On the Organ of Jacobson in *Sphenodon*.

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(Plates 41 & 42.)

Though something is known of the Organ of Jacobson in Lizards and Snakes, principally through the researches of Kitchen Parker (1), Born (2), and Seydel (3), scarcely anything has been published, so far as I am aware, concerning the organ in *Sphenodon*. Osawa (4) figures a transverse section showing the relations of the organ in the adult animal, and the mode of its opening into the choane, and he correctly states:—"Eine papillenartige knorpelige Einragung in das Organ wie bei der *Lacerta* kommt bei der *Hatteria* nicht vor." The bone which lies above the organ he incorrectly calls the "turbinale." This bone has since been shown by Howes and Swinnerton (5) to be the "septo-maxillary." In their paper on the development of the skeleton in *Sphenodon* they figure a section through Jacobson's organ showing the relations of the organ to the cartilages and bones, and state that whereas in *Sphenodon* "Jacobson's organ is completely roofed in cartilage, in the lizard, according to Parker, the septo-maxillary fulfils that function." Seydel (3), in his recent work on the organ of Jacobson in *Echidna*, refers to the condition in *Sphenodon*, and though he has evidently only superficially examined the organ, he has made the following highly important observations:—"Das Jacobson'sche Organ von *Hatteria* ist schlauchförmig und ist dem unteren Rande des Septums eingelagert. Seine Oeffnung liegt in der Nähe des vorderen Randes der Apertura interna; nach hinten endet der Schlauch blind. Das Organ erinnert also in Form und Lage an das der Mammalier; ob sich die Aehnlichkeit auch auf den inneren Bau erstreckt, weiss ich nicht. Jedenfalls ist die Thatsache bedeutungsvoll, dass bei einem recenten Reptil bei verhältnissmässig primitivem Zustande des Gaumens ein den Mammaliern ähnliches Jacobson'sches Organ besteht."

Through the kindness of my friend Prof. Dendy, who has very generously allowed me to freely examine his beautiful sections of *Sphenodon* embryos, I am fortunately in a position to give a

detailed account of the relations of the organ, and to confirm Seydel's opinion as to its mammalian affinities. The sections which most satisfactorily show the relations of the organ are a series of transverse sections of the head of an embryo of Dendy's stage R. At this stage the bones of the head are well ossified, and the organs in young animals have their relations in a more satisfactory condition for enabling comparisons to be made than at later stages, when the primitive structure becomes frequently somewhat obscured by specialization.

In a transverse section through the premaxillaries, the bones are seen to be separated by a feebly developed portion of the internasal cartilaginous septum. A similar condition is met with in *Echidna*, but is not present either in the lizard, snake, or tortoise.

Immediately behind this plane, the nasal septum is found to be greatly expanded in its lower half as seen in fig. 1 (Pl. **41**). It is continued externally into the delicate little cartilage that supports the external nasal opening.

A short distance behind the plane illustrated by fig. 1, the lower part of the median cartilage is found to have four openings—two large ones above for the accommodation of the anterior parts of Jacobson's organ, and two smaller ones for the anterior ends of the prevomers. Figs. 2 & 3 illustrate sections in this region, and fig. 3 shows the lower part of the cartilage forming a cartilaginous support for the papilla. The presence of a papillary cartilage is unknown in Lizards or Snakes, nor has it, so far as I am aware, been found in Chelonians or Birds, but it is met with in the Crocodile. Among Mammals a papillary cartilage has been shown by Wilson to be present in the fœtal *Echidna*; and I have shown that a well-developed cartilage is present in the majority of Marsupials, and among higher forms in *Macroscelides* and *Miniopterus*.

