THE NASAL CAPSULE IN NATRIX CYCLOPION

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INTRODUCTION

Thus far little work has been done on the chondrocrania of reptilia. More investigations have been made upon fishes and amphibia than on the reptiles, birds and mammals.

Kunkel (1912) on "The Development of the Skull of Emys lutaria" gives a good description of the chondrocranium of this reptile, and includes several plates. Parker (1878) describes the structure and development of the common snake, Tropedonotus Natrix; and again in 1879 discusses in considerable detail the skull of the lizard. Parker gives more attention to the character of the older stages and less to the actual developmental process of the earlier larvae, thus making his contribution of less value to this investigation since he has little concern for the ethmoidal region. Gaupp (1900) describes the chondrocranium of Lacerta agilis, one of the lizards, showing a typical ethmoidal region which in some ways is a repetition of the work of Born (1876) on the nasal organ and the related structures of both the amphibia and certain amniota. Seydel (1896) gave several new facts concerning the nasal capsules.

Higgins (1920) in his work on "The Nasal Organ in Amphibia" figures a capsule of an older Amblystoma which bears a striking resemblance to that of Natrix, as will appear in the sequel.

This paper was undertaken with the idea of ascertaining the relation of the reptiles to the more specialized amphibia as well as to the higher amniota. Natrix cyclopion was selected as the reptilian type; although perhaps not the most primitive, yet it possesses certain characters that relate it to primitive conditions.

The material which forms the basis of this study consists of two embryos of different ages which were secured through the kindness of Prof. L. A. Adams of the University of Illinois. The method of removing the embryos from the females is most satisfactory, for it insures complete identity of the species thus worked upon. The

work was done in the Knox Biological Laboratory, and the writer regrets very much that earlier and later stages were not available so that a more complete study of the development of the capsule could be made.

These embryos, measuring respectively 75mm. and 63mm., have been sectioned and studies made upon the development of the nasal capsules and their relation to the nasal organs. Reconstructions by the Born wax-plate method have been made of these structures in both embryos. Drawings of these models and the sections of the nasal organs have been made showing the relation to the capsule itself.

This work was carried on under the supervision of Dr. G. M. Higgins, to whom the writer is indebted greatly, not only for his invaluable assistance during the preparation of this paper, but also for his inspiring influence.

In the younger of the two embryos, that of 63mm. total length, chondrification is not complete, and the deeper structures of the head are exposed through large gaps in an incomplete chondrocranium. The nasal capsules with which this investigation is primarly concerned, consists in this stage of two curving plates of cartilages, connected to each other in the median line.

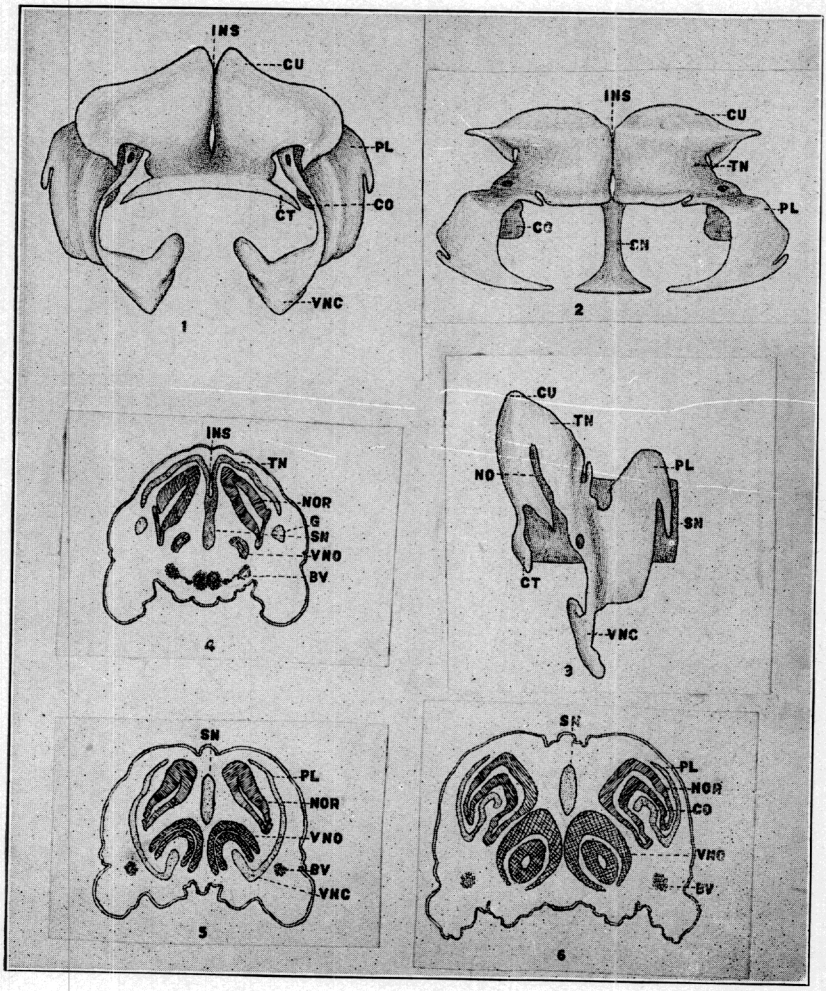
The trabeculae, which form the floor of the chondrocranium in the brain region, unite anteriorly to form a prominent bar of cartilage, the septum nasi, which separates the two nasal organs from each other (Figs. 2, 4). This structure probably represents a prism of the paired trabeculae which form so important a part of the nasal capsules of the amphibia. Anteriorly this septum nasi expands along its ventral margin into a pair of small perpendicular plate-like cartilages, which extend laterally a considerable distance and end in prominent processes ventral to, but in a plane with the external naris (Figs. 1, 3). It would appear that these cartilages are remnants of primitive cornu trabeculae, so prominent in capsules of lower forms, but have lost in the reptiles all association with the nasal organ itself, being considerably ventral and anterior to the nervous structures.

