead (1909), Lebedkin (1918), (arises late).
Phocæna	de Burlet (1913*a*).
Balænoptera	de Burlet (1914*a*).
Megaptera	Honigman (1917).
Globiocephalus	Schreiber (1915).
Lagenorhynchus	de Burlet (1914*b*).
Tatusia	Fawcett (1921).
Bradypus	Weber (1927).
Halicore	Matthes (1921*a*).
Perameles	Cords (1915).
Didelphys	Töplitz (1917) (arises late).

It is obvious from this list that although the basicochlear fissure is not universal in mammals (it is absent in Erinaceus (Fawcett, 1918*a*), as well as in Sorex), its distribution is so wide as to suggest that it is a more or less typical feature of mammalian development.

Before proceeding to evaluate this embryological evidence, and to draw evolutionary conclusions from it, attention may be paid to the morphology of the medial limits of the auditory capsule in the chondrocranium of Sorex. Anteriorly, the alicochlear commissure, as a representative of the trabecula, marks a place which can be regarded as a medial limit to the capsular material. Proceeding straight backwards from this spot, mounting the roof of the cochlear capsule (and paying no attention to the basicochlear sulcus, which marks the position of the basicochlear fissure of other forms), one arrives at the anterior root of the suprafacial commissure. This is a remnant of the original side wall of the skull, and as such, might be taken to mark another medial limit to the capsular material. Still further back, in the same line prolonged, is the apertura medialis of the recessus scalæ tympani. This is a part of the fissura metotica, and consequently there is no doubt that it marks the medial boundary of the auditory capsule.

The result of this inquiry is to show that GAUPP's theory would fit the facts provided that a satisfactory explanation could be found for the basicochlear fissure in those forms which possess it. The presence of the basicochlear fissure might be regarded as a developmental adaptation to a condition which is shared by all the higher mammals, viz., the great increase in the size of the brain, for expansion of the cranial cavity in the hinder region of the skull can only be obtained by pushing out the auditory capsule. Since the ductus cochlearis is an integral part of the membranous labyrinth, it is conceivable that when the latter together with its capsule were displaced to the side, the cartilaginous envelope of the ductus cochlearis accompanied it, and became separated from the rest of the basal plate.

But the basicochlear fissure may, on the other hand, be regarded as a remnant of the original basicapsular fenestra separating the auditory capsule from the basal plate, and it is to be noted that if this is the case, the adaptive significance described above will fit it just as well as if the basicochlear fissure were a new formation. If then GAUPP's theory is rejected and the second alternative is accepted, regarding the envelope of the cochlear capsule as a true part of the auditory capsule, it becomes necessary to explain why: 1st, the trabecula (alicochlear commissure) becomes attached to the auditory capsule; and 2nd, why the suprafacial commissure rests not upon the basal plate but upon the auditory capsule. With regard to the alicochlear commissure and its relations, it may be mentioned that in Talpa, NOORDENBOS (1905) showed that it develops by growing freely backwards, and it is to be supposed that in the primitive state the alicochlear commissure (trabecula) grew back on to the basal plate (parachordal), as in lower vertebrates. Now, it is of the greatest interest to find that this condition, viz., of the alicochlear commissure connecting not with the cochlear part of the auditory capsule but with the basal plate, actually occurs in the Cetacea. In Balænoptera and in Lagenorhynchus it has been shown by DE BURLET (1914*a*, 1914*b*, 1916) that the basal plate broadens out in the anterior region forming a shelf overlying the cochlear capsule on each side. This shelf is the lamina supracochlearis, and it is on to it that the alicochlear commissure is attached. In another whale, Megaptera, HONIGMAN (1917) showed that the lamina supracochlearis arises quite independently of the cochlear capsule and in continuity with the basal plate. In other mammals, the lamina supracochlearis seems to have disappeared, and it is replaced by the cochlear capsule. The alicochlear commissure growing backwards therefore becomes attached to the cochlear part of the auditory capsule. The loss of the lamina supracochlearis in these mammals must be associated with the fact that the cochlear capsules have grown in beneath the lateral edges of the basal plate, and the latter have become superfluous. The attachment of the alicochlear commissure on to the cochlear capsule may therefore be explained as due to the loss of the lamina supracochlearis and its replacement by the cochlear capsule.

Turning now to the relations of the suprafacial commissure, if, as just described, the auditory capsule has grown inwards and substituted itself for the lateral edges of the basal plate, and at the same time the brain-cavity has not decreased (on the contrary, it has certainly increased) it is obvious that the side wall of the skull which is represented by the suprafacial commissure will no longer stand on the lateral edge of the basal plate but on its usurper, the auditory capsule.

That this is the true explanation is rendered very probable by the conditions in Sorex. In the 11 mm. embryo, as already stated, the basicochlear fissure is absent, although its position is marked by the basicochlear sulcus. But in younger embryos, a fissure is plainly visible between the procartilaginous rudiment of the basal plate and the rudiment of the auditory capsule. This can be none other than the basicochlear fissure, corresponding to a basicapsular fenestra. Further, the condensation of tissue which will give rise to the cartilage of the cochlear part of the auditory capsule is perfectly continuous with that surrounding the canalicular part of the capsule. It is therefore to be concluded that NOORDENBOS' theory is correct and GAUPP'S erroneous.

Mention must be made of a curious complication which arises in the case of Didelphys (TÖPLITZ, 1917) and Sus (MEAD, 1909; and LEBEDKIN, 1918), for in the early stages of embryos of these animals there is cartilaginous continuity between the basal plate and the cochlear capsule. Later, however, the basicochlear fissure breaks through, but there appears to be some doubt as to whether this fissure is quite homologous with the basicochlear fissure of other forms (such as the mole, for example).

I. *The Foramen Perilymphaticum and the Fissura Metotica.*

In spite of a certain amount of study, description, and illustration, no easily intelligible account has to my knowledge yet been given of the relations of the fenestra rotunda and the aquæductus cochleæ, nor of the manner in which these openings have been derived by the mammal from the condition in the reptile, in which there is only a single foramen perilymphaticum.

A few words may here properly be said in defence of the terminology adopted in this paper. The term "fenestra cochleæ" seems to be objectionable for two reasons: first, because it has been used on some occasions to mean the reptilian foramen (foramen perilymphaticum), and on other occasions to denote one of the mammalian foramina (fenestra rotunda) which is not the equivalent of the reptilian foramen; and secondly, because "fenestra cochleæ" is too easily mistaken for the aquæductus cochleæ. In order to avoid all possible ambiguity, the term "fenestra cochleæ" has here been discarded altogether.

It is necessary to be clear as to the relations of two apertures, or sets of apertures, in the skull, and to distinguish between them. One of these apertures is the foramen perilymphaticum, and the other is the fissura metotica.

The foramen perilymphaticum is an opening in the hind wall of the cochlear part of the auditory capsule. Its boundaries are the ventral edges of the lateral and medial walls of the auditory capsule, on each side; in front it is bounded by the hind edge of the floor of the cochlear part of the auditory capsule; behind, its boundary is formed by the front edge of the floor of the canalicular part of the auditory capsule. The foramen perilymphaticum is bounded all round by cartilage belonging to the auditory capsule.

The fissura metotica is the elongated space between the lateral edge of the basal plate on the medial side, and the ventral edge of the medial wall of the auditory capsule on the outer side. The boundaries of the fissura metotica are therefore formed by basal cartilage medially and capsular cartilage laterally. In front, the fissura metotica is stopped by the fusion of the auditory capsule with the basal plate; behind, the fissura metotica is enclosed by the occipital arch.

The fissura metotica and the foramen perilymphaticum occur at the same transverse level in the skull, and consequently a transverse section through the skull in this region will pass through both. It is then easy to see that the ventral edge of the medial wall of the auditory capsule forms not only the medial boundary of the foramen perilymphaticum but also the outer or upper boundary of the fissura metotica. The opening of the fissura metotica lies in a more or less vertical plane, while that of the foramen perilymphaticum is more or less horizontal. The result of these relations is that a space, roughly triangular in section, is enclosed between three cartilages, which are: The ventral edge of the lateral wall of the auditory capsule; the ventral edge of the medial wall of the auditory capsule; and the lateral edge of the basal plate. This triangular space is the recessus scalæ tympani.

Between every two of the three cartilaginous boundaries which delimit the recessus scalæ tympani, there is an exit from that recess. Dorsally, the foramen perilymphaticum leads into the auditory capsule; medially, the fissura metotica leads into the cranial cavity; laterally, the apertura lateralis of the recessus scalæ tympani (between the ventral edge of the lateral wall of the auditory capsule, laterally; and the edge of the basal plate, medially) leads to the outside. The apertura lateralis of the recessus scalæ tympani is closed by the secondary tympanic membrane. The description given above is based on the conditions prevailing in the lizard.

The fissura metotica tends to become divided into an anterior and a posterior portion, by an approximation of the lateral edge of the basal plate to the medial wall of the auditory capsule. The anterior part of the fissura metotica so constricted becomes the apertura medialis of the recessus scalæ tympani, while the posterior part becomes the foramen jugulare.

Through the apertura medialis the ductus perilymphaticus enters the cranial cavity, and in some forms the glossopharyngeal nerve emerges. Through the foramen jugulare the vagus, spinal accessory, and in some forms the glossopharyngeal, nerves, and the jugular vein, emerge from the cranial cavity. In Lacerta (GAUPP, 1900) and in the mouse, the fissura metotica remains undivided; in Eumeces (RICE, 1920) and in the shrew, the fissura metotica is subdivided as described above.

The foramen perilymphaticum in reptiles, and in primitive mammals such as Echidna, (GAUPP, 1908) persists as the opening out of the auditory capsule. In other mammals, however, the foramen perilymphaticum becomes superseded by a new opening formed in the following way. A process projects backwards from the hind edge of the floor of the cochlear part of the auditory capsule, in the plane of the apertura lateralis of the recessus scalæ tympani. This process was discovered by FISCHER (1903) in Semnopithecus, and VOIT (1909), who observed it in the rabbit, gave it the unfortunate name of processus intraperilymphaticus. Apart from its clumsiness, this term conveys an erroneous impression of the relations which the process bears to the foramen perilymphaticum. Since this process forms a ventro-lateral wall to the recessus scalæ tympani, it is proposed here to call it simply the processus recessus.

In the cat, TERRY (1917) showed that the processus recessus projects postero-laterally, and ends freely. I am able to confirm these statements from my own model reconstructed from a 32 mm. embryo of the cat. In the mouse the process recessus does not end freely, but fuses with the floor of the canalicular part of the auditory capsule, further back. In this way, a portion of the apertura lateralis of the recessus scalæ tympani becomes delimited and enclosed by cartilage to form the fenestra rotunda. The lateral border of the fenestra rotunda is the ventral edge of the lateral walls of the auditory capsule; its medial border is formed by the processus recessus. Between the processus recessus and the lateral edge of the basal plate there is in the mouse an aperture closed by membrane. Indeed, this membrane, which also extends over the mouth of the fenestra rotunda, is none other than the secondary tympanic membrane of the reptile. The condition in the shrew is carried one stage further than the mouse, for the processus recessus is here not a slender rod as in the mouse but a broad plate, and its medial edge fuses with the lateral edge of the basal plate. In this way the opening between the processus recessus and the basal plate is closed over, and a space, the recessus scalæ tympani, which in the reptilian skull is extracapsular, becomes in the mammal incorporated in the auditory capsule.

The fenestra rotunda is therefore an aperture in the (now cartilaginous) lateral wall of the recessus scalæ tympani. The original foramen perilymphaticum is still there, but it now no longer leads from the auditory capsule to the outside, because the space into which it leads (recessus scalæ tympani) has been incorporated, as described above.

The fissura metotica, or its anterior portion the apertura medialis of the recessus scalæ tympani, persists, and places the recessus scalæ tympani in communication with the cranial cavity. Through this opening the ductus perilymphaticus (which enters the recessus scalæ tympani from the cavum cochleare through the foramen perilymphaticum) passes from the recessus scalæ tympani into the cranial cavity. This passage comes to assume the form of a tunnel in the following manner—the floor of the canalicular portion of the auditory capsule is at a higher level than that of the cochlear portion, and it projects forward like a shelf into the cavity of the latter ; this shelf forms part of the roof of the recessus scalæ tympani, and therefore of the tunnel through which the ductus perilymphaticus passes. The floor of the tunnel is formed by the processus recessus, where its medial edge is fused with the lateral edge of the basal plate. The tunnel may now be known as the aquæductus cochleæ. The aquæductus cochleæ may therefore be considered as the apertura medialis of the recessus scalæ tympani, together with part of the recessus scalæ tympani itself which lies beneath the cartilaginous floor of the canalicular part of the auditory capsule.

The anterior edge of the floor of the canalicular part of the capsule, which has been described above as projecting like a shelf into the cavity of the cochlear part, is a structure of interest. This edge is morphologically the posterior boundary of the original foramen perilymphaticum. The anterior boundary of the foramen perilymphaticum in the reptile is the hind edge of the floor of the cochlear capsule. In the mammal, the position of this hind edge is difficult to find, because the floor of the cochlear capsule has extended backwards to form the processus recessus. Its position may be taken as running along a line in the floor of the cochlear capsule, on a level with the anterior edge of the fenestra rotunda. The lateral boundary of the foramen perilymphaticum coincides with the lateral (or upper) boundary of the fenestra rotunda. The medial boundary of the foramen perilymphaticum runs along a line on the medial wall of the auditory capsule just in front of the aquæductus cochleæ.

It is now possible to consider the relations of the mammalian recessus scalæ tympani and to compare them with those which hold in the lizard. The floor and side wall of the recessus in Sorex are formed by the cartilage of the processus recessus, leaving an aperture, which is the fenestra rotunda, covered by the secondary tympanic membrane. Medially, the recessus communicates with the cranial cavity through the aquæductus cochleæ. Postero-dorsally the recessus is bounded by a cartilaginous roof which is the floor of the canalicular part of the auditory capsule. Posteriorly the recessus comes to an end where the floor (processus recessus) and roof (floor of the canalicular capsule) meet. Antero-dorsally, the floor of the canalicular capsule stops, its edge forming the posterior boundary of the foramen perilymphaticum. In this region, therefore, the recessus is not bounded, but communicates through the foramen perilymphaticum directly with the cavum cochleare.

