

XXVII. *On the Communications between the Cavity of the Tympanum and the Palate in the Crocodilia (Gavials, Alligators and Crocodiles).*

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THERE are three perforations which succeed each other along the middle line of the base of the cranium in the Crocodilian Reptiles. The hindmost (Plate XL. fig. 1, *v*), situated in the basioccipital, near the condyle, is the smallest and least constant in size and existence: it gives passage to a vein, which traverses a vertical canal in the bone homotypal with the vertical vascular canal that opens upon the under surface of the bodies of the vertebræ of the trunk. The next foramen in advance, *e*, is larger and on a lower level; it is constantly present and is regular in its size and position: it perforates the fore part of the basioccipital close to the basisphenoid. The third or anterior foramen, *n*, is the largest, and opens on a still lower plane: it is formed entirely by the pterygoids, which it perforates in a forward direction, and is the posterior aperture of the nasal passages.

There exists a difference of opinion as to the nature of these latter foramina, and especially as to the function of the middle foramen, *e*, viz. that which perforates the basioccipital close to the basisphenoid. CUVIER describes it in his celebrated chapter on the Osteology of the Crocodile, in the last volume of the ‘*Ossemens Fossiles*,’ p. 78, 4to, 1824, as leading to “a canal which traverses the body of the sphenoid, and terminates by two branches opening into the ‘*sella turcica*,’ and, at p. 133, he refers to it in the cranium of the ‘*Gavial de Caen*’ (*Teleosaurus cadomensis*, GEOFFROY), as an arterial foramen (‘*le trou des artères*’).” The continuators of CUVIER, in the posthumous edition of the ‘*Leçons d’Anatomie Comparée*,’ t. ii. p. 523, describe the foramen in question more accurately, as leading to a canal which bifurcates as it ascends; one of the branches traversing obliquely the body of the sphenoid, whilst the other perforates the basilar part of the occipital, and opens into the cavity of the internal ear. They do not state where the branch terminates which traverses the basisphenoid\*, nor what passes through either canal.

In the description of the tympanic cavity of the Crocodile†, no mention is made of this communication, or of the Eustachian tube, which is described in the Saurians

\* I use here, and throughout this paper, the English equivalents of the French phrases defining the bones of the Crocodile’s skull, according to the table of synonyms, No. 1, in my work ‘*On the Archetype of the Vertebrate Skelton*,’ 8vo, 1848.

† *Op. cit.*, tom. iii. p. 512.

generally as communicating with the palate by a wide and short canal (p. 511). But in a supplementary paragraph to CUVIER's description of the foramina in the base of the skull of the Crocodile, the osseous aperture of the Eustachian tube is stated to be perforated in the exoccipital, near its junction with the basioccipital, and to be situated below the anterior condyloid foramen\*.

In the 'Report on British Fossil Reptiles,' communicated to the British Association in 1841†, I described the foramen in the basioccipital, *e*, as the common terminal canal of the Eustachian tubes, and the foramen in advance of it, *n*, as the posterior aperture of the nasal canals.

In the 'Abhandlungen über die Gavial-artigen Reptilien des lias-formation,' fol. 1841, by Professors BRONN and KAUP, it is argued at great length (pp. 12, 16, 24) that the median foramen, *e*, is the true posterior aperture of the nostrils; and a letter from Professor DE BLAINVILLE, dated December 8th, 1841, is cited by those authors in support of their view, in which letter CUVIER's determination, that it was 'an arterial foramen,' is rejected, and Professor BRONN's opinion is stated to be completely confirmed by the appearances in the original fossil skull of the *Teleosaurus* from Caen, described and figured by CUVIER.

Besides the median foramina above specified, there are several lateral foramina, in symmetrical pairs, in the same part of the base of the skull of the Crocodile. One on each side the base of the condyle, Plate XL. fig. 1, *p*, is the 'precondyloid foramen,' which gives exit to the hypoglossal nerve: external to this is a larger foramen, *t*, through which pass the eighth pair of nerves and a vein from the tympanic cavity; below these, and still in the exoccipital (2), is the foramen, *c*, described by the continuators of CUVIER as the bony outlet of the Eustachian canal; and still lower down, in the suture between the basioccipital (1) and basiphenoid (5), is the foramen, *el*, which I have not found noticed by any anatomical author.

