THE NASAL CAPSULE IN BUFO AMERICANA

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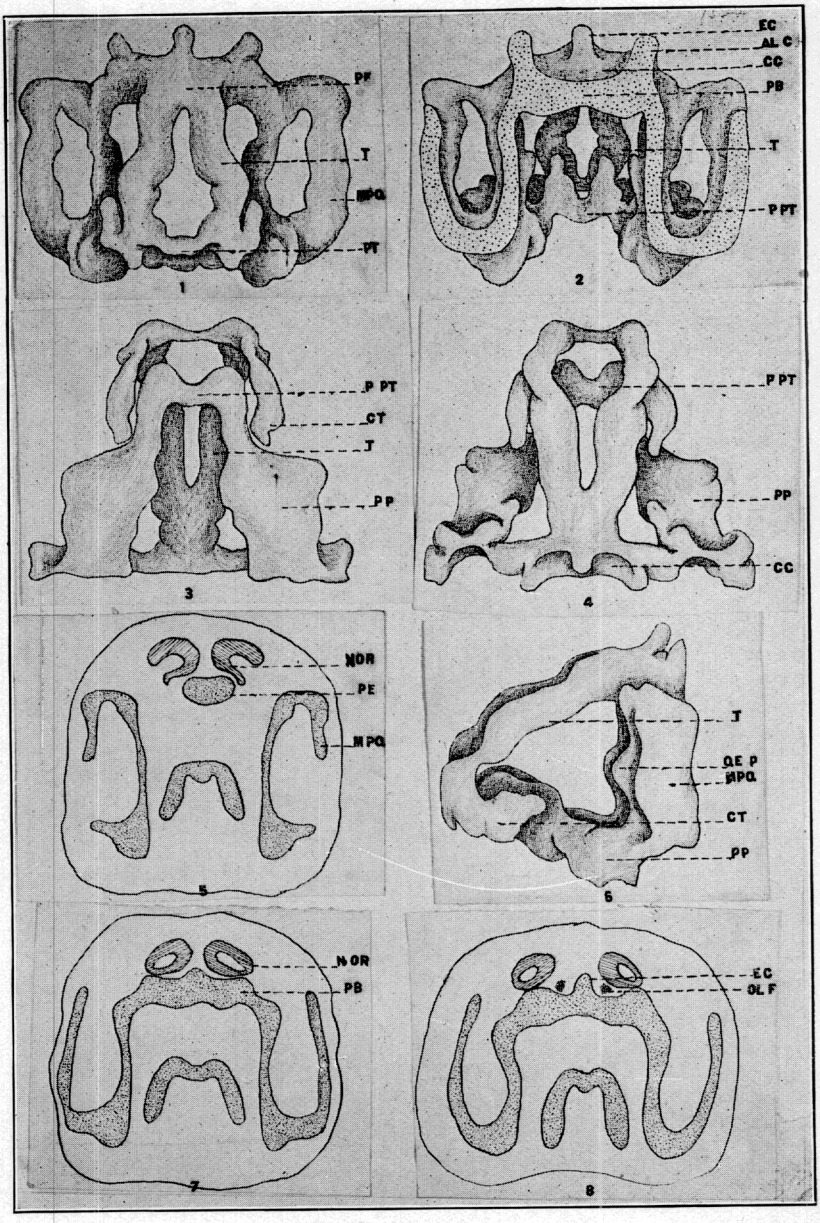
INTRODUCTION

The literature up to the present time on the development of the chondrocranium of fishes and amphibia is considerable. More work, however, has been done upon the latter class of vertebrates, the Urodeles and the Anura especially.

The first adequate account of the development of the skull in the Anura was given by Parker in a paper published in 1871. This paper, with three others published in 1876, 1877, and 1881, fail to give any very detailed account of the process of chondrification. Born (1876) describes in detail the chondrification of the skull in Triton cristatus, and Stőhr (1879) also describes this process in Triton. Terry (1906) compares the process of chondrification in Amblystoma with that of Triton, finding that the two agree closely. Gaupp (1893) gives a thorough-going detailed study of the skull of Rana fusca.

Most of the work on the developing chondrocranium of amphibia has been made on the later stages, rather than upon the early larvae. Considerable work has been done upon the earlier stages of Rana, but a less amount of intimate detail is available for use on the early chondrification of the toad. Later stages have been described by Higgins (1920); but nothing is known of the early process of chondrification in this order. Since such knowledge is indispensable to a complete understanding of the proper system of classification, the writer approached this study of the toad to determine if possible what light, if any, the study of the nasal organ would shed on this problem of relations drawn from previous workers on classifications of the Anura.