In figs. 2 & 3 is seen the moderately well-developed septo-maxillary bone. It forms the floor of the anterior part of the nasal cavity, and to some extent protects the roof of Jacobson's organ. In its relations it is seen to be strikingly dissimilar to the septo-maxillary of either the lizard or the snake. In the Squamata the organ of Jacobson is never roofed by cartilage as in *Sphenodon*, and the septo-maxillary bone is highly developed to protect the very large organ. The bone is firmly attached to the nasal septum and usually surrounds the upper part of the

organ, but never shows on the outer surface of the skull as in *Sphenodon*. In snakes the septo-maxillary is more largely developed than in lizards, and to a considerable extent supports the nasal septum beyond the limits of the organ of Jacobson.

A septo-maxillary bone has not hitherto been described as such in any mammal, but it appears to occur in the immediate ancestors of the Mammals, the Cynodonts, and is known to be present in the more primitive Therocephalians and Pelycosaurians. No trace of the bone has been found, however, in any Anomodont. In 1896 I discovered a nasal-floor bone in the Armadillo (*Dasypus villosus*), but did not at the time recognize its true significance. Fig. 9 represents a section through the bone; and if this be compared with figs. 2 & 3, it will be seen that there is considerable reason for regarding the "nasal-floor bone" of the Armadillo as homologous with the septo-maxillary of *Sphenodon*. The fact that the septo-maxillary is seen from the *Sphenodon* condition to be primarily a nasal-floor bone, and that the bone occurs in the mammalian ancestors, renders it exceedingly probable that the bone in *Dasypus* is a true septo-maxillary.

The organ of Jacobson, as illustrated in figs. 3, 4, 5, & 6, is seen to be relatively much less developed than in lizards and snakes, and to differ very much from the type found in the Squamata. It is a flattened lens-shaped organ which lies near the base of the nasal septum, between the prevomer and the nasal cavity. The anterior part of the organ, as seen in figs. 3 & 4, is supported below by the paraseptal cartilage, and above by a special roofing-cartilage. The plane of the organ looks upwards and slightly outwards. At a point near the middle of the outer side, the organ opens into the anterior end of the lower part of the nasal cavity, as seen in figs. 4 & 5. The lachrymal duct opens into the same part of the nasal cavity from the outer side. On passing farther backwards the organ is seen to be rather narrower than in front (see fig. 6). It ends quite abruptly and not, as is the rule in Mammals, by becoming a gland-duct.

The differences between the organ in *Sphenodon* and that in the typical representatives of the Squamata are much greater than might have been expected, considering the many lizard-like characters of *Sphenodon*. In the Lacertilia and Ophidia the organs are formed on a common type, and the differences, either

in structure or relationships, are comparatively slight. The organ is usually of large size, and has a well-developed turbinal process passing into it from its anterior and under side, and it is roofed by the large septo-maxillary bone. It usually opens more or less directly into the mouth, and it is only indirectly connected with the nasal cavity. In the Geckonidæ, which are probably the most primitive of living lizards, the organ opens with the lachrymal duct into a cavity which is connected with the nasal chamber, and in this group the septo-maxillary, though it forms the roof of the organ and articulates with the nasal septum, is considerably smaller than in the typical lizards. The Gecko thus shows a nearer affinity with *Sphenodon* than do the other lizards, and helps us to understand how the lizard type of organ may have developed from something like the *Sphenodon* type.

In the way in which the organ opens into the anterior part of the lower portion of the nasal cavity, the resemblance is much closer to the mammalian condition than to the lacertilian. In the mammal the resemblance is slightly obscured by the formation of the secondary palate by which the anterior part of the nasal cavity becomes the naso-palatine canal. In the mamma. the organ of Jacobson normally opens into the naso-palatine canal. This condition is found in the Monotremes, all Marsupials (except *Æpyprymnus* and *Notoryctes*), Ungulates, Carnivores, Insectivores, Bats, and Lemurs. It does not occur, however, in Rodents, *Dasypus*, or Man. The roofing of the organ by cartilage, though exceptional in Mammals, is by no means uncommon. It is met with in the Monotremes, a few Marsupials, and a number of Eutherians. In Mammals the organ only very exceptionally extends in front of the opening. In *Ornithorhynchus*, however, about as much of the organ lies in front of the duct as behind it, and the way in which the anterior part of the organ excavates the lateral cartilage is not unlike the condition seen in *Sphenodon*; and in *Ornithorhynchus* the cartilage is supported by the prevomer or "dumbbell bone," just as in *Sphenodon* it is supported by the bone usually, but I believe erroneously, called the "vomer." In no higher mammal does the organ extend much in front of the duct, but it does to a slight extent in *Perameles* and *Macroscelides*. A striking difference between the organ in *Ornithorhynchus* and *Sphenodon* is that in the former there is a well-developed turbinal passing