The decisive test of the nature of these latter foramina, *el*, and of the different opinions respecting the foramina, *c*, *c*, and the median foramina, *e* and *n*, was, of course, to be sought for in the results of an accurate anatomical examination of the parts in the recent Crocodile. I have, accordingly, availed myself of the opportunities liberally afforded to me by the Council of the Zoological Society, to dissect for this purpose specimens of an Alligator (*Alligator lucius*) and a Crocodile (*Crocodilus acutus*) which have died at the Zoological Gardens; the examination being made after injecting the vessels of the head with coloured wax.

The entocarotid arteries (Plate XL. fig. 2, *c*) enter the foramina (fig. 1 *c*, *c*) situated, one in each exoccipital bone, 2, at the side of the base of the condyle, below

\* "Le trou condyloïdien est dans l'occipital latéral, et en dehors de lui est un trou assez grand pour des vaisseaux. L'ouverture osseuse de la trompe d'Eustache est au dessous des précédents, aussi dans l'occipital latéral, et tout près du point de réunion de cet os avec le basilaire et le sphénoïde."—Leçons d'Anat. Comp. tom. ii. p. 524, 1837.

† Reports, 8vo, p. 96.

the outlet for the hypoglossal and eighth pair of nerves, *t* and *p*. In a young Crocodile, with a head of eleven inches in length, the common trunk, fig. 2, *cc*, of both carotids is continued along the under surface of the cervical vertebræ as far as the dentata, where it bifurcates into the two carotids: these diverge, ascend, inosculate with the vertebral artery, *v*, and subdivide into the ectocarotid, *ec*, and entocarotid. The latter artery, *c*, at the first part of its course, extends obliquely forwards inwards and upwards, protected by a bony canal, half an inch in length, which terminates by projecting freely as a tube of a line in length (Plate XLI. fig. 4, *c*), opening into the cavity of the tympanum beneath the bony plate, 16, to which I have restricted the term 'petrosal\*.' The artery emerging from the bony canal extends forward across the base of the tympanic cavity, covered only by a reflexion of its lining membrane, for about a third of an inch, and then enters a second bony canal, opening into the fore part of the tympanum, and continued to the 'sella turcica,' where the carotid enters the cranial cavity, as is shown in Plate XL. fig. 3, *c*.

No artery enters the single median foramen, Plate XL. fig. 1, *e*, situated close to the suture between the basioccipital and basisphenoid. The soft palate which covers this part, immediately behind the true posterior nares, forms a subcircular protuberance with a single central aperture (Plate XLI. fig. 5); this aperture is also partly closed by a valvular membranous prominence, *x*, which reduces its area to a crescentic form. This orifice in the soft palate is not, as I had supposed, continued exclusively from the bony orifice in question, *e*, immediately above it; but is the common palatal outlet of three canals, one of which, *e*, is median, extending into the bony canal, figs. 6 and 7, *e*, which ascends into the substance of the basisphenoid; the other two, *el*, are membranous for the extent of eight lines, and diverge as they ascend to penetrate the fissures, fig. 7, *el*, one on each side of the larger median foramen, and which lead to canals, fig. 7, *el'*, extending upwards between the basioccipital and basisphenoid.

From the inferior openings, Plate XL. fig. 1, *el*, of these canals in the dry skull, grooves lodging their membranous prolongations are continued to the common median fossa into which the middle osseous canal, fig. 7, *e'*, opens by the foramen, *e*, in question. Dissections of the recent parts demonstrated that this foramen, like the two lateral canals, communicated by a membranous tube (fig. 5, *e*) with the surface of the palate and would receive air from the mouth. It was next to be determined where the air would be conducted by those tubes; and the passage leading from the median foramen was first traced. In an alligator with a head 14 inches in length, the foramen, *e*, leads to a canal lined by a continuation of the palatal membrane, which ascends along the suture between the basioccipital and basisphenoid, for nearly 2 inches, and then bifurcates; one branch inclining forward into the basisphenoid, the other rising vertically into the basioccipital, and both in the same

\* It was probably the observation of this structure in the dry skull that misled the continuators of CUVIER into the belief that the canal, *e*, was the osseous part of the Eustachian tube.