This work has been done in the Biological department, Knox College, upon Bufo americana (the common toad) which is very abundant in this region. The material used for study was fixed in Bouin's fluid, washed, dehydrated, sectioned, mounted, and stained with Delafields haematoxylin and eosin. A model was made after the Born wax-plate method and then studied. Drawings of the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capsule have been made; also drawings of the nasal organs, showing the relation of the organs to the capsule.

The study of the nasal capsule was undertaken upon the suggestion of Dr. G. M. Higgins, to whom the writer is indebted greatly, not only for the supervision and helpful suggestions of the work and the preparation of this paper, but also for the material used.

In a single toad larva, 14mm. total length, which has formed the basis of this study, a completely chondrified nasal capsule has not yet developed. Several structures, however, are already formed so that satisfactory comparisons may be made, not only with the older stages previously described, but with the capsules of corresponding stages of Rana.

The cavum cranii (CC), the cavity containing the brain, is only partially formed, so that the nasal cavity is practically continuous with that of the brain. The floor of the brain case in its anterior part is formed by a rather thick cartilage plate, the planum basale (PB), which is continuous laterally with the lower margin of the alisphenoid cartilages (AL C).

From the median line of the planum basale, just anterior to the telencephalon, a small cylindrical process extends dorsally (Fig. 2) a short distance, to end in the mesenchymatous tissue above. This is the beginning of the posterior wall of the nasal capsule, and is ultimately to separate the nasal cavity from the cavum cranii. It is quite evident that this process, the ethmoidal column (EC), is the first appearance of that structure later known as the pons ethmoidalis, which connects the dorsal margin of the alisphenoids just anterior to the brain.

Anterior to the ethmoidal column, the planum basale continues into that cartilage plate which forms the Planum ethmoidalis (PE, Fig. 1). This structure, more narrow along its posterior part, gradually increases in its lateral dimension and forms a trapezoid whose anterior margin exceeds the length of the posterior by one third. The medial and posterior portions of each nasal organ rest lightly upon the corresponding lateral surfaces of this planum (N OR, Fig. 5), but the larger part of the organ lies above and lateral to it. This portion of the

capsule, relatively small at this stage, forms in the later larva the entire floor, and supports the nasal organs as well as the nasal glands found within the cavity.

At the anterior end of the nasal organ the planum ethmoidalis bifurcates, forming the cylindrically flattened trabeculae (T, Figs. 1, 6), which diverge forward, pointing ventrally in the mouth region. The trabeculae, although separated throughout their entire length by a triangular internasal space, are joined distally by a cartilaginous plate, the pons trabeculae (PT, Fig. 1). At the region of the junction of the pons, each trabecula curves ventrally for a short distance, and then by a broad curve forms a prominent corna trabeculae (CT, Fig. 6), which ends in a small posteriorly directed process closely applied to the pterygoid cartilage of the upper jaw. Contrary to the usual position of the cornu trabeculae of the Urodeles, each cornu of the toad is directed ventrally and posteriorly instead of laterally, although the general shape of these structures is quite identical in these groups. A further contrast is to be noted in the relation of the nasal organs to the cornua. In the Urodeles the external naris is terminal and the anterior portion of the nasal organ lies directly upon the cornu trabeculae which thus supports it. In the toad, on the other hand, the narial aperture is more dorsal and considerably back from these anterior parts of the capsule, so that here there is no intimate association between the nasal sac and the cornu. Later, however, it is probably true that as development ensues, each cornu forms an integral part of the capsule, and as the nasal organ assumes greater proportions comes to rest upon it.

Although not definitely a part of the nasal capsule, yet rather intimately connected with it in the earlier larval stages is a prominent curved plate of cartilage connected with the anterior margin of the planum basale at its junction with the alisphenoid cartilage. This is the muscularis process of the quadrate (MPQ, Figs. 1, 6) which in the earlier stages is attached to the anterior portion of the chondrocranium, but later migrates posteriorly and at metamorphosis takes its position in relation to the suspension of the jaws. This structure is

strikingly U-shaped in section (Figs. 7, 8), the other limb being entirely free from the inner except at the anterior margin where both limbs are joined dorsally by a small bar of cartilage. This small cartilage is absent from the skull of Rana, where the limbs of this muscularis process are entirely free from each other except ventrally, where even as in this stage of Bufo they are joined to continue forward to a prominent pterygoid process. The anterior margin of the inner limb of the musculars process bears a prominent round structure which, although lacking any reference to the nasal organ as such, is known as the quadrato-ethmoidalis process, and corresponds with a similar region in the frog (QEP, Fig. 6).