It may be objected that the space enclosed by the processus recessus in mammals is not the recessus scalæ tympani of the lizard because the glossopharyngeal nerve traverses the recessus in lizards but does not traverse the space in question in mammals. To this two answers may be given. In the first place, since the apertura medialis of the recessus scalæ tympani is a part of the original fissura metotica, there is nothing to prevent the glossopharyngeal nerve slipping back into the jugular foramen, and so avoiding enclosure by the processus recessus. This is what must have happened in the evolution of the mammals. But on the other hand, an enclosure comparable to that which the mammalian glossopharyngeal has avoided, seems to have been effected in the Chelonia. KUNKEL (1912) showed that the glossopharyngeal in Emys traverses the posterior region of the cochlear capsule. RICE (1920) suggested that this intracapsular course would be paralleled in the lizard if the apertura lateralis of the recessus scalæ tympani were to be considered as part of the wall of the auditory capsule (which would be the case if a processus recessus were to develop). That this is the explanation is highly probable, for KUNKEL (1912) himself states that there is a posterior extension of the floor of the cochlear capsule. The objection outlined above may therefore be overruled.

Turning to other mammals, a processus recessus is present in Phocæna and Globiocephalus, according to DE BURLET (1914A) and SCHREIBER (1915). In man, MACKLIN'S (1921) description shows that in addition to a process projecting back from the hind edge of the floor of the cochlear capsule, there is also a process which projects forwards from the floor of the canalicular capsule. These processes may be distinguished as the anterior and posterior processus recessus respectively. In Phocæna, DE BURLET (1913*b*) describes a process, but its relations are not quite clear. The cases of the cat and rabbit have already been mentioned. In Microtus and Miniopterus (FAWCETT, 1917 and 1919) structures corresponding to the processus recessus are present, for the fenestra rotunda is formed.

It seems therefore clear that the chief factor in the superseding of the foramen perilymphaticum by the fenestra rotunda and aquæductus cochleæ in the mammals is the development of the processus recessus (anterior, or posterior, or both together), and the consequent incorporation of the recessus scalæ tympani in the auditory capsule.

It now remains to compare the conclusions here arrived at with those of previous investigators. GAUPP (1900, p. 515) believed that "die bei den Sauriern einheitliche Fenestra cochleæ bei den Säugern in zwei Öffnungen, die eigentliche Fenestra cochleæ und den Aquæductus cochleæ, zerlegt wird." In the present terminology, this means that GAUPP thought that the fenestra rotunda and the aquæductus cochleæ were derived from the foramen perilymphaticum by subdivision. The means of this supposed subdivision was discovered by FISCHER (1903), and named by VOIT (1909, p. 445) the processus intraperilymphaticus. The objection to the latter term will now become clear. The process does not subdivide the foramen perilymphaticum at all, but extends ventral to it and encloses the recessus scalæ tympani, leaving the fenestra rotunda as a gap in the side wall of the latter. Therefore the term processus recessus is preferable. Strangely enough, VOIT himself realised that the processus intraperilymphaticus fused " nicht mit dem eigentlichen Hinterrand der Fenestra cochlearis, sondern mit der weiter unten von der Pars canalicularis . . . vorspringenden freien Kante der Crista parotica " (p. 542). His further description shows that he recognised the relations of the structures and apertures correctly.

With regard to the derivation of the fenestra rotunda and aquæductus cochleæ from the foramen perilymphaticum by subdivision of the latter, in a very rough and general way this may be said to be not totally incorrect, and thus far GAUPP perceived an element of the truth, but it must be realised that neither the fenestra rotunda nor the aquæductus cochleæ is really any part of the foramen perilymphaticum. GAUPP was right just in so far as it may be said that the arched handle of a bucket divides the opening of the mouth of the bucket: the exit is divided, but the two new openings are not part of the old one. When the details are worked out, it becomes clear that GAUPP's view is erroneous.

With regard to the secondary tympanic membrane, GAUPP (1900, p. 514) held that the structures bearing this name in reptiles and in mammals could not be homologous because of the difference in their relations. The reptilian membrane covering the apertura lateralis of the recessus scalæ tympani stretches from capsular cartilage laterally to basal cartilage medially; whereas the mammalian membrane covering the fenestra rotunda stretches from capsular cartilage to capsular cartilage (the processus recessus). This opinion is erroneous, and I agree with RICE (1920, p. 152) in regarding the secondary tympanic membranes of reptiles and mammals as homologous, although in the mammal the membrane is reduced owing to the formation of cartilage (processus recessus) in the remainder of the floor of the recessus scalæ tympani.

GAUPP was therefore wrong both in deriving the fenestra rotunda from the foramen perilymphaticum and in denying the homology of the reptilian with the mammalian secondary tympanic membrane. It is doubtful whether he would have fallen into these associated errors if he had realised that the recessus scalæ tympani, which is extracapsular in reptiles, is intracapsular in mammals. This is all the more remarkable because he definitely referred (1900, p. 514) to the fact that the perilymphatic sac in the mammal is confined to the auditory capsule and cranial cavity, whereas in the reptile the perilymphatic sac emerges from the auditory capsule into the recessus scalæ tympani before communicating with the cranial cavity.

Attention may here be called to what I believe to be a mistake in FISCHER's text-fig. 1 (1903, p. 394). FISCHER describes the processus recessus (not given a special name by him) and states that the fenestra rotunda is covered by a dense membrane. The figure, however, shows a membrane covering not the fenestra rotunda but the original foramen perilymphaticum, the ductus perilymphaticus in the aquæductus cochleæ being thereby excluded from the cavum cochleare.

It may be mentioned that the views developed here with regard to the relation between the reptilian foramen perilymphaticum and the mammalian fenestra rotunda, are in agreement with those put forward by VERSLUYS (1898) regarding the fenestra rotunda of the hen, which according to him has no homologue in the lizard. He says (p. 357) that the fenestra rotunda is "bestimmt nicht das Loch, durch das der Ductus perilymphaticus aus der Labyrinthhöhle in den Recessus tritt." On the same page he maintains that the fenestra rotunda is a part of what he calls the foramen jugulare externum, which corresponds to the apertura lateralis of the recessus scalæ tympani. If this be so, the fenestra rotunda of the hen and of the mammals may be regarded as comparable structures.

J. *The Processus Opercularis.*

The processus opercularis is a remarkable structure, which (so far as I know) has been found only in Talpa and Microtus, besides Sorex. In Talpa, according to FISCHER (1901), NOORDENBOS (1905) and FAWCETT (1918*a*), it has the same relations as in Sorex, *i.e.*, it is a plate of cartilage in the sagittal plane stretching up to the side of the place where the orbitoparietal commissure is attached to the auditory capsule. It is attached by its base to the tegmen tympani and crista parotica, and to the side wall of the auditory capsule, on a level with the tegmen tympani, and behind the latter structure; its anterior and superior edges are free. It is altogether lateral to the true cranial wall, and between it and that wall the lateral jugular vein (or emissarium temporale) passes on its way down from the foramen jugulare spurium (superior occipito-capsular fissure) to the region of the future postglenoid fossa. The only difference is that the processus opercularis in Sorex appears to be a little larger. In Microtus, FAWCETT (1917) has shown that a cartilage which occupies a similar position is derived from the supraoccipital cartilage. Here therefore the "operculum," as he calls it, is attached above and its ventral margin is free, but it has the same relations to the lateral jugular vein.

In discussing the question as to what this cartilage represents, it may be mentioned that VAN BEMMELEN (1901) considered that the canal between the processus opercularis of Talpa and the side wall of the auditory capsule might be equivalent to the temporal canal of the monotremes. This view, however, raises too many difficulties, and the problem would seem to be narrowed down to a consideration of whether the processus opercularis is a local formation, or whether it is really some other element which has been shifted into that position. The former alternative is difficult to uphold, because there is no precedent for any cartilage arising in that position lateral to the real side wall of the skull, which is here as it were duplicated. The latter explanation therefore appears to be the more probable, and I am inclined to regard the condition in Microtus as an indication of what has happened in Talpa and Sorex. In these two genera, the opercular cartilage has no connexion with the supraoccipital cartilage, but the presence in Sorex of a fissure at its base, where it is attached to the side wall of the auditory capsule, suggests that it is not an upgrowth *in situ* but a downgrowth which has become attached to the side wall of the auditory capsule, and which has then lost all connexion with the supraoccipital cartilage.

In Microtus, the opercular process serves as an attachment for certain muscles connected with the pectoral girdle, and the same is true in Sorex. The variation in the degree of fusion of the opercular process itself with the neighbouring cartilaginous structures is therefore probably associated with function.

K. Comparison of the Chondrocrania of Insectivora.

The chondrocrania of a number of Insectivora have now been studied by modern methods, viz., Erinaceus (FAWCETT, 1918*a*), Talpa (FISCHER, 1901, and FAWCETT, 1918*a*), Tupaia (HENCKEL, 1928*b*), and Sorex (present paper). All these show a certain similarity of general form, from which, however, Tupaia departs the most. In all, it is remarkable that the main axis of the skull lies in a line which is almost straight, instead of being more or less acutely bent in the region of the dorsum sellæ (as in Primates for example).

Leaving Tupaia aside, as differing more from the remaining three genera than they differ among themselves, it remains to estimate the relative differences between the latter. It must be admitted that the similarities outweigh the differences, but the following can be made out, and are for convenience established in tabular form.

Structure.	Sorex	Talpa	Erinaceus
hypophysial fenestra	present	absent	present
basicochlear fissure	absent	present	absent
foramen epiphaniale	absent	present	absent
processus opercularis	present	present	absent
ala hypochiasmatica	absent	absent	present
secondary cartilage in mandible	present	present	absent
condition of tectum posterius	specialised	specialised	primitive

On considering this table, it is apparent that Sorex shares characters with Erinaceus that Talpa does not possess, and *vice versa*. It is to be noticed, however, that those characters in which Sorex and Erinaceus agree and differ from Talpa, are such that can easily be explained as quantitative differences of development, perhaps due to a matter of relative age. On the other hand, the characters which Sorex and Talpa have in common and which Erinaceus lacks (such as the processus opercularis, and the absence of an ala hypochiasmatica) are qualitative differences, which may be held to express relationship. These considerations lead to the conclusion already expressed by PARKER (1885, p. 198) that hedgehog, mole, and shrew, "may easily have arisen from one common stock, and the mole comes in as a connecting link between the well-developed hedgehog and the scant and stinted form of the shrew."

Finally, attention may be drawn to a feature which indicates the primitive nature of the chondrocranium of Sorex, viz., the intercommunication of the posterior and lateral semicircular canals by means of a perforation in the septum semicirculare posterius. The perforation is due to the fact that the septum is incomplete, and it is interesting to note that in phylogeny this septum (semicirculare posterius) is the last to be formed. GAUPP (1900, p. 517) draws attention to the fact that this septum is incomplete in Lacerta, in Chelonia and in birds, while in Triton the septum is wholly wanting. As far as I know, Sorex is the only mammal in which this feature has as yet been observed.

V. SUMMARY.

In the chondrocranium and early osteocranium of Sorex, the following points can be made out :—

1. The posterior paraseptal cartilages are still almost independent of the lamina transversalis posterior.

2. A zona annularis is present.

3. The planum antorbitale has been pressed so far back that the roots of the ala orbitalis rest on it and not directly on the central stem.

4. The pterygoid cartilage is in direct cartilaginous continuity with the processus pterygoideus of the ala temporalis.

5. A small "pterygoid" bone is present in addition to the pterygoid cartilage.

6. It is concluded that the pterygoid cartilage is secondary cartilage representing a dermal bone, and from its relations this dermal bone is homologous with the pterygoid of reptiles.

7. It is concluded that the small "pterygoid" bone represents the basitemporal, or detached lateral wing of the parasphenoid.

8. It is concluded that the so-called mammalian pterygoid is a composite structure, and evidence in favour of this view is presented from the work of other investigators.

9. The palatine processes of the premaxilla have relations which are identical with those which are described for the dumb-bell-shaped bone of Ornithorhynchus.

10. It is concluded that the so-called palatine process of the premaxilla of mammals is really a composite structure, of which the posterior portion represents an originally

independent prevomerine ossification. The term prevomerine process is suggested for this portion.

11. Vestiges of the posterior basicranial fenestra are present in young embryos.

12. Anterior clinoid processes are present.

13. The ala temporalis, processus alaris, and central stem are in uninterrupted cartilaginous continuity.

14. The alicochlear commissure is to be regarded as the posterior part of the trabecula.

15. The carotid foramen and the internal carotid artery are to be regarded as homologous with the structures bearing similar names in lower vertebrates.

16. A secondary facial foramen is present.

17. The relations of the cavum epiptericum and cavum supracochleare are defined and discussed.

18. The relations of the auditory capsule to the basal plate are probably to be interpreted in NOORDENBOS' sense, that the cochlear portion is a part of the true auditory capsule which has grown inwards, and is often separated from the basal plate by a basicochlear fissure, and not in GAUPP's sense.

19. There is in Sorex no basicochlear fissure in the chondrocranium, but the fissure is present in the procartilaginous stage.

20. A processus opercularis is present.

21. The original foramen perilymphaticum of the reptile is superseded by the fenestra rotunda and the aquæductus cochleæ, neither of which are to be regarded as subdivisions of the foramen perilymphaticum.

22. The foramen perilymphaticum can still be traced in the mammal, but it no longer opens directly to the outside, but into the recessus scalæ tympani.

23. The recessus scalæ tympani, which is outside the auditory capsule in reptiles, is in mammals incorporated in the capsule by the development of the process recessus, which forms the cartilaginous floor of the recessus scalæ tympani and the medial border of the fenestra rotunda.

24. The aquæductus cochleæ represents the apertura medialis of the recessus scalæ tympani (anterior portion of the fissura metotica) together with a portion of the recessus scalæ tympani.

25. The secondary tympanic membrane of mammals is homologous with that of reptiles, but only its lateral portion persists, covering the fenestra rotunda.

26. A very small vestige of the jugal bone is present, unattached to any other bone.

27. The chondrocranium of Sorex has more points of similarity with that of Talpa than with that of Erinaceus.

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VII.—EXPLANATION OF LETTERING.