median plane. I followed out the further course of these canals in the skull of a *Crocodilus acutus* of about the same size as the recent Alligator. Figure 7, Plate XLI. shows the common median canal extending from *e* to *e'*, where it divides. Each of these branches subdivides, and sends its subdivisions, one to the right the other to the left, to communicate with the tympanic cavity. The lateral canals, *el'*, which commence below at *el*, one on each side of the median foramen, communicate with the lateral subdivisions, *eo*, of the posterior or basioccipital branch of the common median canal; a small rhomboidal sinus, *eo'*, being formed at their point of union, from which a short canal is continued to the tympanic cavity. Thus each lateral canal, *el'*, with each posterior lateral subdivision, *eo*, of the basioccipital branch of the median canal, has a common opening into the base of the tympanic cavity of its own side. Each lateral subdivision, *es*, fig. 8, Plate XLII., of the anterior or basisphenoid branch of the median canal opens into the tympanic cavity at *es*, fig. 10, in advance of the preceding orifice. The lining membrane of these several canals here becomes continuous with that of the tympanic cavity.

Thus it was seen that no passage from the median orifice or canal in question, *e*, figs. 1 and 7, between the basioccipital and basisphenoid, conducted to the nasal passages, but that all the branches from that common orifice opened into the tympanic cavity: at the same time it was demonstrated, that the communication between the tympanum and the palate, commonly called the 'Eustachian tube,' was more complex in the Alligator and Crocodile than had been suspected, or than was known to exist in any other animal. It may be described as follows:—From each tympanic cavity two passages are continued downward, one from the fore part, Plate XLII. fig. 10, *es*, the other from the floor, *ib. eo*, of the cavity. The anterior canal, *es*, passes downwards and inwards, expands and again contracts before it unites with its fellow from the opposite side at *es'*, fig. 8, to form a median canal, *es'* to *e'*, which passes from the basisphenoid to the space or broad suture between that bone and the basioccipital, where it terminates in the single subvertical canal, *e'* to *e*, descending along that suture to the median foramen in question, *e*, fig. 1.

The opening at the floor of the tympanic cavity, *eo*, fig. 10, leads to a short canal, *eo*, figs. 7 and 8, which curves towards its fellow from the opposite tympanum, but first swells into the rhomboid sinus, fig. 7, *eo'*; and divides; one branch descends almost vertically, *el'*, and terminates by the small foramen, *el*, fig. 1, in the osseous groove or channel leading to the central aperture and fossa; the other branch, *eo* to *eo'*, fig. 8, continues the course inwards and downwards until it meets its fellow at the median line of the basioccipital at *eo'*, and forms the posterior primary division of the common median canal, *eo* to *e*: this soon joins the anterior division, at *e'*, to form that common canal, which then descends and terminates by slightly expanding into the foramen, *e*, at the middle of the fossa between the basioccipital and basisphenoid; which fossa receives also the grooves lodging the membranous canals from the lateral fissures. Finally, the three bony canals terminate by their membranous continuations

*e* and *el*, fig. 5, Plate XLI., in the single Eustachian valvular outlet, *x*, on the soft prominence behind the posterior nares, *n*.

The canals from the lateral orifices, *el*, are partially divided by a longitudinal ridge of bone projecting into them from their anterior wall: and the dilated lateral branches of the alisphenoid division of the median canal, *es*, are impressed by a longitudinal groove. I may also remark, that at the upper part of their place of confluence or termination, there is a median fossa leading to a small vascular canal.

The tympanum of the Crocodiles, Plate XLII. fig. 10, is very extensive, by reason of the air-cells continued from it, not only into the mastoid, but across the basioccipital and basisphenoid\*, and into the exoccipital, supraoccipital†, alisphenoid and parietal bones‡.

By the dissection of a young Gavial of the Ganges, preserved in spirits, and a comparison of this with sections of the cranium of a full-grown specimen, I have satisfied myself that the third median system of Eustachian tubes, as well as the two lateral tubes, exist in the Gavials as in the Alligators and true Crocodiles; only in the Gavial the common terminal canal of the median system is shorter, as is shown in Plate XLII. fig. 9, *e*, *es*, *eo*.