From the anterior third of the dorsal margin of the septum nasi, two curving plates of cartilages, separated

by a narrow internasal space, extend upward a short distance and curve laterally and ventrally to cover the anterior portion of the nasal organ (Figs 1, 2). This structure is a complete cupola and forms the anterior wall of the chondrocranium. It is connected ventrally in front with the dorsal margin of the cornu trabeculae, above described, its upper margin extending laterally a considerable distance to form the anterior wall of the naris (Fig. 1). Lateral to the narial opening, the margin of the cupola extends ventrally and terminates in a prominent process, so that a broad deep notch is included between it and the lateral margin of the cornu trabeculae (Fig. 1).

The roof of the capsule, formed, as above indicated, from the septum nasi and continued anteriorly with the cupola, is known as the tectum nasale (Fig. 2). It continues laterally, and inclining somewhat ventra-posteriorly, is reduced to a narrow plate of cartilage which forms the lateral wall of the capsule in this region. The remaining portion of the lateral wall is continuous with that portion just described, and consists of a broadly curving plate of cartilage, the planum lateralis, which entirely covers the lateral surface of the posterior part of the nasal organ (Figs. 2, 3). Its anterior ventral margin is curved conspicuously and forms a prominent process which lies slightly lateral and considerably below the ventral margin of septum nasi. This process has an intimate relation to the vomero-nasal organ, as shown in Figure 5, and is known by Gaupp as the Capsule of Jacobsen's Organ.

Two large fenestrae occur within the walls of the capsule. Of these one is dorsal, lying back of the posterior margin of tectum nasale between palnum lateralis and septum nasi; while the other is of irregular shape and lies on the floor of the capsule, continuous with the lateral narial aperture (Fig. 3). Thus the nasal organ, of this stage, is exposed upon its entire ventral and posterior dorsal surface. The anterior part of planum lateralis is pierced by a single foramen, through which the profundus branch of the trigeminal nerve passes to the anterior region of the snout.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In the older stage, that of 75mm. total length, chondrification is more advanced. The nasal capsule of this stage consists of two curving plates of cartilages connected in the median line, forming the body of the capsule as in the earlier stage.

The trabeculae, which form the floor of the chondrocranium in the region of the brain as before, unite anteriorly to form the septum nasi, now considerably broader and longer than in the earlier stage (Fig. 8). The cornu trabeculae, which are the anterior expansions of the septum nasi, are more elongate and extend ventrally and somewhat posteriorly, ending in a process ventral but still in a plane with the external naris (Fig. 7).