into the organ from the outer side. It also occurs in *Echidna* but no higher mammal retains it. The appearance of the cartilages in the Marsupials and Edentata, however, suggests the belief that the higher forms are descended from animals which had a turbinal in the organ. The relations of the posterior part of the organ to the septum in *Sphenodon* are typically mammalian.

With regard to the structure of the organ, so far as can be made out from the sections of the embryos I have examined, the affinities are much more with the Squamata than with the Mammalia. The lower wall of the organ is composed of two or three layers of rounded epithelial cells, apparently without cilia: the upper and inner wall is formed of closely-packed bunches of neuro-epithelium, as in the Squamata. In Mammals the sensory epithelium is usually confined to the inner and lower wall of the organ, but in the Monotremes it covers also the upper wall of the organ.

The study of the organ of Jacobson and its relations helps considerably towards the solution of the problem of the affinities of *Sphenodon*. By Huxley, Osawa, and others, *Sphenodon* has been held to be a true lizard. By Gadow and many others it has been looked upon as an extremely primitive reptile not very far removed from the Batrachians, and belonging to an order from which almost all other reptiles have descended. It will probably only be possible to definitely settle the position of *Sphenodon* when palæontology has advanced much further than at present, but it seems to me that enough can be said on each side of the question to demand for the opposing views most careful consideration. In many respects *Sphenodon* bears a closer resemblance to the lizards than to other reptiles, but the characters which they have in common are probably primitive and shared by most of the early lizard-like forms. It seems impossible that lizards with a distinct prosquamosal can have descended from a *Sphenodon*-like form in which that bone is lost; but lizards and *Sphenodon* may both have had a common ancestor in Permian times which had a distinct prosquamosal and a fully-roofed temporal region. Such an ancestor would probably not be far removed from the Cotylosaurians, one of which was the remote mammalian ancestor. *Sphenodon*, though it has advanced far from the Cotylosaurian state, still retains a number of the primitive characters, and the organ of Jacobson

is probably still of the same type as that possessed by the Cotylosaurians. In the Squamata the organ has become greatly developed and specialized, and more or less completely separated off from the nose.

The condition of Jacobson's organ in *Sphenodon* is of further interest in that it affords additional evidence, if such be any longer required, of the Reptilian affinities of the Mammalia. The palæontological evidence that Mammals are descended from a primitive but true reptile seems to be pretty conclusive; but, owing to most living reptiles having been much specialized, the relations of the mammal to the reptile are not so striking when one only studies the ordinary living types. In *Sphenodon* we have a reptile nearer to the primitive type than any other at present alive, and it is thus particularly interesting to find in it a type of Jacobson's organ so near to that of the mammal. In the mammal, possibly as the result of the large development of the incisor teeth, the organ has been forced to lie along the base of the nasal septum, and while degenerating as a sense-organ it has been retained largely as an excretory duct for the nasal glands.

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(2) G. Born.—Die Nasenhöhlen und der Thränenausgang der amnioten Wirbelthiere. Morph. Jahrb., Bd. v. (1879) pp. 62–140, & viii. (1883) pp. 188–232.

(3) O. Seydel.—Ueber Entwickelungsvorgänge an der Nasenhöhle und am Mundhöhlendache von *Echidna*. Semon, Zool. Forschungsreise, 1899.