It appears to have been still shorter in the extinct *Teleosauri*; the posterior primary division of the canal which penetrates the basioccipital forms, in the section of the skull of the Caen Teleosaur, a subcircular depression, which is filled with the matrix in the Parisian specimen. The anterior primary division, answering to *es*, fig. 9, plainly perforates the substance of the basisphenoid, as it ascends obliquely forwards, and therefore can by no means be regarded as the posterior termination of the nasal passages, which, in the *Teleosauri*, are surrounded exclusively by the pterygoids, as in all the existing forms of *Crocodylia*.

With regard to the homologies of the above described complex Eustachian or palato-tympanic air-passages in the *Crocodylia*, the lateral bony canals, *el*, fig. 7, terminating at the grooves, *el*, answer to the simple Eustachian tubes of lizards and mammals: the median canal, *e*, *e'*, with its dichotomous divisions, is a speciality peculiar to the *Crocodylia*.

I forbear, with my present limited experience of the living habits and actions of the Crocodylian Reptiles, to offer any hypothesis as to the function of the complex canals which conduct the air and would convey its sonorous vibrations from the nose to the ear: but one peculiarity I may suggest, as being probably related to the structures in question, in which the Crocodiles and Gavials differ from all the Lizard-tribe, viz. that of habitually floating with the operculated meatus externus submerged, and only the eyes and the prominent nostril exposed above the surface of the water. Any noise in the air that might reach the floating reptile would, under such conditions, be conveyed to the tympanum by the canals conducting to that cavity from near the

\* On the Archetype of the Vertebrate Skeleton. 8vo. VAN VOORST, fig. 9, p. 22, 1 and 5.

† *Ibid.* 3.

‡ *Ibid.* fig. 19, p. 120, 6 and 7.

hinder opening of the long nasal passage ; and it may also be remembered, that there is a peculiar valve in the Crocodiles which shuts off all communication between that passage and the mouth.

#### DESCRIPTION OF THE PLATES.

#### PLATE XL.

Fig. 1. A view of the hinder part of the base of the skull of a Crocodile, showing :—

- v.* The venous foramen.
- e.* The median Eustachian foramen.
- el.* The lateral Eustachian foramina (the canal, *el'*, is laid open on the right side).
- n.* The posterior nasal aperture.
- c.* The carotid foramina.
- p.* The precondyloid nervous foramina.
- t.* The foramen jugulare.
- 1. The basioccipital.
- 2. The exoccipital.
- 5. The basisphenoid.
- 24. The pterygoid. The bristle ending at this figure is passed through the median canal and right subdivision of its basioccipital branch through the sinus of communication with the lateral canal, which is laid open between *t* and *c*.

Fig. 2. A view of an injected preparation of the *Crocodilus acutus*, showing the course of the carotids *cc*, vertebral artery *v*, and entocarotid *c*, to its foramen, and through the posterior bony canal into the tympanic cavity.

Fig. 3. Showing the emergence of the entocarotids, *c*, from their anterior bony canals opening into the sella turcica, their sinuous course forwards, and confluence into the single artery continued into the rhinencephalic division of the cranium.

#### PLATE XLI.

Fig. 4. A section of the skull of a *Crocodilus biporcatus*, showing the free or prominent tubular termination of the posterior bony carotid canal in the tympanic cavity ; *c*, a style passed through the canal ; 16, the petrosal.

Fig. 5. A section of the bony and soft parts of the palate of an Alligator (*All. lucius*), showing the posterior nares, *n*, the common median valvular aperture, *x*, of the median, *e*, and the two lateral, *el*, Eustachian canals ; bristles are passed along the membranous portions of these tubes.