(The abbreviations explained here apply to the text-figures as well as to the figures in the Plates.)

a	atlas vertebra.
aai	arteria alveolaris inferior.
ac	aquæductus cochleæ.
aca	accessory cartilage (of nasal capsule).
acc	alicochlear commissure.
acp	anterior clinoid process.
afp	position of anterior border of original foramen perilymphaticum.
aio	arteria infraorbitalis.
alt	ala temporalis.
am	ascending portion of maxillary bone.
ao	ala orbitalis.
ap	ascending process.
apc	anterior paraseptal cartilage.
apl	apertura lateralis of recessus scalæ tympani.
apm	apertura medialis of recessus scalæ tympani.
app	ascending portion of premaxillary bone.
ar	anterior root of 1st ethmoturbinal.
arc	arytenoid cartilage.
asc	anterior semicircular canal.
at	atrioturbinal.
ax	axis vertebra.
b	brain.
bc	bar of cartilage forming anterior boundary of foramen pretransversale.
bcf	basicochlear fissure.
bcs	basicochlear sulcus.
bf	basicranial fenestra.
bh	basihyal.
bo	basioccipital bone.
bp	basal plate.
bs	basisphenoid bone
btp	basitrabecular process.
ca	cupula anterior of nasal capsule.
cac	canalicular part of auditory capsule.
cc	cavum canaliculare of auditory capsule.
cca	cricoid cartilage.
cf	crista falciformis.
cfo	carotid foramen.
cg	crista galli.
cgn	ciliary ganglion.
ch	ceratohyal.
cic	crista intercribrosa.
cJo	cavity in anterior paraseptal cartilage lodging Jacobson's organ.
cnf	condylar foramen.
coc	cochlear part of auditory capsule.

VII.—Explanation of Lettering (continued).

cp	cupula posterior of nasal capsule.
crp	crista parotica.
cs	crista semicircularis.
cse	commissura sphenethmoidalis.
cst	central stem.
ct	chorda tympani.
d	dentary bone.
dc	ductus cochlearis.
de	ductus endolymphaticus.
dm	dura mater.
dp	deep petrosal or internal carotid nerve.
dw	deficiency in wall of auditory capsule.
e	eye.
eam	external auditory meatus.
efc	edge of floor of cavum canaliculare.
ejv	external jugular vein.
eo	exoccipital bone.
Et	Eustachian tube.
et 1	1st ethmoturbinal.
et 2	2nd ethmoturbinal.
et 3	3rd ethmoturbinal.
f	frontal bone.
fai	foramen acusticum inferius.
fas	foramen acusticum superius.
fb	fenestra basalis of nasal capsule.
fbp	foramen in basal plate.
fcc	floor of cochlear capsule.
fd	fenestra dorsalis of nasal capsule.
fe	foramen endolymphaticum.
ffp	primary facial foramen.
ffs	secondary facial foramen.
fg	facial ganglion.
fh	fenestra hypophyseos.
fj	foramen jugulare.
fjs	foramen jugulare spurium.
fm	foramen magnum.
fn	fenestra narina.
fo	fenestra ovalis.
foc	fissura occipito-capsularis superior.
fp	false palate
fpr	foramen perilymphaticum
fpt	foramen pretransversale.
fr	fenestra rotunda and secondary tympanic membrane.
fs	fossa subarcuata.
ft	frontoturbinal.

VII.—EXPLANATION OF LETTERING (continued).

gg	glossopharyngeal ganglion.
gl	glottis.
gsp	greater superficial petrosal (or palatine) nerve.
hf	hypoglossal foramina.
hh	hypohyal.
i	incus.
ica	internal carotid artery.
id	incipient division of foramen acusticum inferius.
ijv	internal jugular vein.
iof	infraorbital foramen.
ip	interparietal bone.
ir	inferior root of 1st ethmoturbinal.
ive	inturned ventral edge of paries nasi.
j	jugal bone.
Jo	Jacobson's organ.
Jod	duct of Jacobson's organ.
l	lachrymal bone.
ljv	lateral jugular vein.
lm	lateral portion of maxillary bone.
lsc	lateral semicircular canal.
lsp	lesser superficial petrosal nerve.
lta	lamina transversalis anterior.
ltp	lamina transversalis posterior.
m	maxillary bone.
ma	malleus.
man	massa angularis.
Mc	Meckel's cartilage.
mm	arteria meningea media.
mma	manubrium of malleus.
mt	maxilloturbinal.
n	nasal bone.
nld	nasolachrymal duct.
npp	nasopharyngeal passage.
ns	nasal septum.
nt	nasoturbinal.
nV3	notch in ala temporalis for mandibular branch of trigeminal nerve.
oa	occipital arch.
ocp	openings through cribriform plate.
of	optic foramen.
og	otic ganglion.
onf	orbitonasal fissure.
op	opercular process.
opc	orbitoparietal commissure.
p	premaxillary bone.
pa	planum antorbitale

VII.—EXPLANATION OF LETTERING (continued).

pac	palatine cartilage.
pal	processus alaris.
par	parietal bone.
pas	processus alaris superior.
pb	pterygoid bone.
pc	pterygoid cartilage.
pF	processus Folii.
phc	pharyngeal cavity.
pia	pila antotica.
pit	pituitary body.
pl	palatine bone.
pla	processus lateralis anterior.
plv	processus lateralis ventralis.
pma	processus maxillaris anterior.
pn	paries nasi.
pop	postpalatine commissure.
pp	parietal plate.
ppa	pterygoid process of ala temporalis.
ppc	posterior paraseptal cartilage.
ppm	palatine process of maxillary bone.
ppp	palatine process of premaxillary bone.
ppr	processus paracondyloideus.
pr	posterior root of 1st ethmoturbinal.
prc	processus recessus (processus intraperilymphaticus).
prm	promontorium of cochlear capsule.
pro	preoptic root of ala orbitalis.
psc	posterior semicircular canal.
psh	parasphenoid bone.
pso	postoptic root of ala orbitalis.
ptr	processus transversalis.
pua	prominentia utriculo-ampullaris inferior.
pv	prevomer bone.
pvp	prevomerine process of premaxillary bone.
ra	recessus anterior of nasal capsule.
rcdnp	rudiment of cartilago ductus naso-palatini.
rf	recessus frontalis of nasal capsule.
rg	recessus glandularis of nasal capsule.
rm	recessus maxillaris of nasal capsule.
rsa	recessus supra-alaris.
rsc	recessus supraconchalis of nasal capsule.
rst	recessus scalæ tympani.
s	squamosal bone.
sa	stapedial artery.
sac	saccule.
sc	secondary cartilage of dentary.

VII.—EXPLANATION OF LETTERING (continued).

scc	septum of cochlear capsule.
sfc	suprafacial commissure.
sl	sinus lateralis.
sm	septomaxillary bone.
smf	stylomastoid foramen.
smg	submaxillary ganglion.
snl	sulcus for nasolachrymal duct.
so	supraoccipital bone.
soc	supraoccipital cartilage.
spf	septoparaseptal fissure.
spg	sphenopalatine ganglion.
ssm	sulcus for stapedial muscle.
st	stapes.
stm	stapedial muscle.
stp	styloid process.
sv	sulcus ventralis.
t	tympanic bone.
tc	tympanic cavity.
tg	trigeminal ganglion.
tgt	tegmen tympani.
thc	thyroid cartilage.
thl	thyrohyal cartilage.
tn	tectum nasi.
tnp	tectum nasi posterius.
tp	tectum posterius.
trc	trabecula cranii.
ts	tooth-socket.
tt	tensor tympani muscle.
u	utricle.
v	vomer bone.
vc	Vidian canal.
ve	ventral edge of median wall of auditory capsule.
vel	ventral edge of lateral wall of auditory capsule.
vg	vagus ganglion.
vn	Vidian nerve.
II	optic nerve.
III	oculomotor nerve.
IV	trochlear nerve.
V 1	profundus (or ethmoid) branch of trigeminal nerve.
V 2	maxillary branch of trigeminal nerve.
V 3	mandibular branch of trigeminal nerve.
VI	abducens nerve.
VII	facial nerve.
VIII	auditory nerve.
XII	hypoglossal nerve.

VIII.—EXPLANATION OF PLATES.

Cartilage is stippled; dermal bone is shaded with lines; cartilage-bone is shaded with dots.

PLATE 94.

FIG. 1.—Dorsal view of the model reconstructed from an 11-mm. embryo of Sorex. The bones are shown on the right side only.

FIG. 2.—Ventral view of the model.

PLATE 95.

FIG. 3.—Lateral view of the model showing the cartilage without the bones.

FIG. 4.—Lateral view of the model showing the cartilage with the bones attached.

PLATE 96.

FIG. 5.—Lateral view of the nasal capsule.

FIG. 6.—Internal view of the nasal capsule. The capsule has been cut transversely and the observer is looking forwards at the posterior face of the anterior portion of the capsule.

FIG. 7.—Internal view of the nasal capsule. The observer is looking backwards at the anterior face of the posterior portion of the capsule.

PLATE 97.

FIG. 8.—Lateral view of the orbitotemporal region of the model.

FIG. 9.—Median view of the auditory capsule.

PLATE 98.

FIG. 10.—Internal view of the auditory capsule. The capsule has been cut transversely, and the observer is looking backwards at the anterior face of the posterior portion of the capsule. The outline of the original foramen perilymphaticum is indicated by a broken line.

FIG. 11.—Ventral view of the auditory capsule of the skull of Lacerta (from GAUPP's model reconstructed by ZIEGLER) showing the relations of the foramen perilymphaticum and the fissura metotica.

FIG. 12.—Ventral view of the auditory capsule of a model reconstruction of the skull of an embryo cat (32 mm. long), showing the relations of the processus recessus.

FIG. 13.—Ventral view of the auditory capsule of the model of Sorex, showing the formation of the fenestra rotunda by the fusion of the processus recessus with the canalicular capsule.

Text-figures 1 to 37 represent a series of transverse sections through an embryo of Sorex araneus, of 11 mm. crown-rump length. The numbers beneath the figures refer to the number of the sections in the author's collection.

Fig. 2.

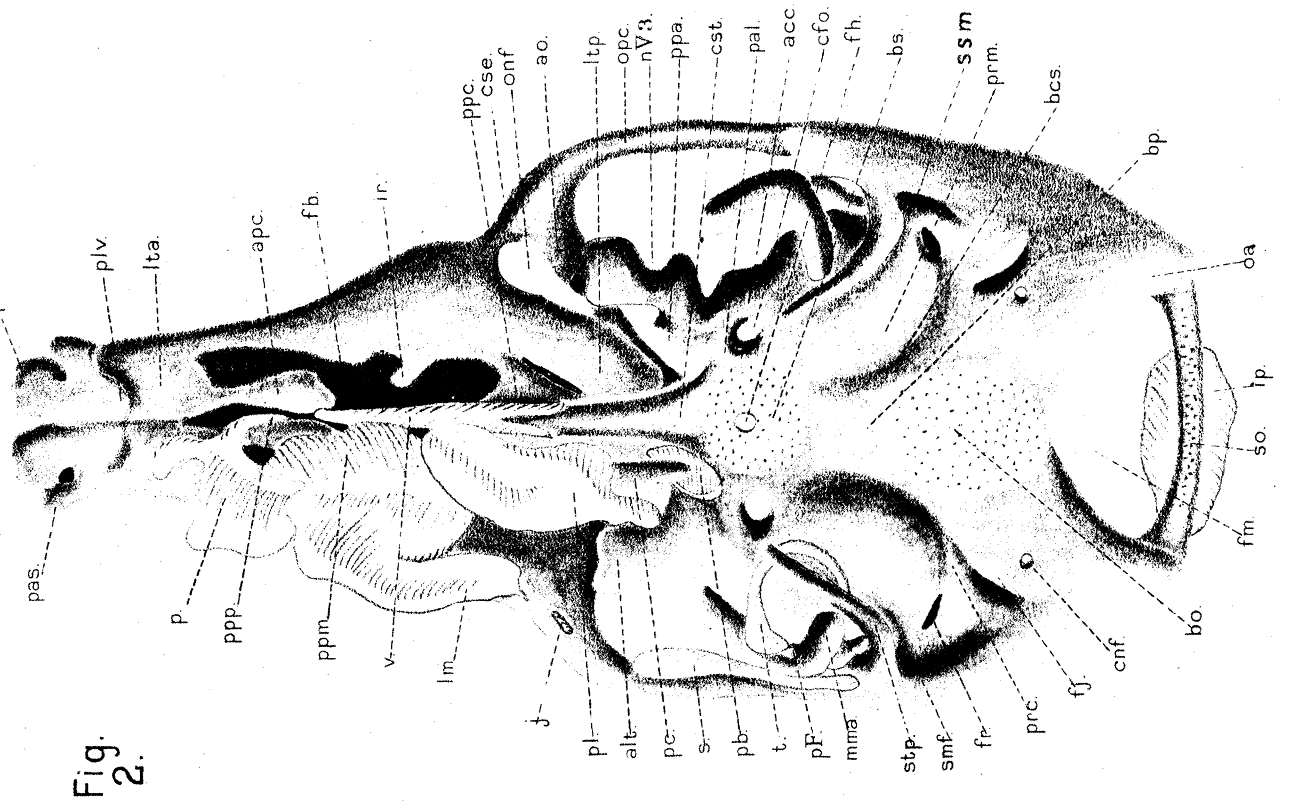
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Fig. 1.