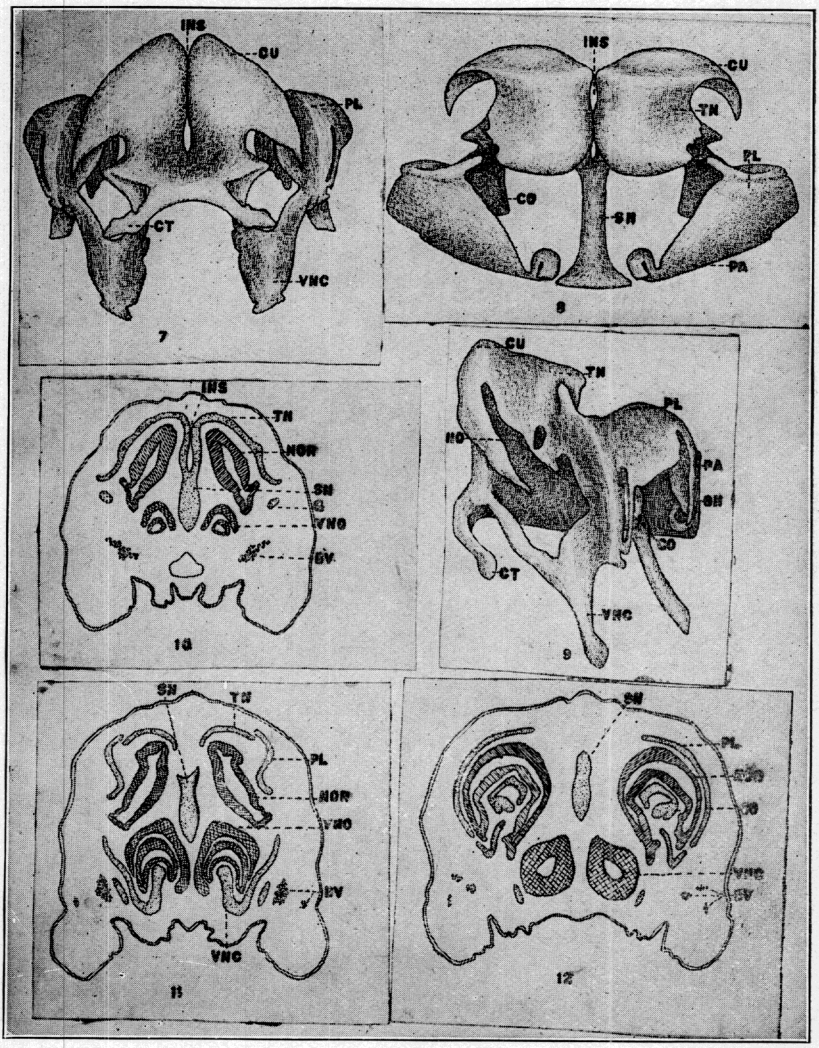
The part of the nasal capsule which covers the anterior portion of the nasal organ is now more curved in appearance. The tectum nasale reaches more posteriorly, and bending ventrally covers a considerable portion of the nasal organ (Figs. 8, 10). Anteriorly, it is continuous with the cupola, as in the younger stage, which forms the anterior covering of the nasal organ, and forms part of the wall of the capsule in this region (Fig. 9). The prominent process formed by the ventral extension of the cupola lateral to the narial opening curves posteriorly, and although ending bluntly here, would in all probability unite with the small lateral process of the tectum nasale to form a complete oval narial fenestra (Fig. 9). Such a fusion has already occurred in the older lizard embryo described by Gaupp, and no doubt is true here as well.

The planum lateralis, which forms the lateral wall of the posterior part of the capsule, becomes more expanded than before, and bending in a median ventral direction, ends in a knob-like process which makes a conspicuous U-shaped bend closely applied to, but not connected with the septum nasi (Figs. 8, 9). This new plate covering the posterior parts of the nasal organ now forms the posterior wall of the nasal capsule, and following the terminology of authors may well be called the planum antorbitale. The lateral and ventral margin of this curved planum antorbitale is conspicuous by three deep indentations, thus giving it a marked serrate appear-

ance. These notches appear to be unrelated to any nervous structure and may simply represent regions of incomplete chondrification.

Anteriorly, in a plane midway to the anterior end of the capsule, this planum lateralis bends abruptly ventrally and forms a vertical plate, extending laterally and ventrally so that the cavum nasi may be said to be roughly divided into two regions, the anterior one related to the cupola and tectum nasale above described, the posterior covered by planum lateralis and antorbitale (Fig. 9). The dorsal margin of this vertical portion of planum lateralis continues medially into a cylindrically shaped process, which as a small beak is inclined anteriorly and is superimposed upon a small enlargement of the posterior margin of tectum nasale (Figs. 8, 9). Thus there is formed between the two a small bay, continuous with the large fenestra in the roof of the capsule. No nervous structures were found to be associated with this bay. Just below this beak-like process, the medial part of the ventral margin of planum lateralis is continued by a broad cartilage plate into the posterior lateral angle of the tectum nasale forming the only cartilage support for the nasal organ in this region. It is pierced, however, by a small foramen, the homologue of a similar opening described in the earlier stage (Fig. 9).