*Crocodilus acutus*

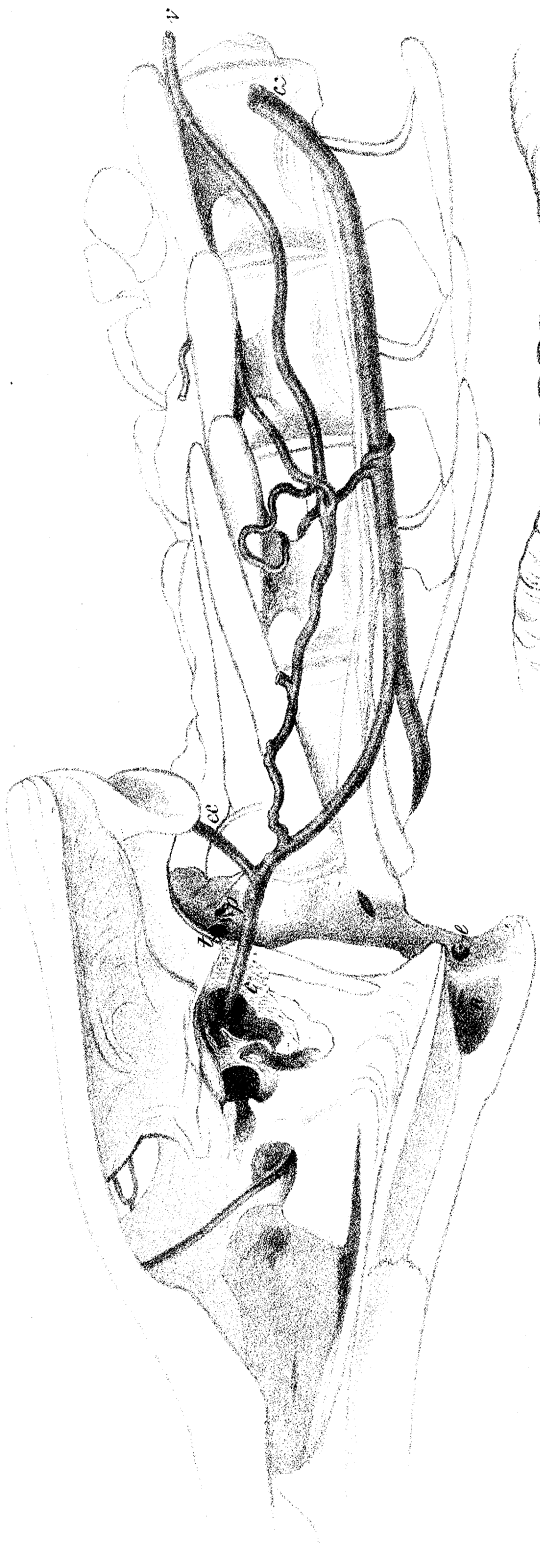


Fig. 2.

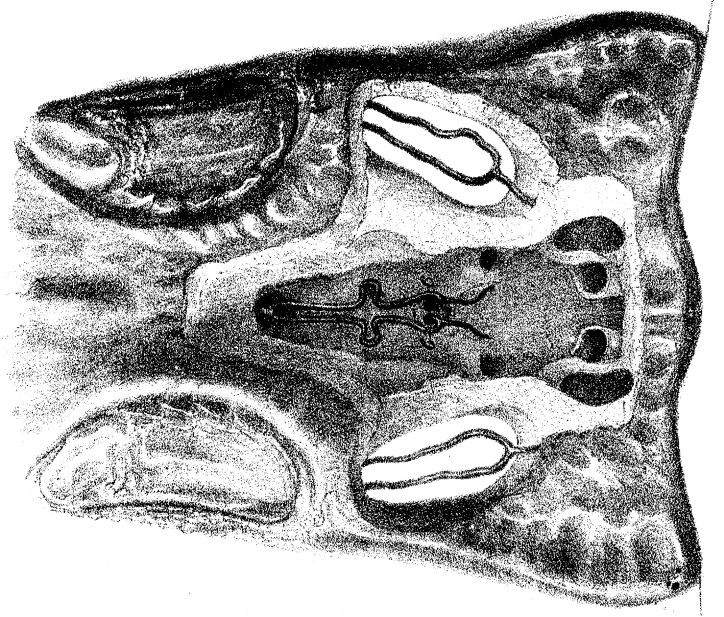


Fig. 3.