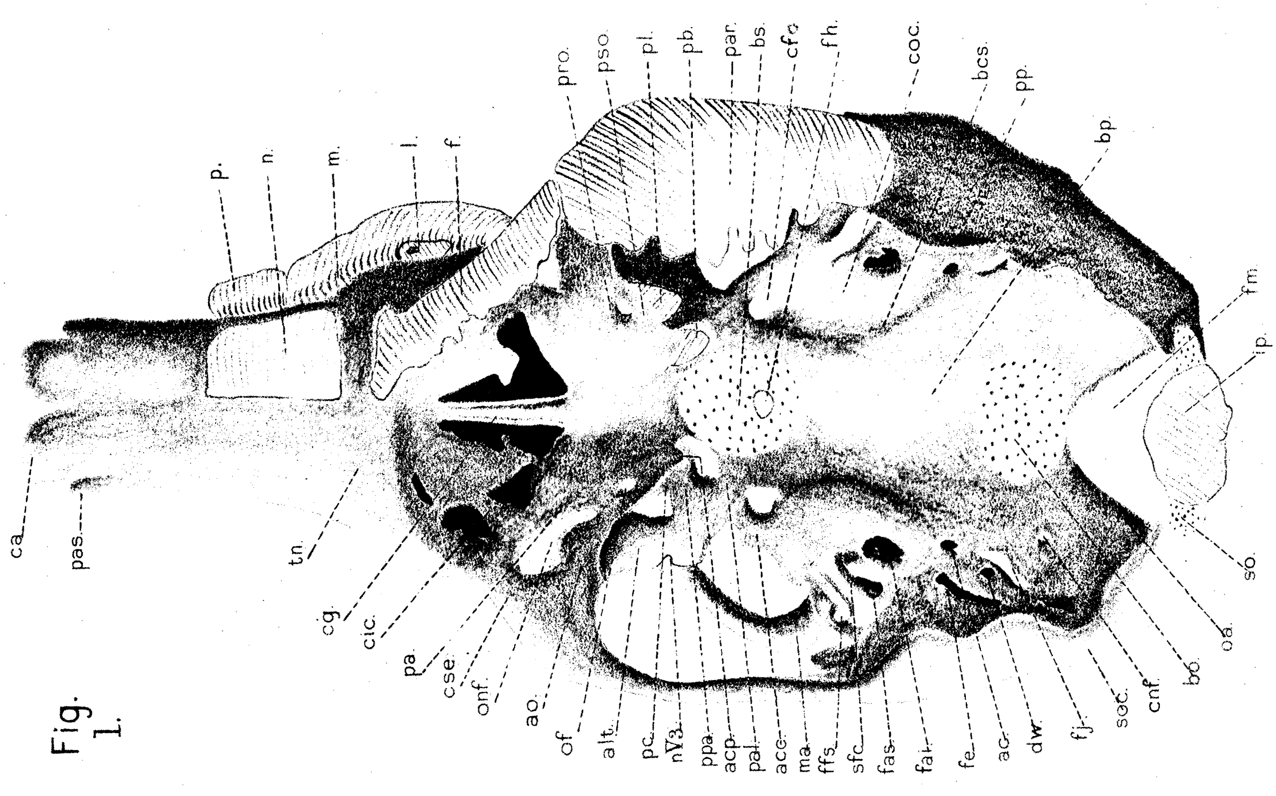
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Fig. 3.

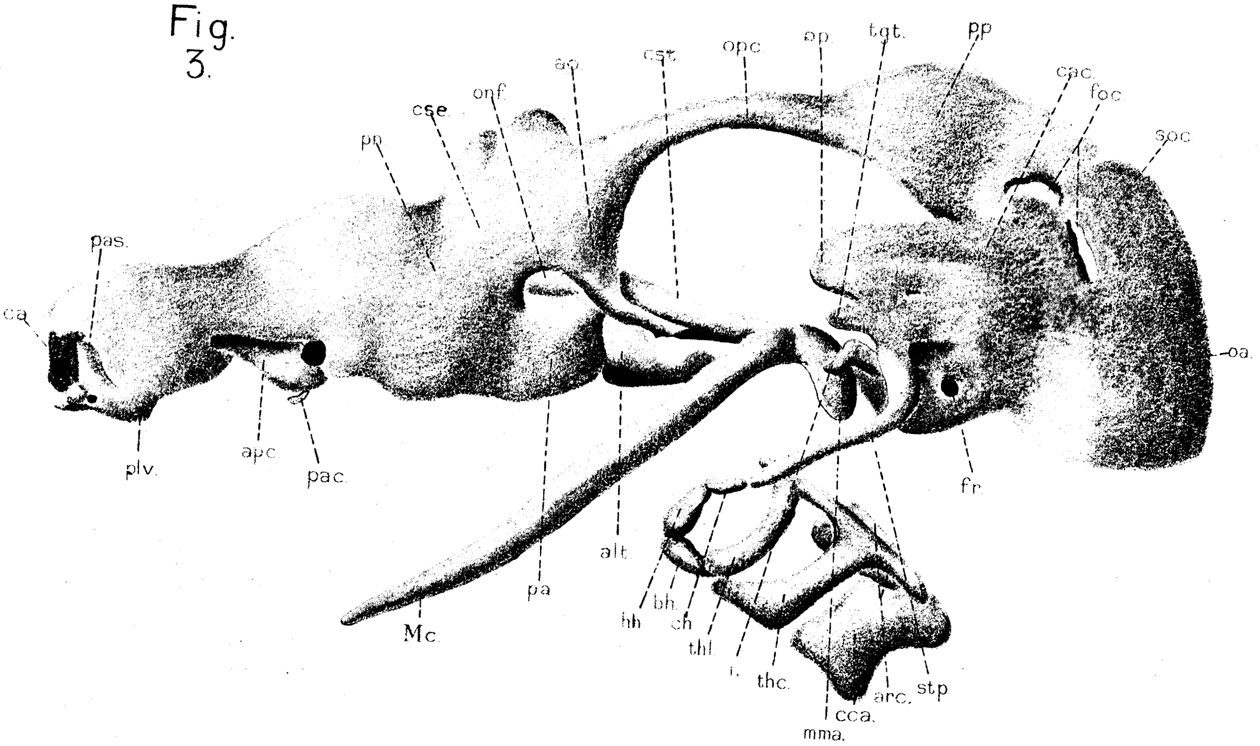
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Fig. 4

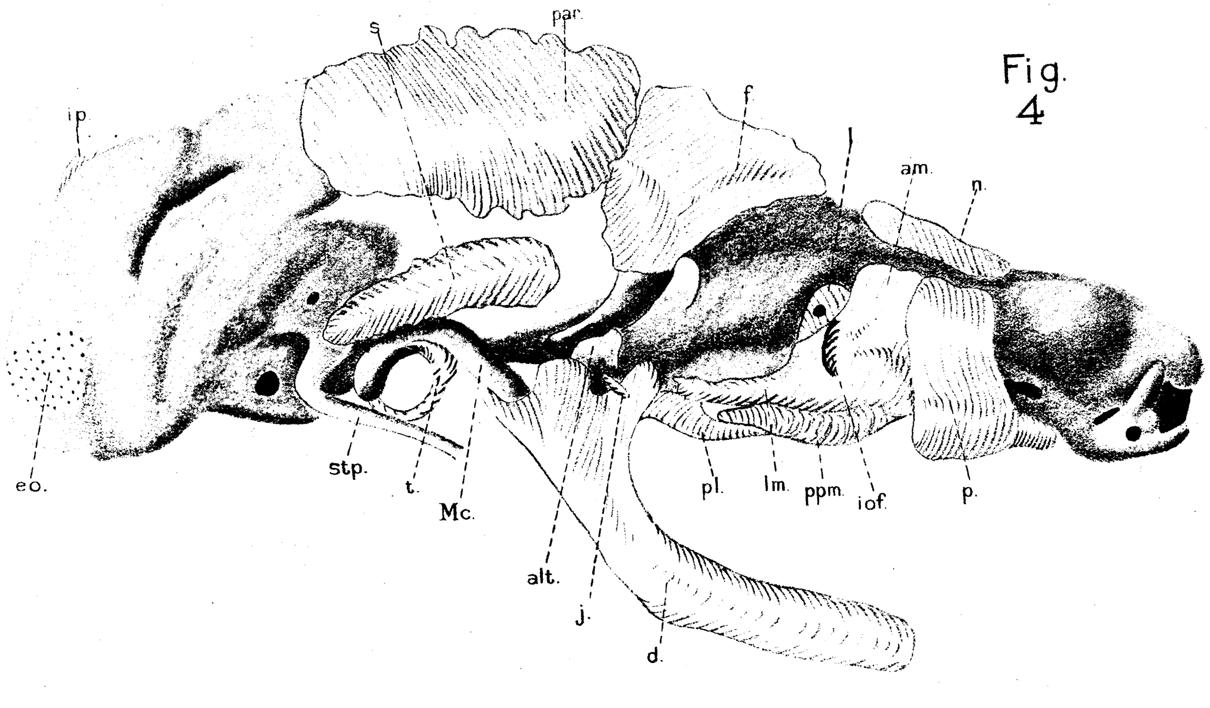
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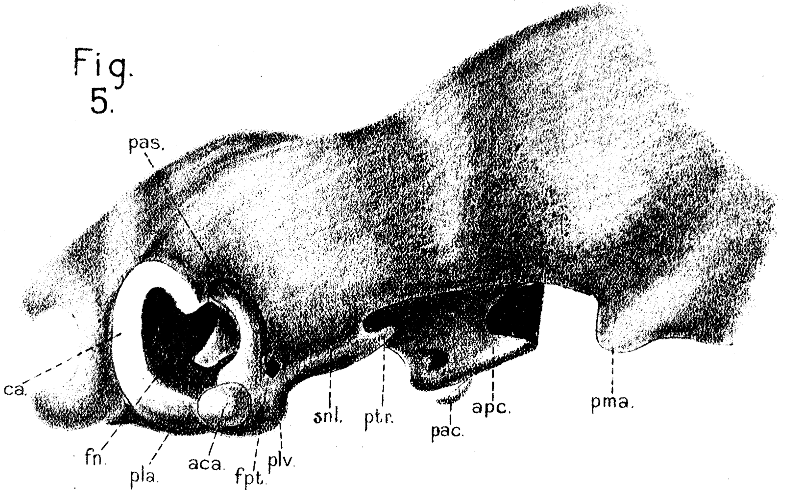
Fig. 5.



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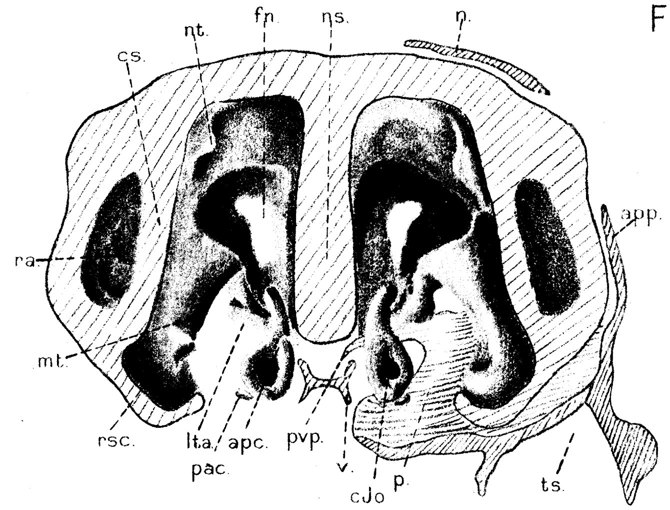

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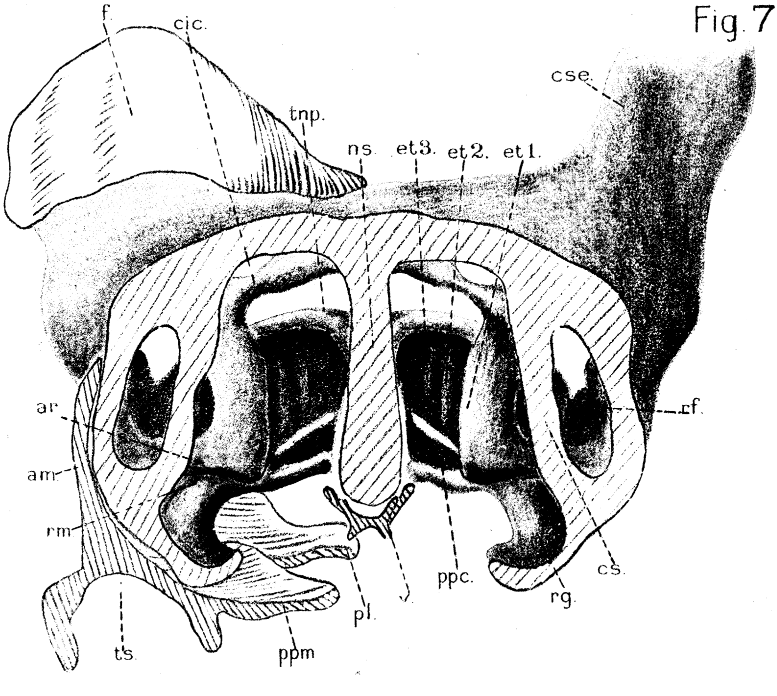