(4) G. Osawa.—Beiträge zur Anatomie der *Hatteria punctata*. Arch. mikr. Anat., Bd. li. (1898) pp. 481–691.

(5) G. B. Howes & H. H. Swinnerton.—On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*, etc. Trans. Zool. Soc. xvi. 1. (1901) pp. 1–86, pls. 1–6.

EXPLANATION OF THE PLATES.

C.c.n., cartilage of the external nares; *c.n.*, external nares; *J.O.*, Jacobson's organ; *l.d.*, lachrymal duct; *l.J.c.*, lower part of Jacobson's cartilage; *Mx.* maxilla; *Na.*, nasal; *n.c.*, nasal cartilage; *n.f.c.*, nasal-floor cartilage *n.s.*, nasal septum; *Pmx.*, premaxilla; *p.s.c.*, paraseptal cartilage; *P.Vo.*, prevomer; *S.Mx.*, septo-maxilla; *u.J.c.*, upper part of Jacobson's cartilage.

Plate 41.

Fig. 1. Transverse section of nose of embryo *Sphenodon punctatus*, Stage R, showing the broad expansion of the lower part of the nasal septum immediately behind the premaxillaries. The section is through the anterior nares, and a portion of the supporting cartilage is seen above and below.

2. Transverse section a short distance behind fig. 1. The lower part of the septal cartilage shows four excavations. The upper two are for Jacobson's organ, the lower for the prevomers. The section shows the anterior part of the septo-maxillary.

3. Transverse section a little behind fig. 2. The anterior part of Jacobson's organ is seen, also the prevomers. The lower part of the septal cartilage is now seen forming a papillary cartilage (*p.c.*). The septo-maxillary is of large size, and forms part of the external wall of the skull.

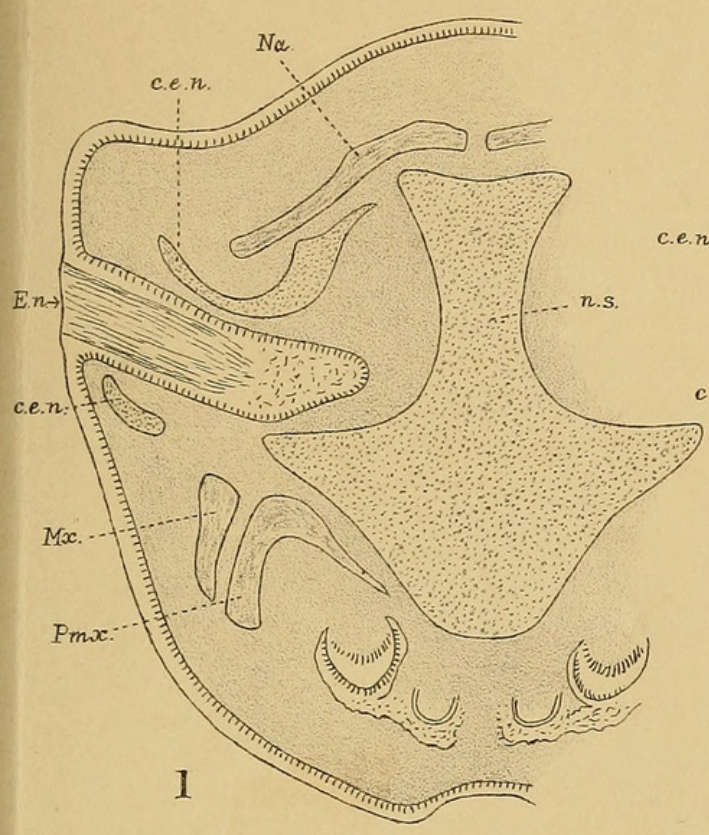
Fig. 4, fig. 5, and fig. 6 are almost consecutive sections a little behind fig. 3. Fig. 4 shows a section of the organ where it is opening into the anterior and inferior corner of the nasal cavity in common with the lachrymal duct. The organ is roofed above and below by cartilage.