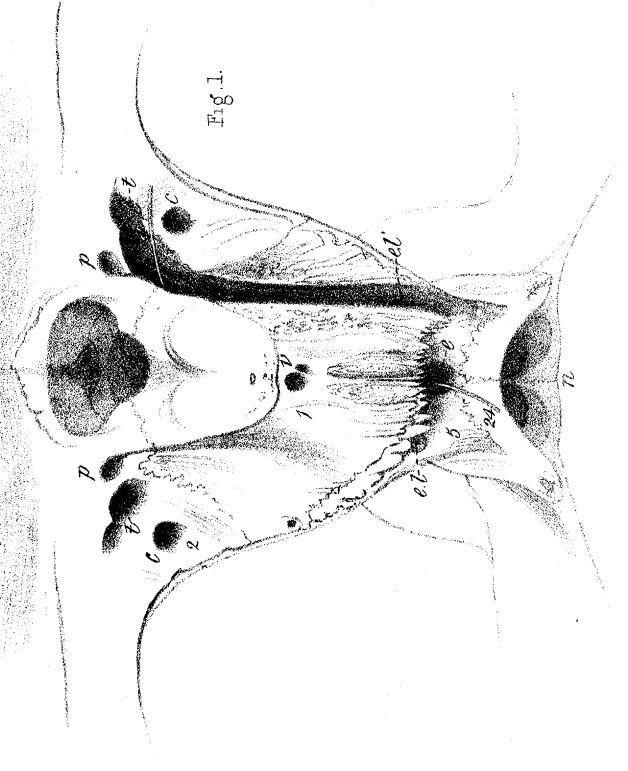


Fig. 1.

*Crocodilus acutus*

*Crocodilus biporcatus*

Fig. 5.

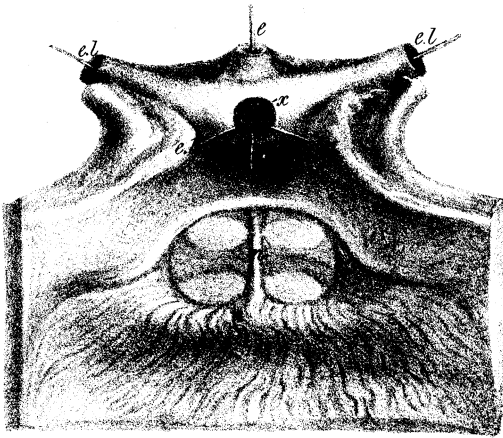
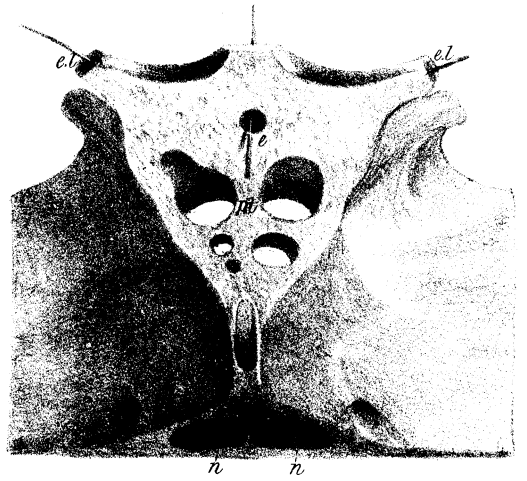


Fig. 6.

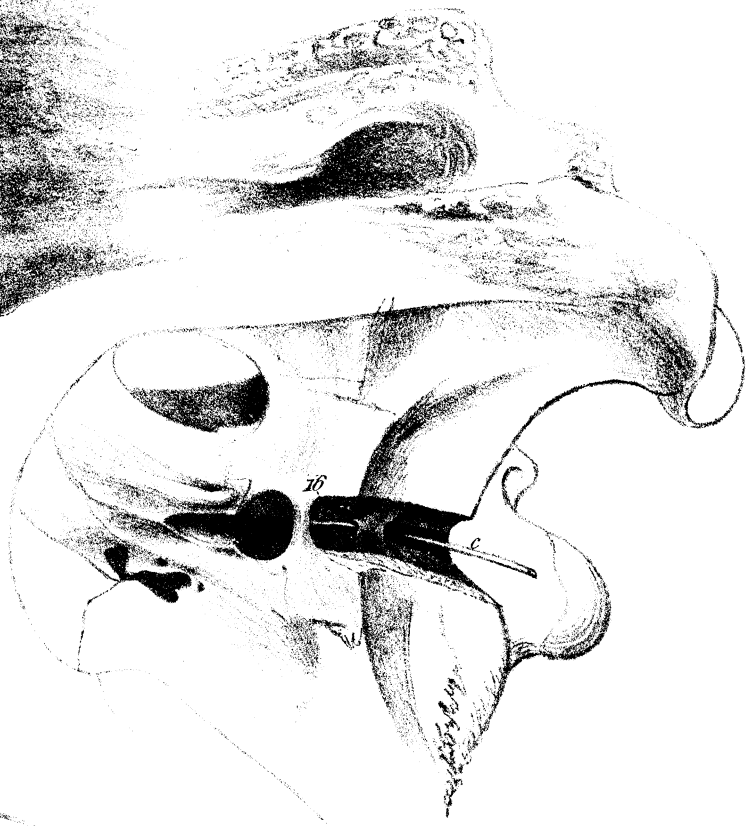


*Alligator lucius*

Fig. 7.