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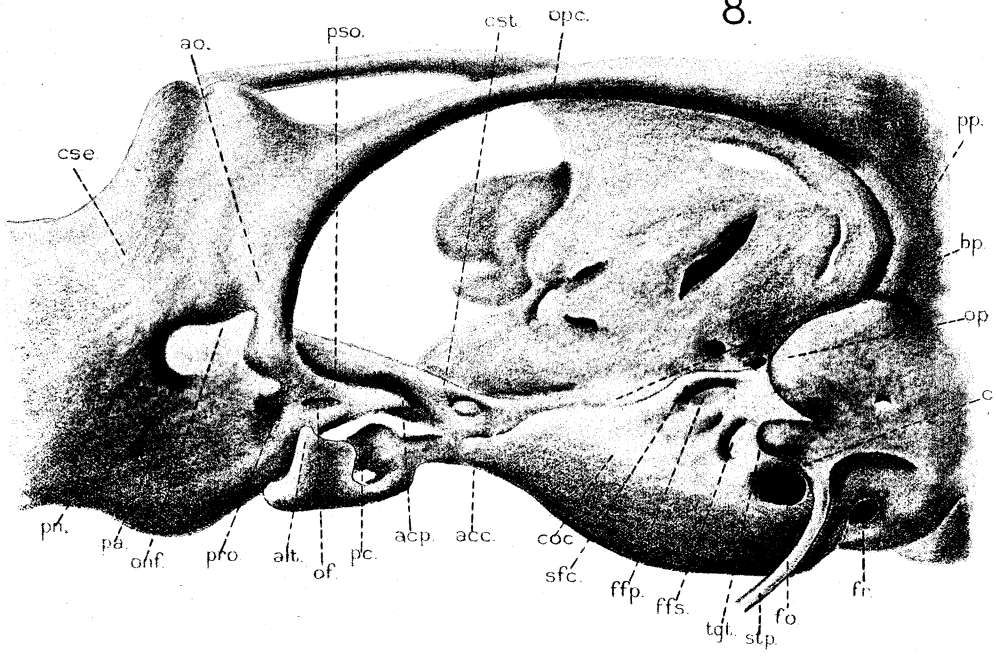
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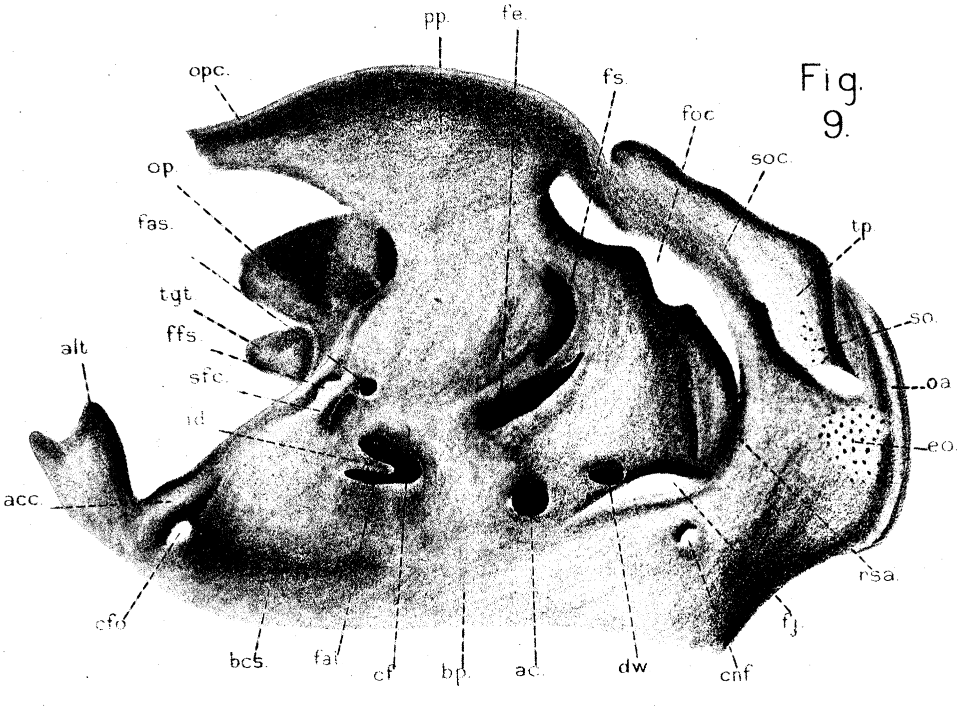
Fig. 9.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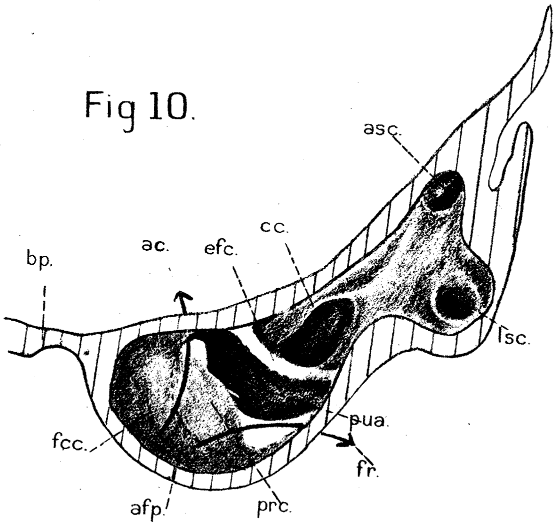
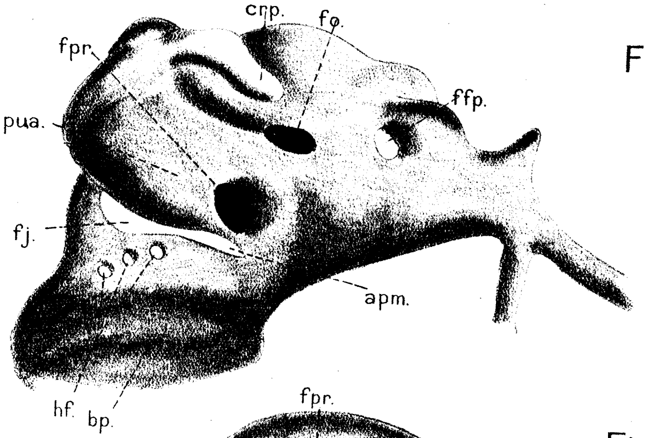


Fig 10.

Fig. 11.



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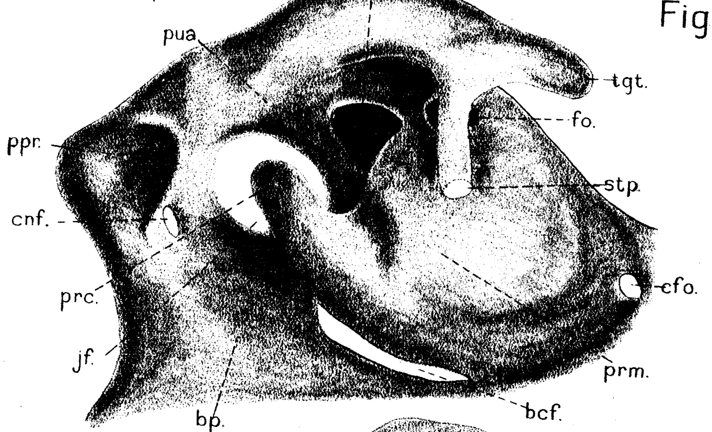

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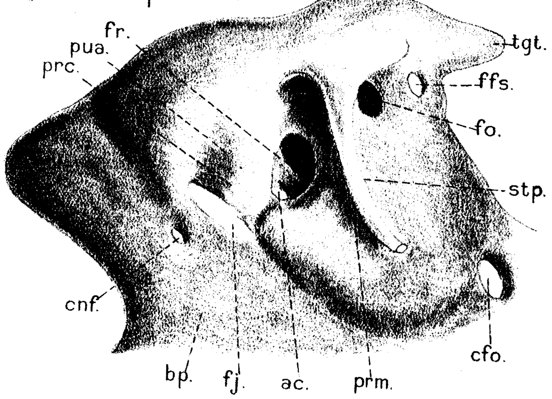


Fig. 1.

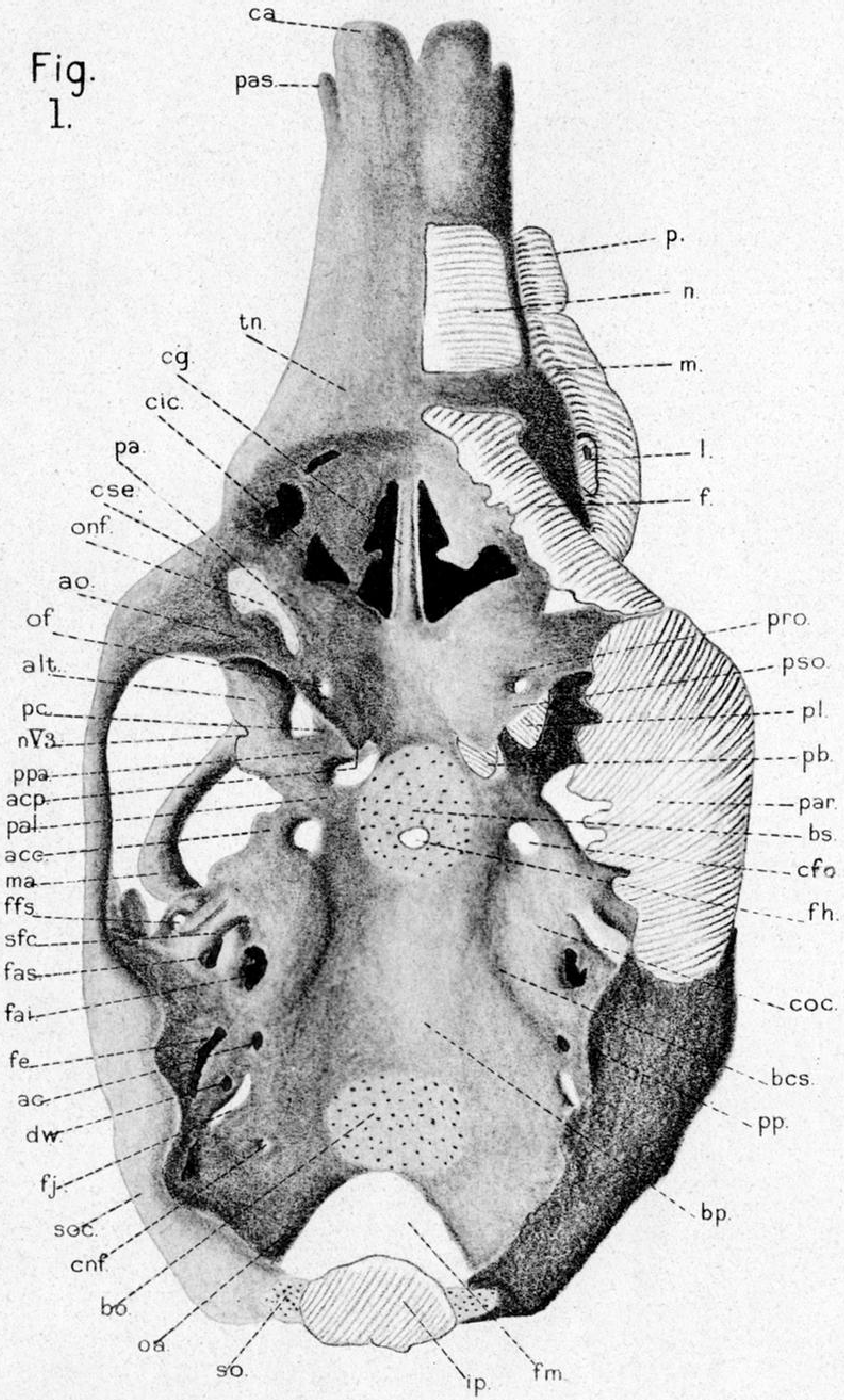


Fig. 2.

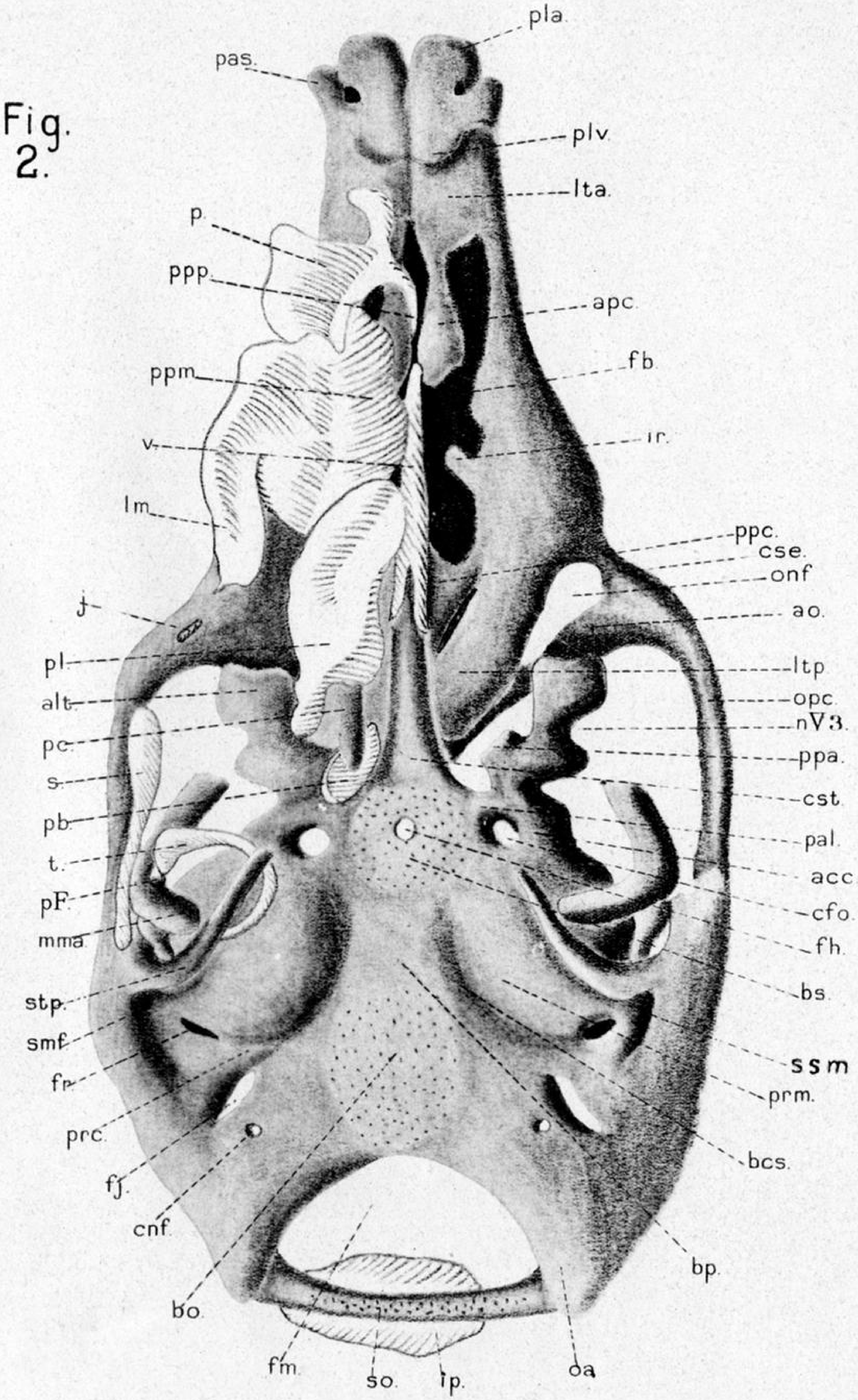


Plate 94.

Fig. 1.—Dorsal view of the model reconstructed from an 11-mm. embryo of Sorex. The bones are shown on the right side only.

Fig. 2.—Ventral view of the model.

Fig. 3.