Plate 42.

Fig. 5 shows the organ just behind its opening into the anterior part of the nasal cavity; the cartilage of the organ shows an upper and a lower part, the lower being manifestly the paraseptal cartilage. The lower part of the nasal cartilage is separated as a nasal-floor cartilage, almost exactly as is seen in most mammals. Fig. 6 is a section which in almost every respect is typically mammalian. With the exception of the fact that the mode of opening of the lachrymal duct is different, the section might pass for a section through the snout of a marsupial. In the marsupial, as in most mammals, Jacobson's cartilage is supported by the palatine process of the premaxilla: here the supporting bone is the prevomer.

Fig. 7. Transverse section a considerable distance behind fig. 6. The paraseptal cartilage is small and the prevomer large. The lachrymal duct is seen below the maxilla and the prefrontal.

8. Transverse section of snout of *Dasypus villosus*. Below the base of the true nasal septum are seen the anterior portions of the cartilages which become Jacobson's cartilages. Along the inner part of the nasal floor is seen the well-developed bone which is believed to be the septo-maxillary (*S.Mx.*). A little farther back it lies inside of the premaxillary, and has no connection with any other bone.



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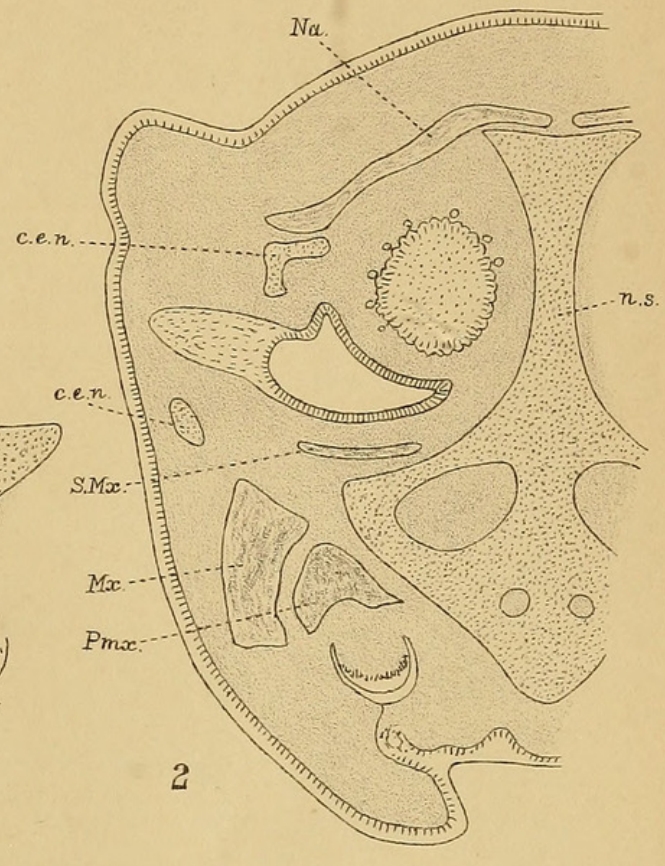