Fig. 4.

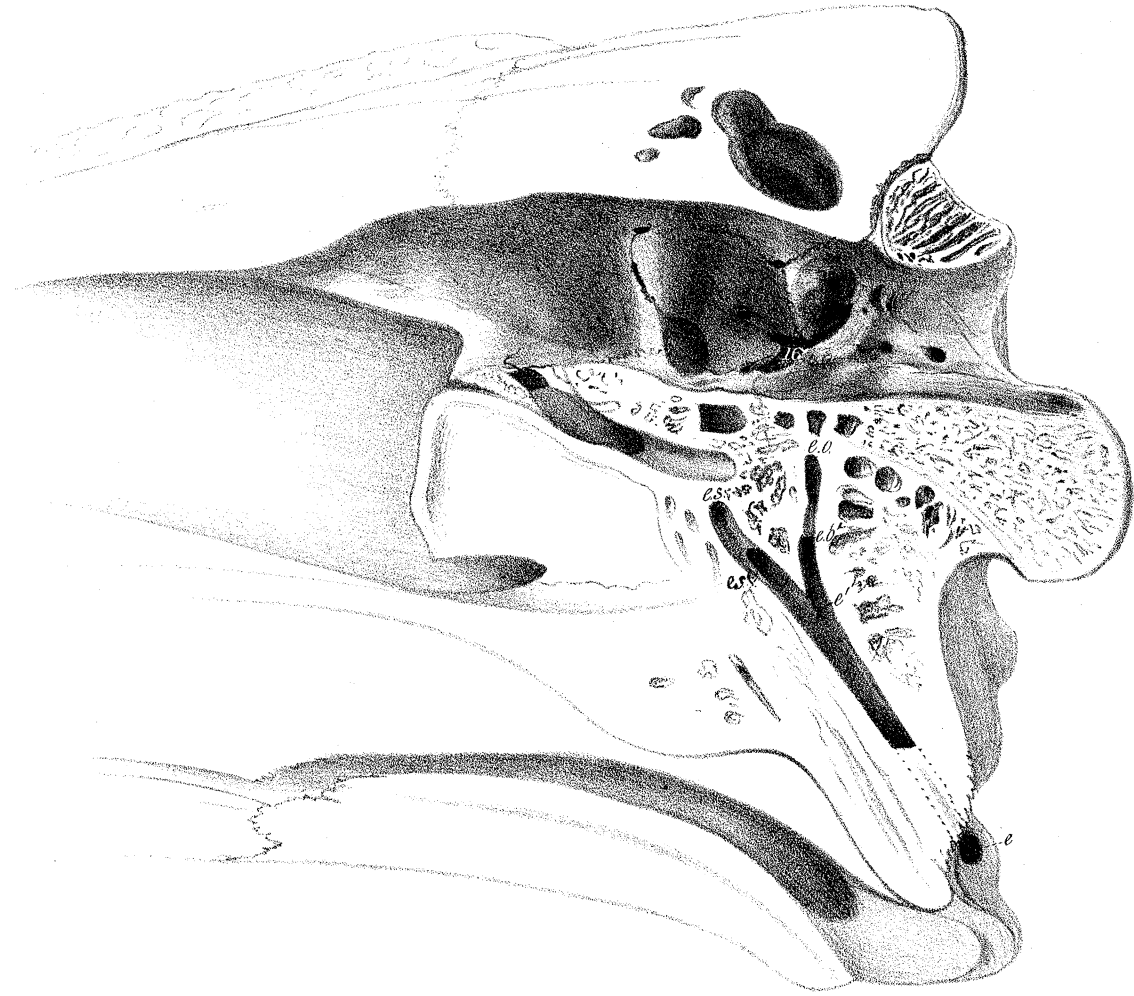


*Crocodilus acutus.*

*Crocodilus biporcatus*



Fig.8.



*Crocodilus biporcatus.*

Fig.10.