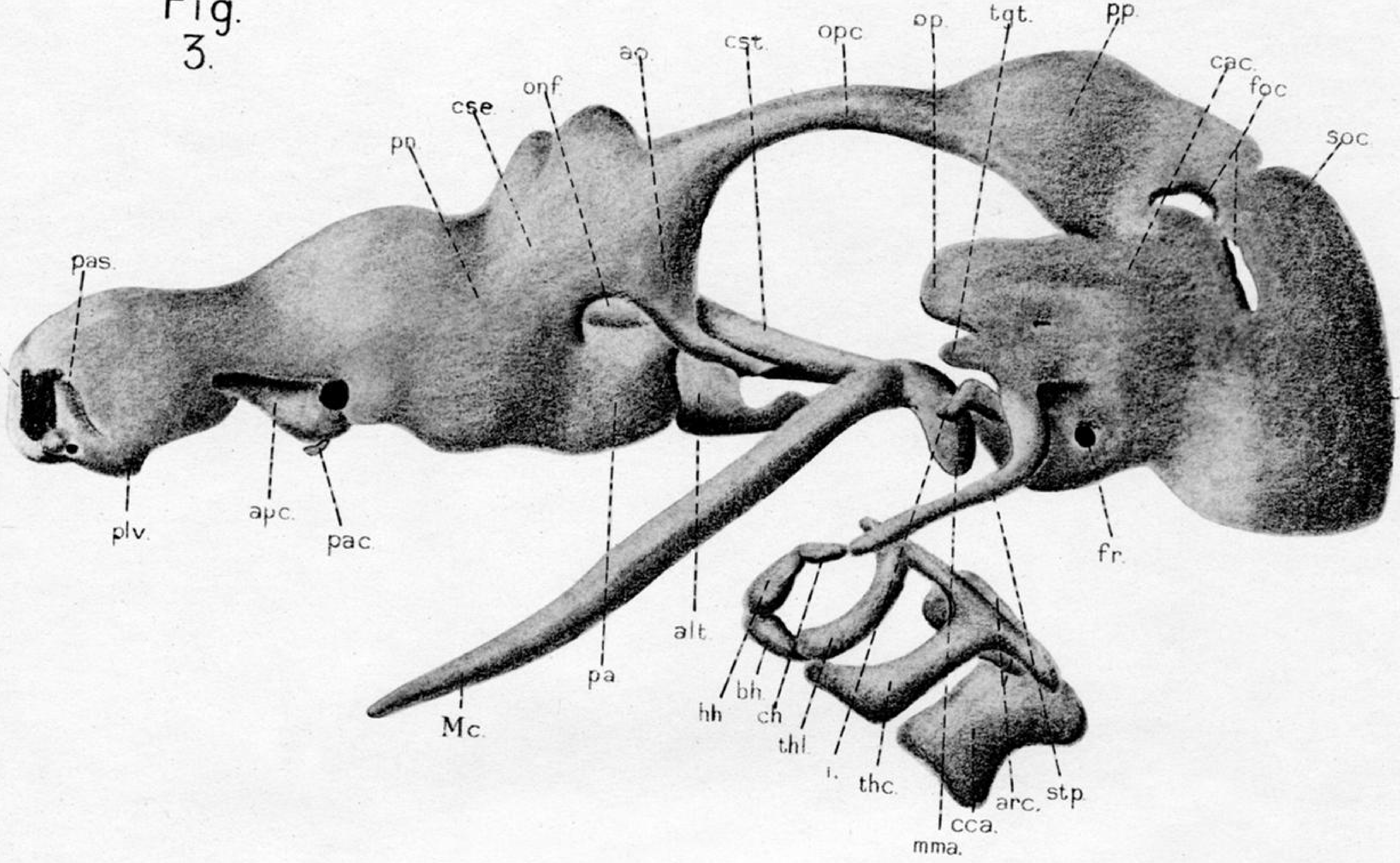


Fig. 4

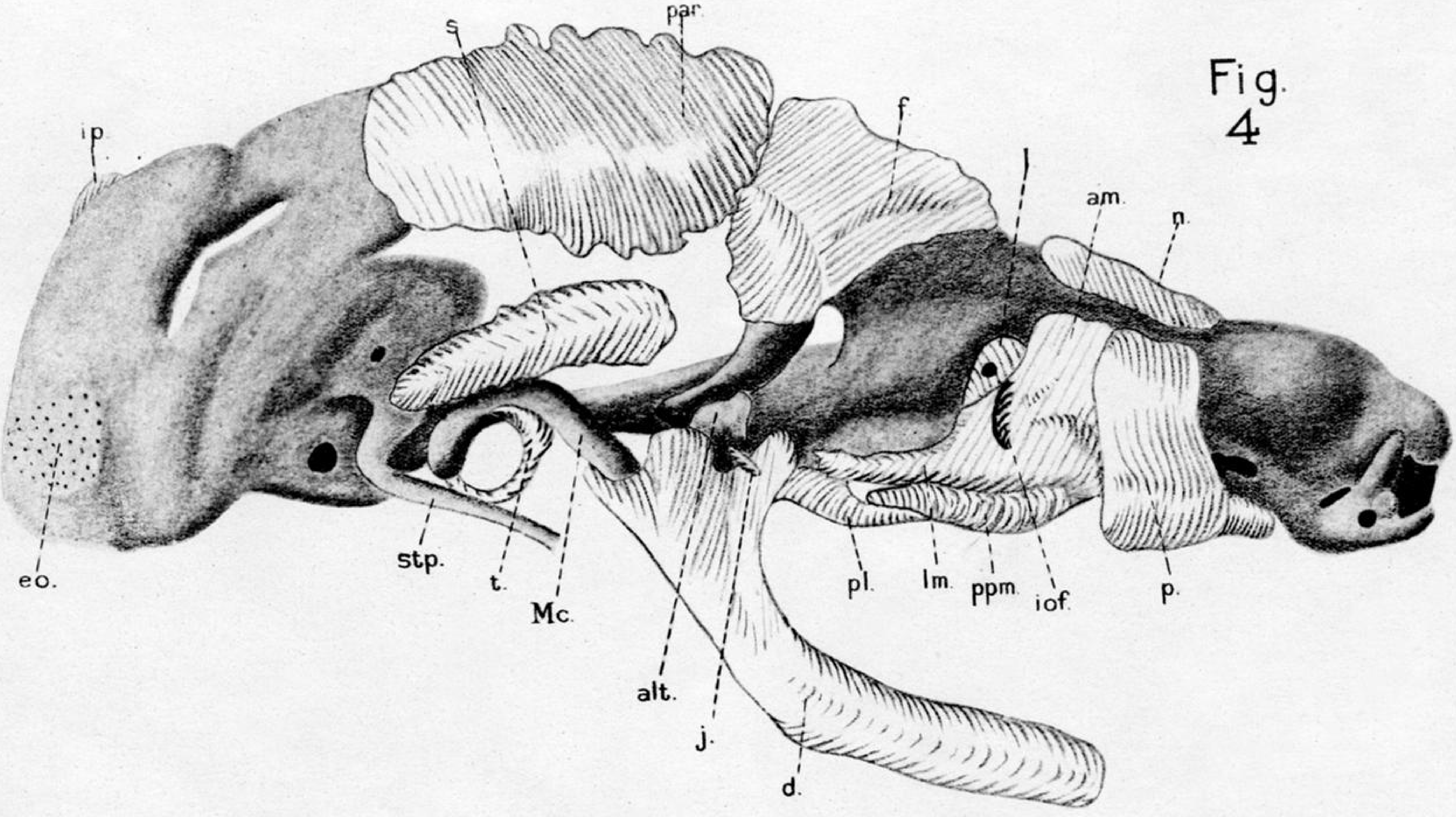
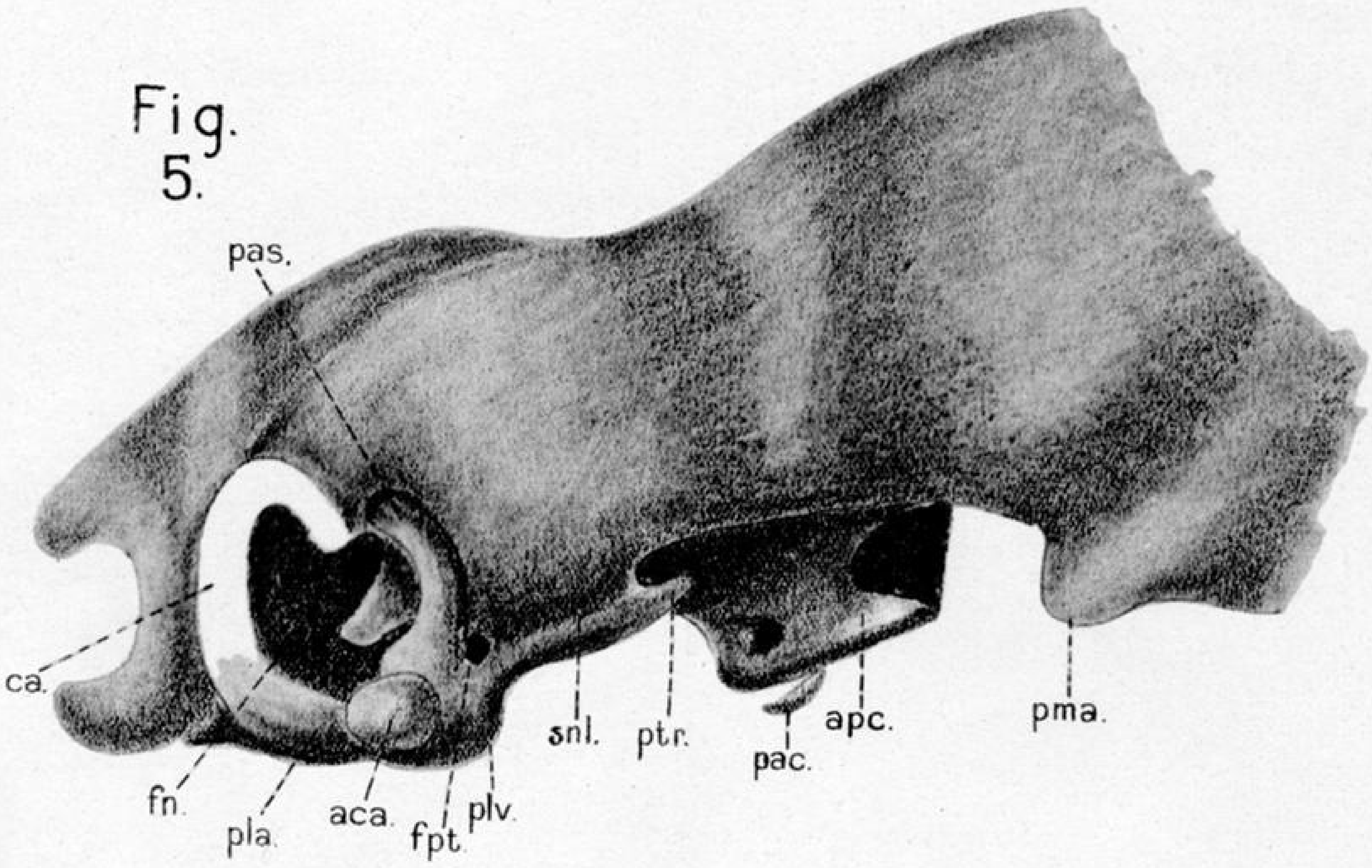


Plate 95.

Fig. 3.—Lateral view of the model showing the cartilage without the bones.

Fig. 4.—Lateral view of the model showing the cartilage with the bones attached.

Fig. 5.



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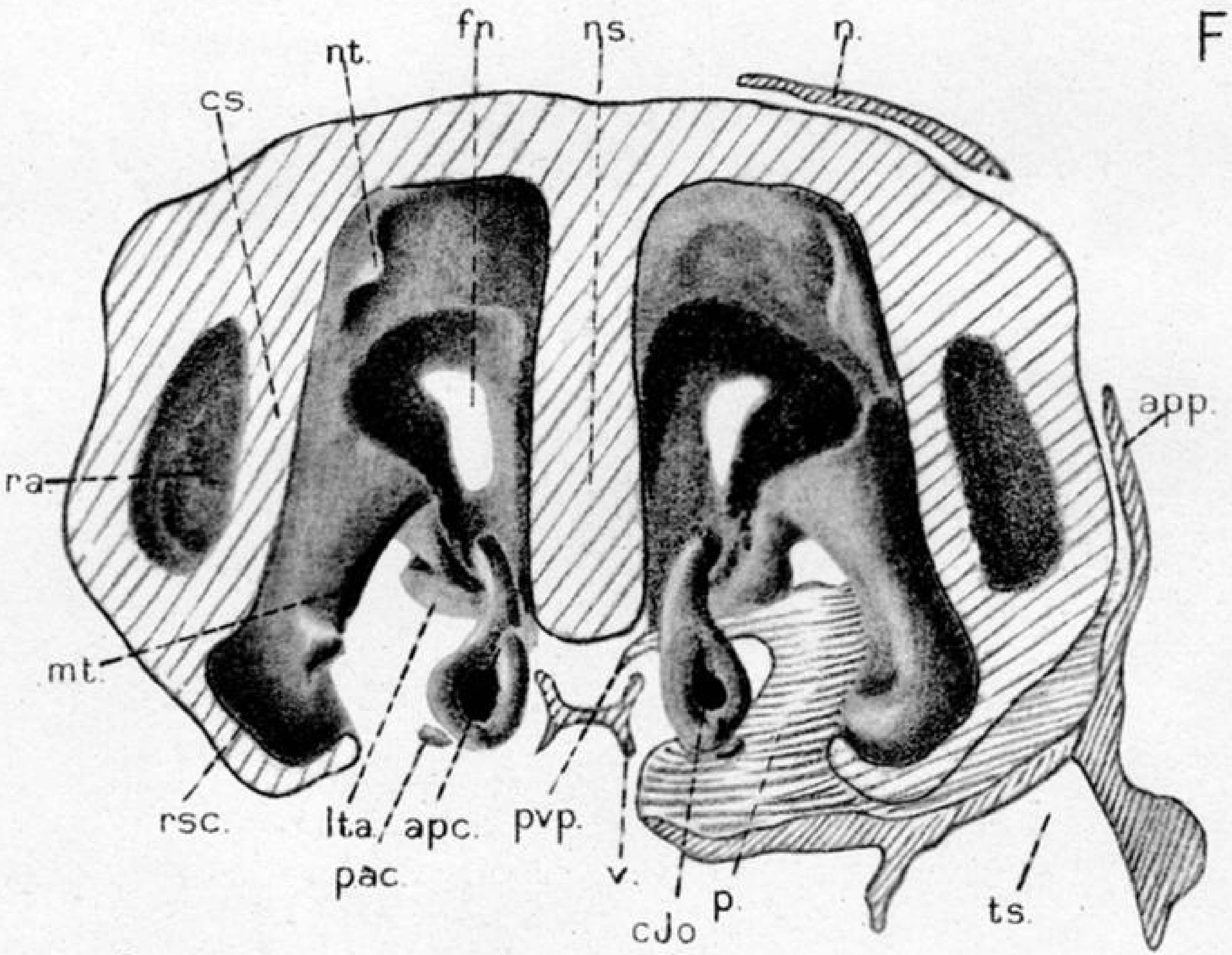


Fig. 7.