The ventral margin of this vertical plane continues forward into a prominent curved process which lies ventrally, medially and below the plane of the ventral margin of the septum nasi (Fig. 7, 9). Following Gaupp, who figures a similar structure in the skull of the lizard, this process, closely applied to the anterior surface of Jacobsen's organ, as well as the part of it extending into the organ, may be called the vomeronasal capsule (Fig. 11). The vomeronasal capsule arises from the planum lateralis by a narrow arm which widens ventrally and turns posteriorly midway between planum lateralis and the septum nasi, and becomes more elongate and more pronounced than in the earlier stage. From the ventral margin of this capsule a prominent process curves posteriorly and ends in the surrounding tissue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limiting it in this region. It is connected with the cupola by a cylindrically shaped rod which bends medially and laterally, forming an obtuse angle, and uniting with the ventral margin of the cupola at its junction with the cornu trabeculae (Figs. 7, 9).

The ventral half of the planum lateralis, just before it bends to form the anterior vertical plate, is pierced by a long slit-like foramen which appears to be unrelated to any nervous structure and may represent merely an incomplete chondrification here (Figs. 7, 9). On the posterior median surface of this vertical plate is an S-like formation which has just started to form in the younger stage (Figs. 6, 12). This structure is continuous with the planum lateralis. In the older stage a rod-shaped cartilage bar extends from the upper portion of it posteriorly at an angle of 45 degrees to the median line of the skull (Fig. 9). This is unquestionably a nasal concha, and is evidently homologous to that concha shown by Gaupp (1900) in his description of the skull of the lizard.

This description of the development of the nasal capsule of the snake is of considerable interest in itself; but its greater interest lies in the comparisons that exist between it and the other capsules of the reptilian class as well as capsules among the amphibia. In following Kunkel in his description of Emys, it appears that considerable identity of structure exists in the ethmoidal regions. The chondrocranium of the turtle is apparently more compact than that of the snake, although homologous regions may be identified readily. Furthermore, it would appear that considerable similarity exists between the capsules of certain urodeles and this capsule of Natrix cyclopion. To attempt to establish any basis of phylogenetic continuity upon such a resemblance would be unscientific; and yet one cannot fail to note this relationship. In both, the roof of the capsule is pierced by a large rhonmboidal fenestra which appears to be bounded by homologous regions. Similar capsules cap the anterior end of each organ, and similar internasal spaces separate the two.

The special attention of the writer is drawn to that portion of the capsule which forms the posterior wall. In the work of Higgins (1920) the term planum tectale is used to designate that same portion of the capsule which Gaupp in his discussion of the lizard has called planum antorbitale, a term continued in use throughout this discussion. Regarding the use of the term antorbitale, the writer recalls the fact that in all the nasal capsules of the amphibia, where the facts are known, the antorbital process arises from the trabecula as a lateral diverticulum just posterior to the choana. Subsequently this structure unites with other portions of the capsule to form this posterior wall. In the reptiles there is no association between these two regions, and it would seem that the structure known as planum antorbitale could not have arisen as a normal antorbital process, and consequently the use of this term is questioned.

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EXPLANATION OF PLATES.

Fig. 1. Anterior view of model of nasal capsule of Natrix cyclopion, 63 mm. ×58.

Fig. 2. Dorsal view of model of nasal capsule of Natrix cyclopion, 63 mm. ×58.

Fig. 3. Lateral view of model of nasal capsule of Natrix cyclopion, 63 mm. ×58.

Fig. 4. Cross section through tectum nasale of Natrix cyclopion, 63 mm. ×35.

Fig. 5. Cross section through vomeronasal capsule of Natrix cyclopion, 63 mm. ×35.

Fig. 6. Cross section through nasal concha of Natrix cyclopion, 63 mm. ×35.

Fig. 7. Anterior view of model of nasal capsule of Natrix cyclopion, 75 mm. ×58.

Fig. 8. Dorsal view of model of nasal capsule of Natrix cyclopion, 75 mm. ×58.

Fig. 9. Lateral view of model of nasal capsule of Natrix cyclopion, 75 mm. ×58.

Fig. 10. Cross section through tectum nasale of Natrix cyclopion, 75 mm. ×35.

Fig. 11. Cross section through vomeronasal capsule of Natrix cyclopion, 75 mm. ×35.

Fig. 12. Cross section through nasal concha of Natrix cyclopion, 75 mm. ×35.

BV Blood vessel
CO Nasal concha
CT Cornu trabecula
CU Cupola
G Gland
INS Internasal space
NO Narial Opening
NOR Nasal Organ
PA Planum Antorbitale
PL Planum Lateralis
SN Septum nasi
TN Tectum Nasale
VNC Vomeronasal capsule
VNO Vomeronasal organ