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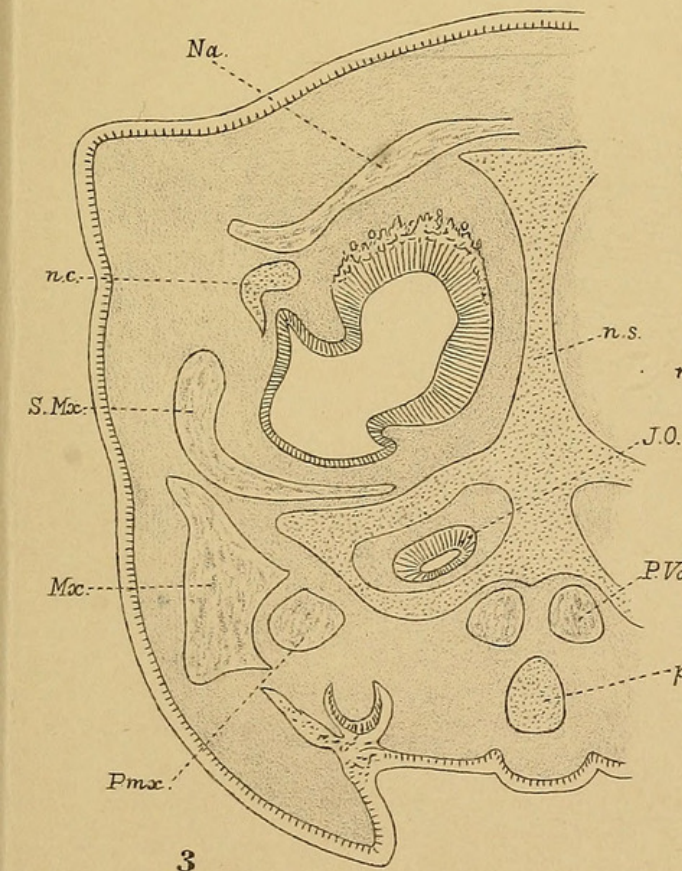

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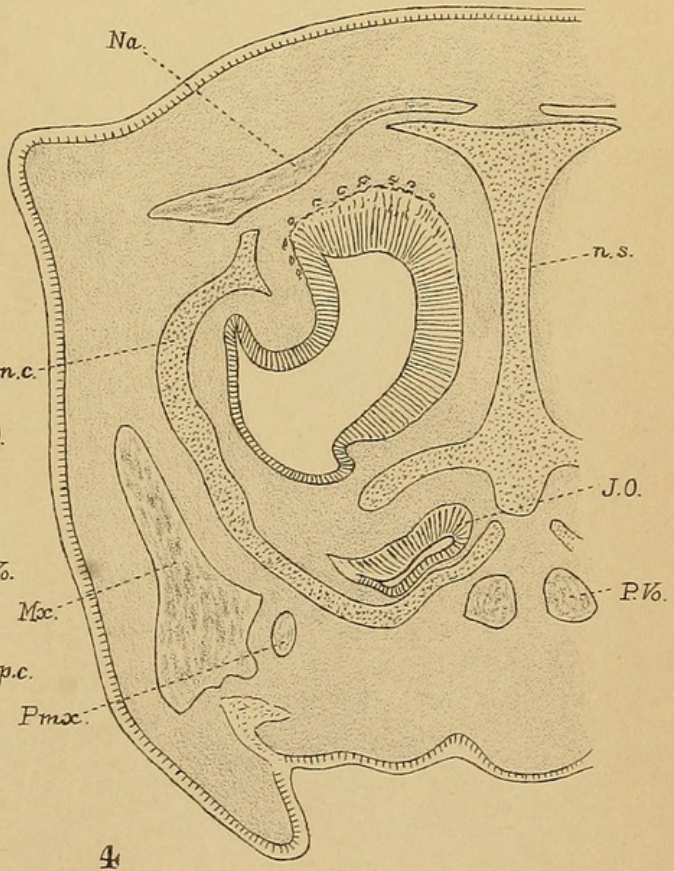