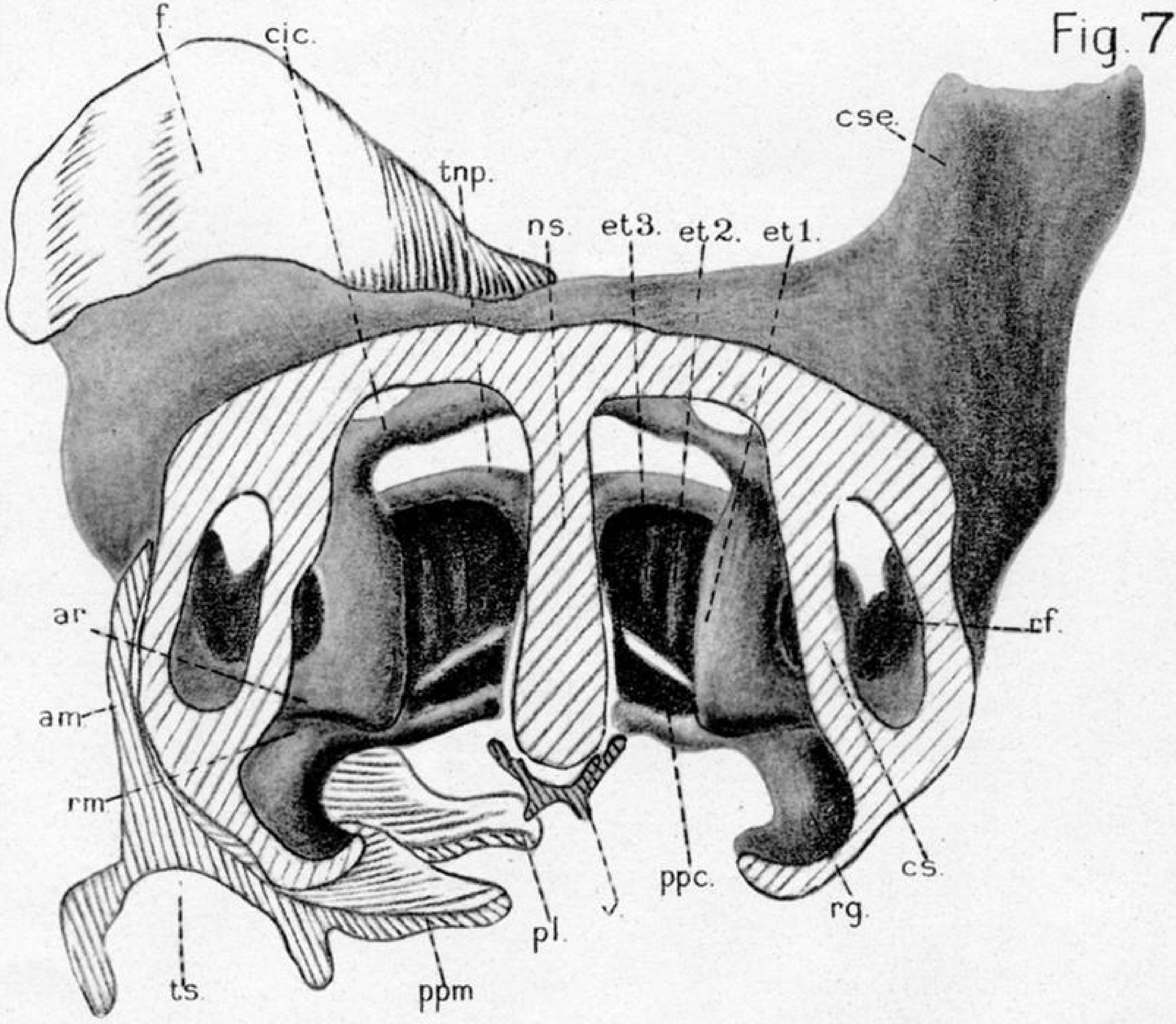


PLATE 96.

FIG. 5.—Lateral view of the nasal capsule.

FIG. 6.—Internal view of the nasal capsule. The capsule has been cut transversely and the observer is looking forwards at the posterior face of the anterior portion of the capsule.

FIG. 7.—Internal view of the nasal capsule. The observer is looking backwards at the anterior face of the posterior portion of the capsule.

Fig. 8.

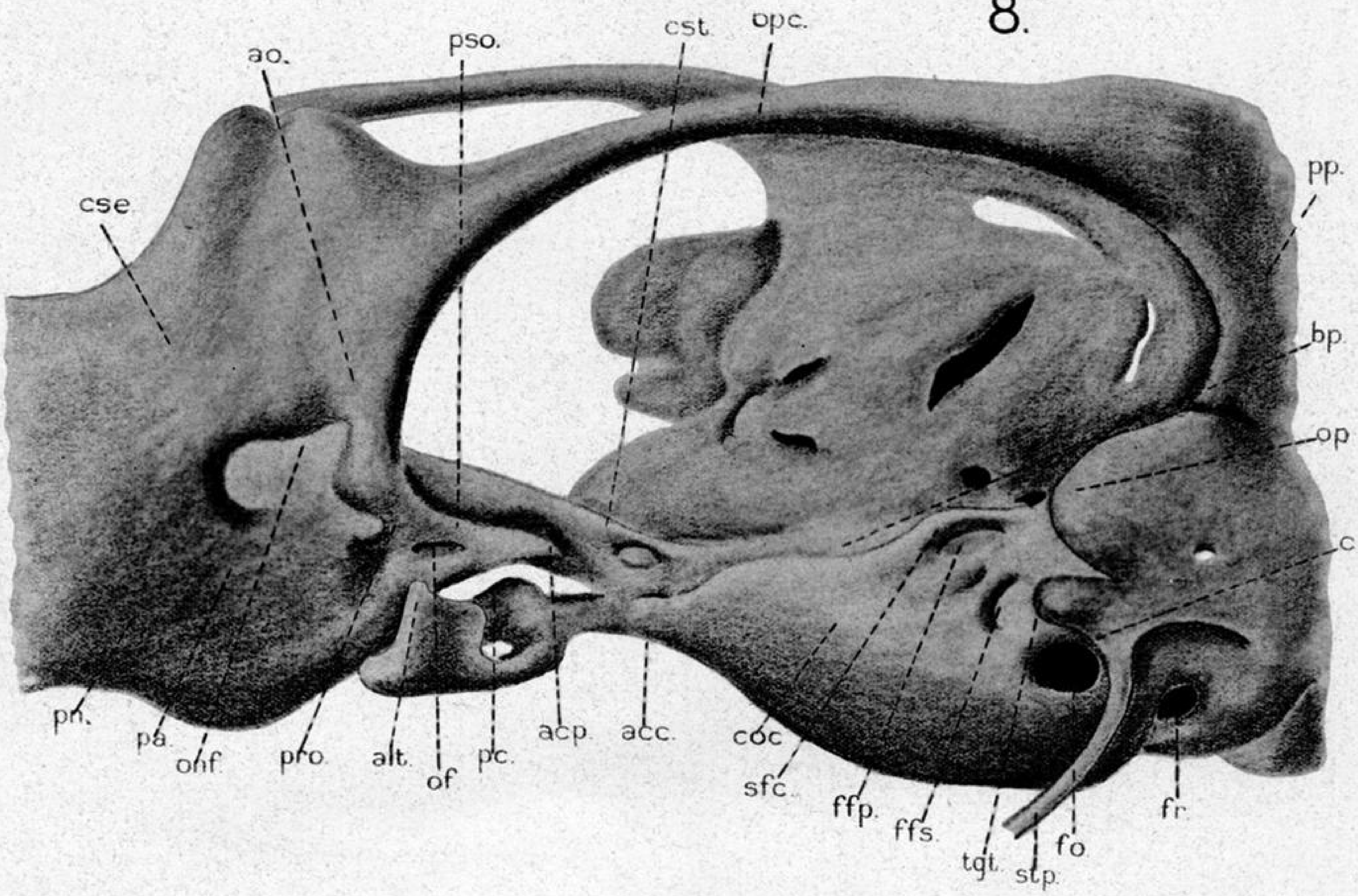


Fig. 9.

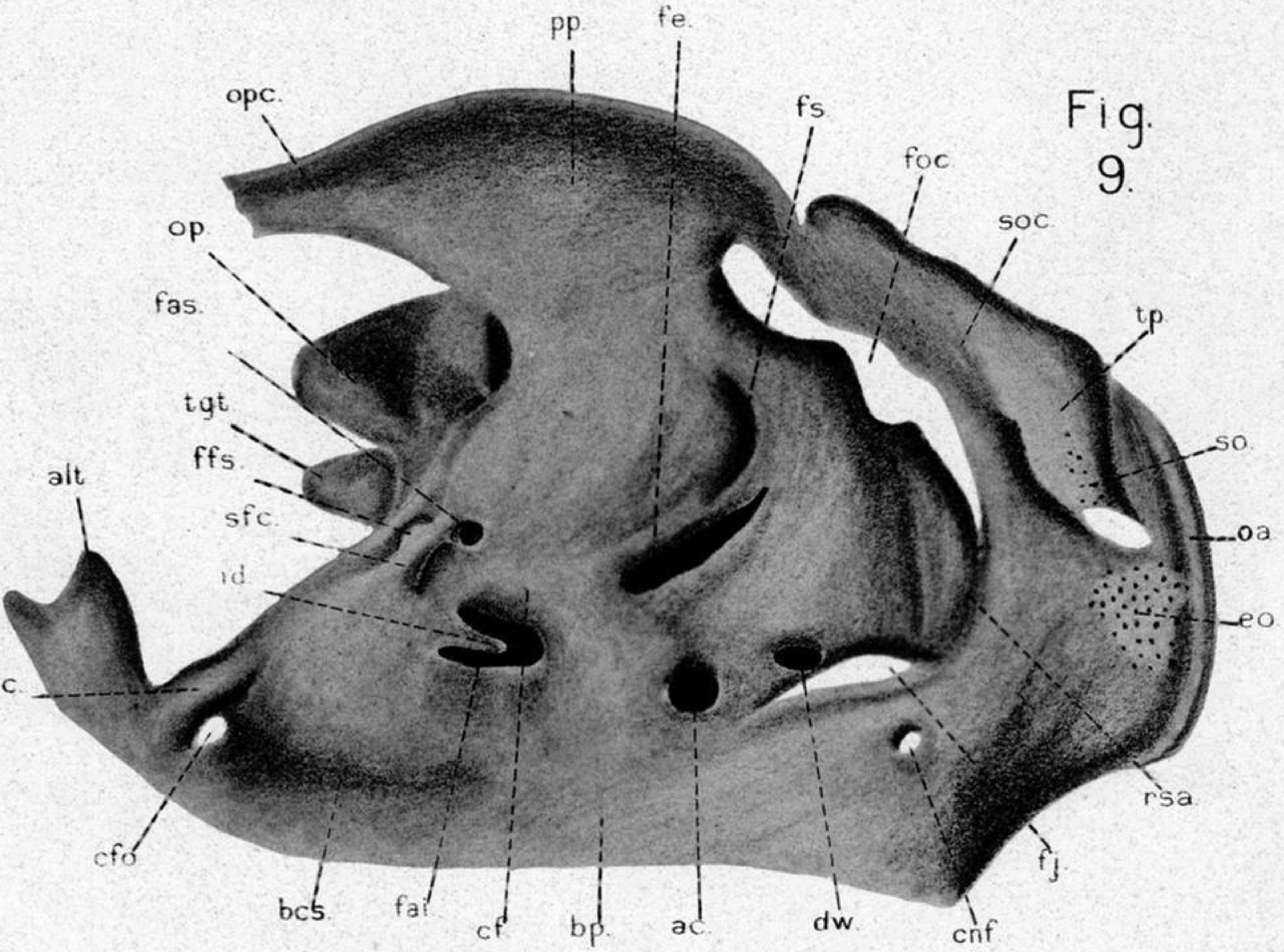
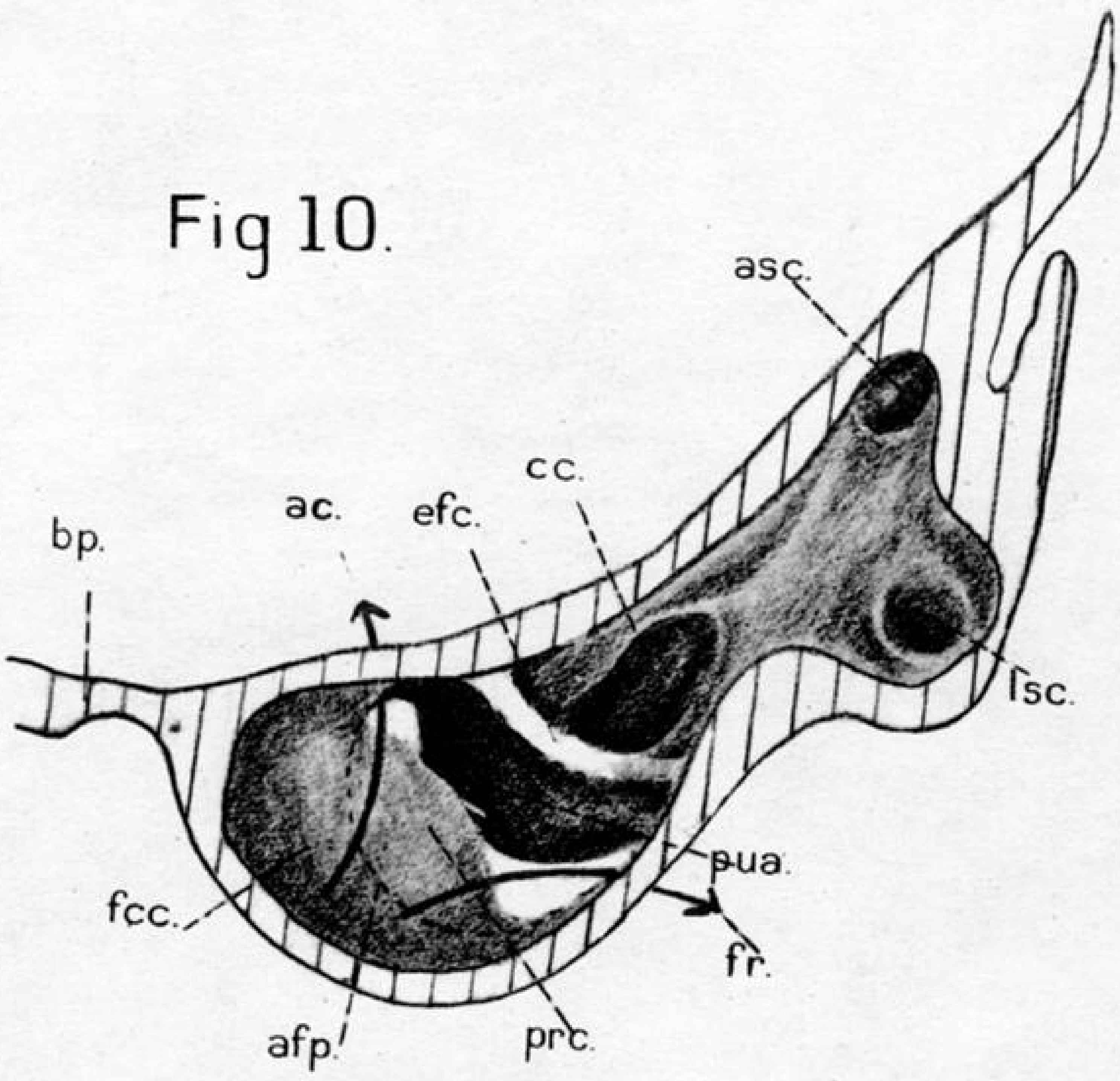


Plate 97.