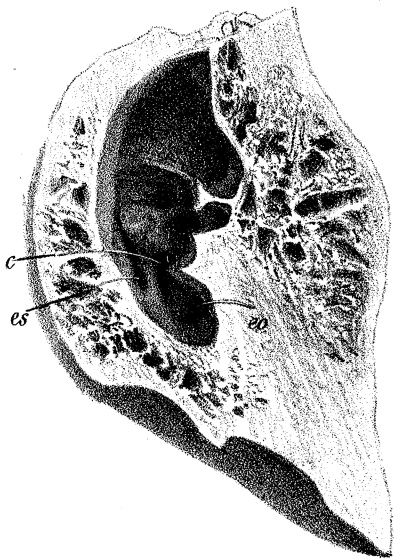
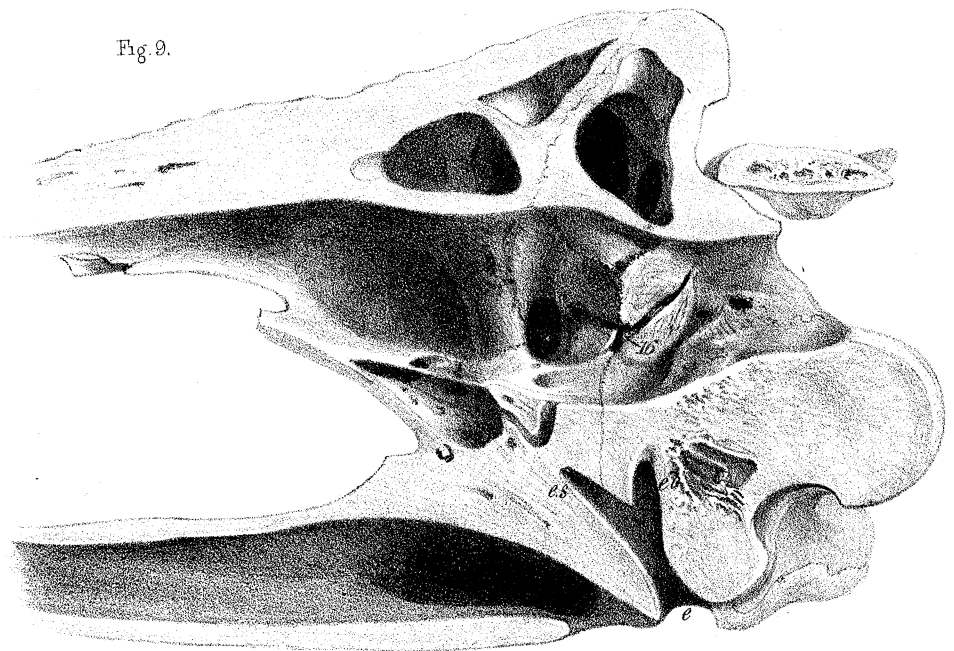


Fig.9.



*Gairalis gangeticus*

Fig. 6. The opposite side of the same section, showing the median bony Eustachian canal, *e*, the lateral membranous Eustachian canals, *el*, cut off where they join the lateral bony canals, and the pterygoid air-cells, *pt*, communicating with the posterior nares, *n, n*.

Fig. 7. A section of the cranium of the *Crocodylus acutus*, showing the course of the median Eustachian canal, *e*, to its bifurcation at *e'*, the division of the basioccipital branch, *e'* to *eo*; the course of the left lateral Eustachian canal, *el'*, to its communication, at the rhomboidal sinus, *eo'*, with the tympanic branch of the basioccipital division of the median Eustachian canal.

#### PLATE XLII.

Fig. 8. A vertical section of the cranium of the *Crocodylus biporcatus*, a little to the left of the median line, showing part of the left tympanic branches, *es, eo*, and the orifices, *es', eo'*, of the right tympanic branches, of the primary divisions of the median canal, *e'* to *e*.

Fig. 9. A vertical median section of the cranium of a Gavial, *Gavialis gangeticus*, showing the basioccipital division, *eo*, and the basisphenoid division, *es*, of the median Eustachian canal, *e*.

Fig. 10. A vertical section of the tympanic cavity of the *Crocodylus biporcatus*, showing bristles inserted into the basioccipital branch, *eo*, and basisphenoid branch, *es*, of the Eustachian tube; *c*, the entry of the entocarotid canal.