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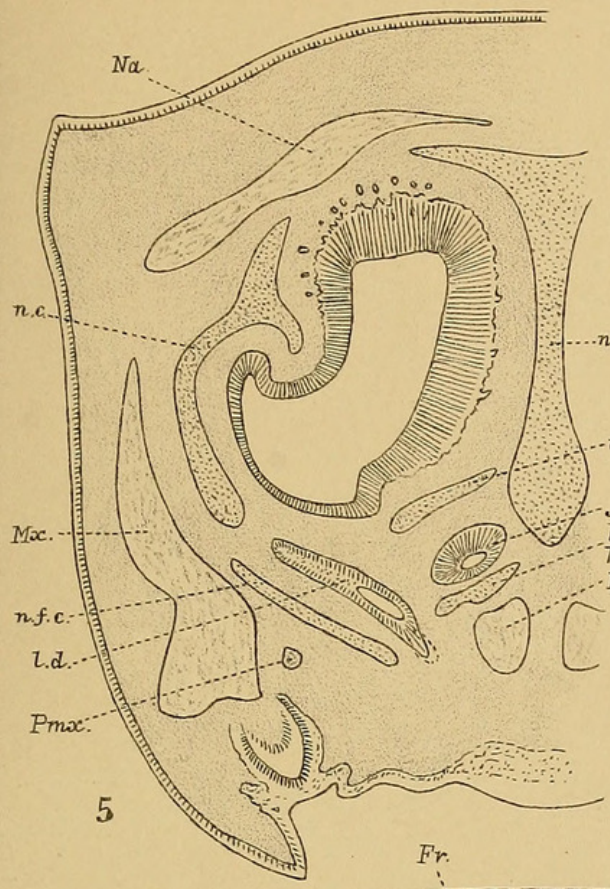
R. Broom del.

M. P. Parker lith.
Parker & West imp.

JACOBSON'S ORGAN IN SPHENODON.



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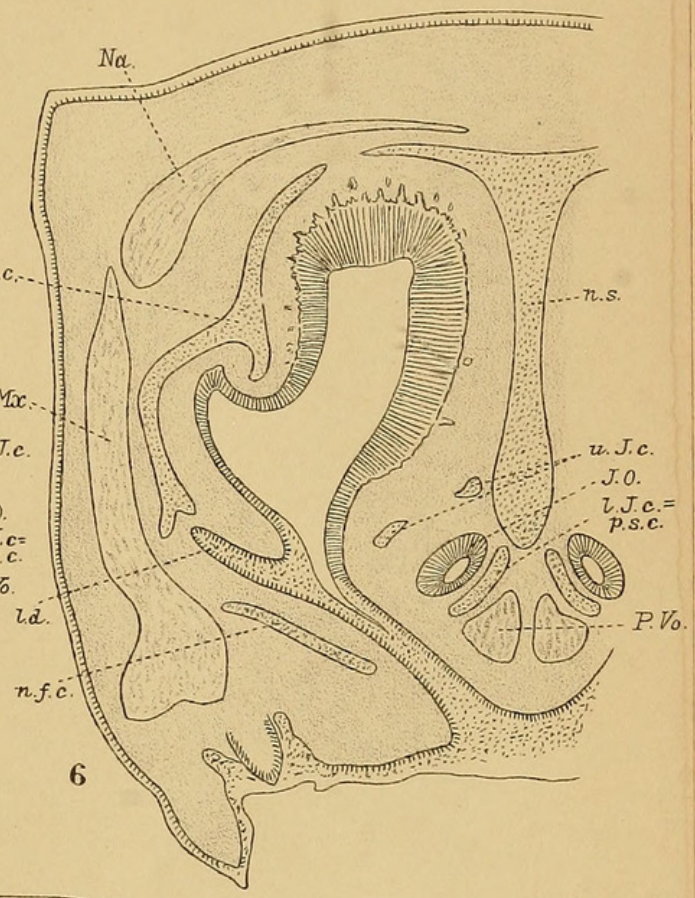