Fig. 8.—Lateral view of the orbitotemporal region of the model.

Fig. 9.—Median view of the auditory capsule.

Fig 10.



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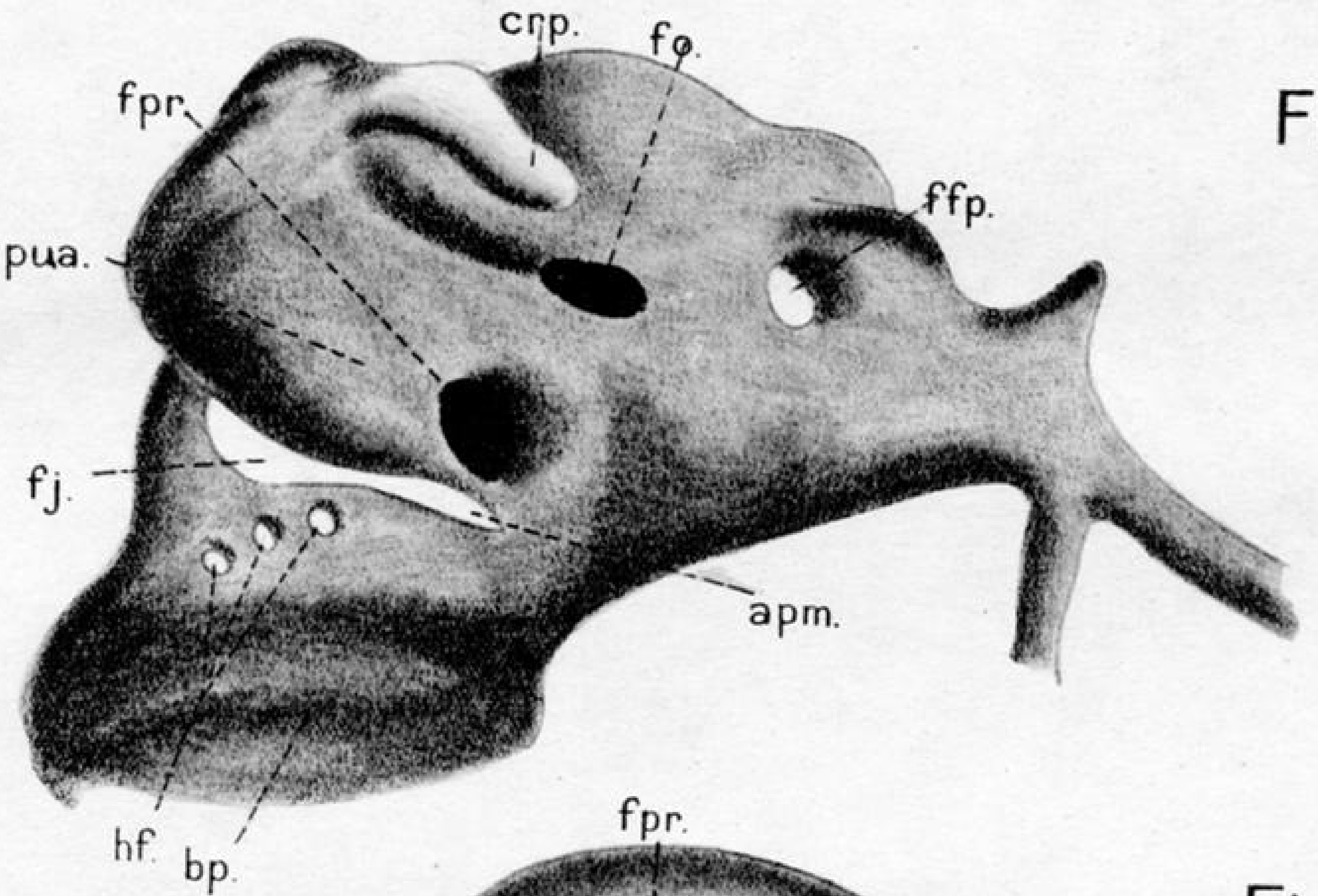

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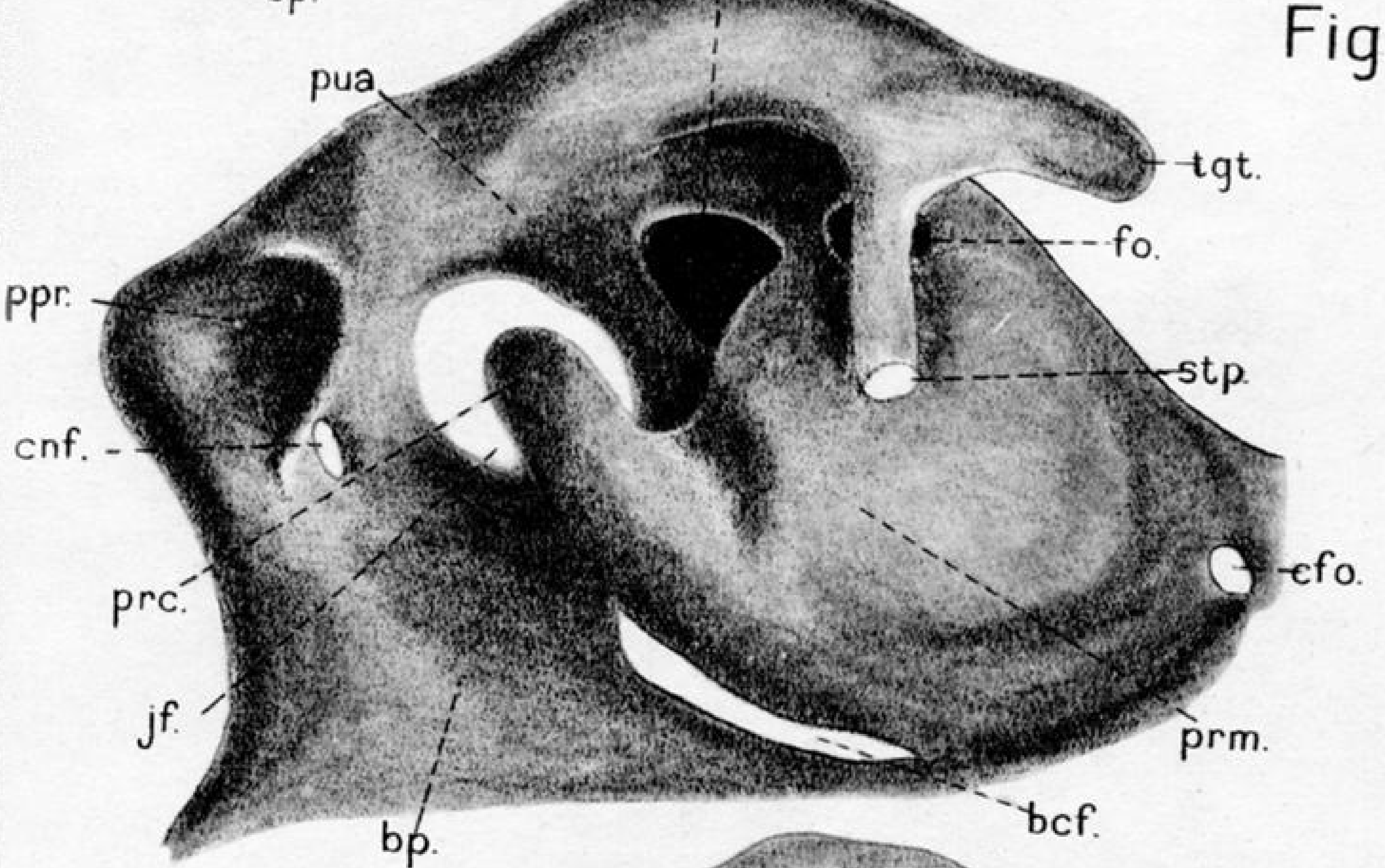

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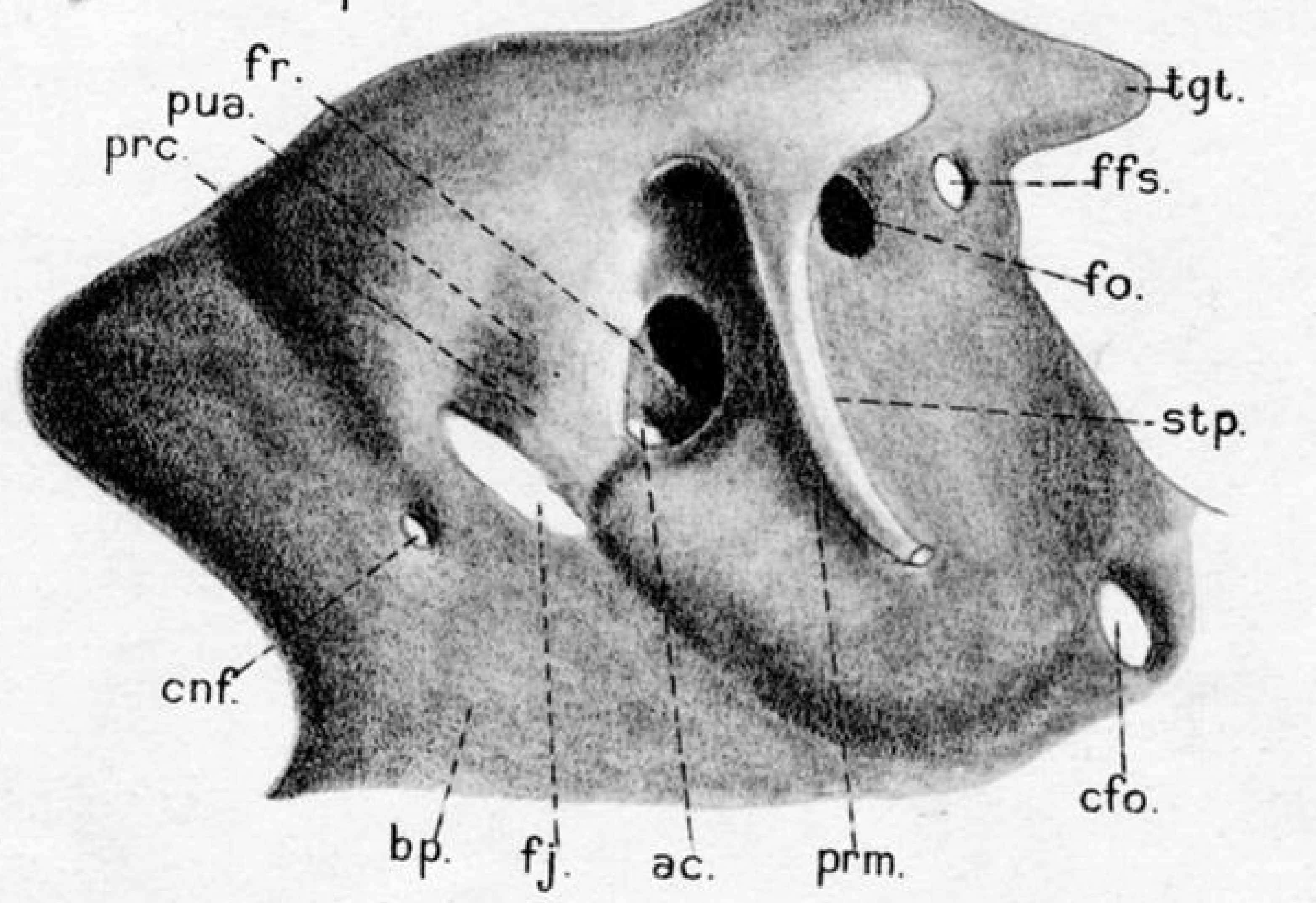

PLATE 98.

FIG. 10.—Internal view of the auditory capsule. The capsule has been cut transversely, and the observer is looking backwards at the anterior face of the posterior portion of the capsule. The outline of the original foramen perilymphaticum is indicated by a broken line.

FIG. 11.—Ventral view of the auditory capsule of the skull of Lacerta (from GAUPP's model reconstructed by ZIEGLER) showing the relations of the foramen perilymphaticum and the fissura metotica.

FIG. 12.—Ventral view of the auditory capsule of a model reconstruction of the skull of an embryo cat (32 mm. long), showing the relations of the processus recessus.

FIG. 13.—Ventral view of the auditory capsule of the model of Sorex, showing the formation of the fenestra rotunda by the fusion of the processus recessus with the canalicular capsule.