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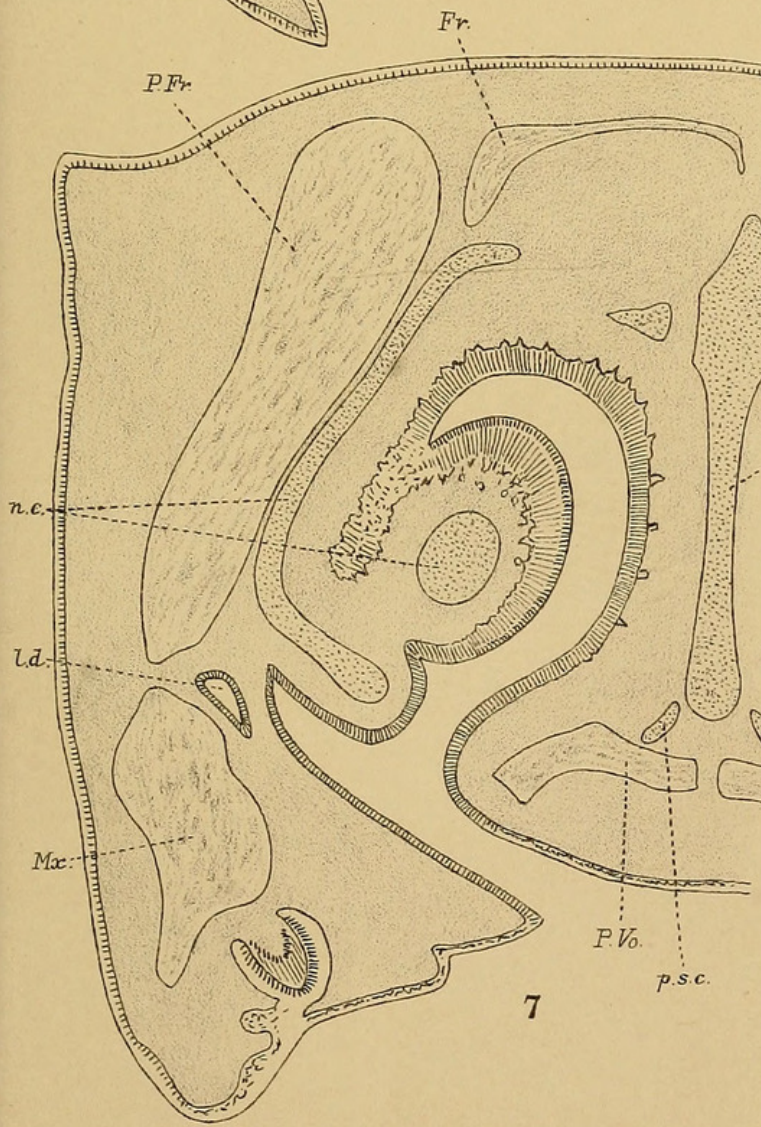

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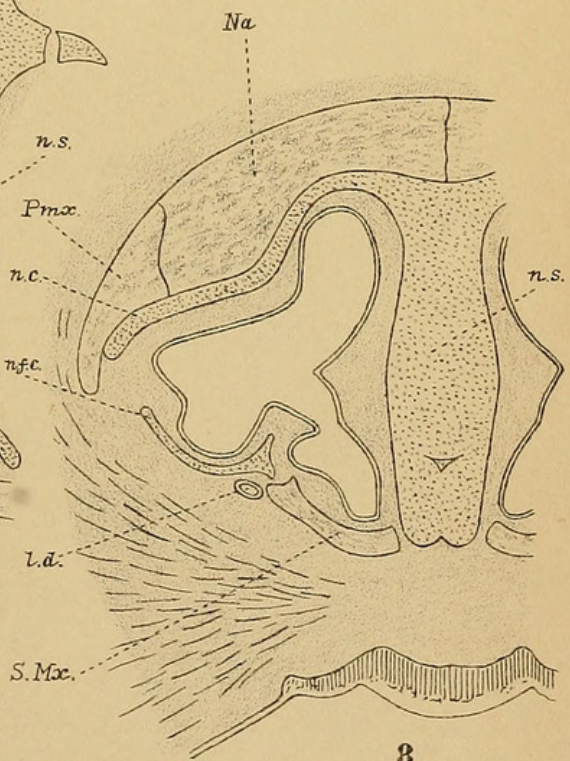

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R. Broom del.

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JACOBSON'S ORGAN IN SPHENODON.