Continuing forward from the anterior ventral surface of the muscularis of the quadrate is a broad band of cartilage, the pterygoid process (PP, Fig. 6). Each pterygoid continues forward to the position of the mouth and joins its mate at a point considerably posterior to the pons trabeculae, above described, and in a manner similar to it, thus forming the pons pterygoidii (PPT, Figs. 2, 3). In its posterior part each pterygoid is conspicuously broad; approximately flat on its upper surface, but possessed of a conspicuous keel on its lower. Just anterior to this broad portion each pterygoid bends abruptly toward the median line and expands into a prominent vertical plate which extends dorsally to a point just below the vertical margin of the trabecula. This portion of the pterygoid (Figs. 3, 6) is conspicuously concave on its external surface, and lies just within the expanded cornu trabeculae, the inner surface of which is markedly convex, so that there comes to be formed a conspicuous oval fenestra between these portions of the capsule. Thus it is evident that the anterior portion of the capsule, consisting of trabeculae, pons and cornua, form a hood-like structure which fits over the anterior portions of the pterygoids and the pons, uniting them (Fig. 3).

As we contrast this nasal capsule, just described, with that of the older toad at the time of metamorphosis, it is quite easy to recognize the changes that have taken place in the transformation. These changes concern only those portions definitely related to the nasal organ, and thus

involve planum basale, ethmoidal column, planum ethmoidalis, the trabeculae and the cornua.

In the adult the nasal organs are entirely separated from each other as well as from cavum cranii by thick cartilage walls, pierced only by foramina for the olfactory nerves. Contrasting the two capsules, it is easy to see that the median vertical plate, the planum verticale, which separates the two nasal organs is but an anterior-dorsal chondrification of the ethmoidal column along the median line of the planum ethmoidalis. At the same time it is evident further that the posterior wall of the nasal capsule, separating the cavum nasi from the cavum cranii, has arisen by a chondrification dorsally of the planum basale, coupled with certain contributions from the alisphenoids, in the transverse plane of the ethmoidal column. In my single stage, although not mentioned in the section describing the capsule, the olfactory nerve passes anteriorly from the telencephalon through the wide notch between the ethmoidal column and the alisphenoid cartilage (Fig. 8, OLF). Later, as chondrification advances, cartilage layers form around this nerve, so that in the adult the olfactory nerves are found to pierce this posterior wall of the capsule, passing thence to the various parts of the nasal organ.

The floor of the nasal capsule of the older toad is considerably larger than the planum ethmoidalis of this stage, and it would appear that it has been formed by a further fusion of the trabeculae forward to the region of the cornua. No trabeculae as such are identified in the older stage, and it follows that they have lost their identity in the formation of the complex anterior part of the older capsule. The floor is wider than before so that a large portion of the nasal organ now rests upon it, giving it support, as well as additional protection. Anteriorly the cornua trabeculae persist even into the adult stage, where they take a more lateral direction and form what are known as the alinasal cartilages which support the anterior part of the nasal organ and form the floor of the external naris.

There remains for consideration the roof of the older stage, and if we may accept the evidence of such types

as Hyla, the tree toad and the earlier stages of Rana, as described by Gaupp, a conclusion entirely warranted, it would appear that the roof of the capsule is but a lateral chondrification of the dorsal margin of the planum verticale. So the entire roof of the capsule, as well as the planum verticale, above described, is but a further chrondrification of the single median ethmoidal column of the earlier larval stage, together with certain additions from the planum ethmoidalis.

The foregoing comparison shows that there is a definite relationship between the younger and the later stages. It was found that the two trabeculae, separated by the internasal space in the younger embryo, were united, later forming the floor of the capsule in the older one. The planum basale, here as well as in the earlier stage, forms the floor of the cavum cranii; also the cornua remain, but have assumed a different position.

It follows that the nasal capsule of the younger toad is but a further development of those structures appearing in my earlier larva. Development is a continuous process, and in the final result a more specialized but reduced capsule is attained.

According to the zoological classification of Amphibia, this class is divided into four orders: Anura, Urodela, Gymnophiona, and Stegocephala. This paper is concerned only with that class Anura and its subdivisions, and upon the evidence of the nasal capsule it would appear that the existing order of Amphibian classification is entirely supported by this investigation.

EXPLANATION OF PLATE.

Fig. 1. Anterior view of model of nasal capsule of Bufo americana, 14 mm. total length. ×54.
Fig. 2. Posterior view of same model.
Fig. 3. Ventral view of same model.
Fig. 4. Dorsal view of same model.
Fig. 5. Transverse section through posterior part of nasal capsule.
Fig. 6. Lateral view of model of Fig. 1.
Fig. 7. Transverse section through planum basale and muscularis process of the quadrate.
Fig. 8. Transverse section through planum basale and olfactory nerve.

ALC Alisphenoid cartilage
CC Cavum cranii
CT Cornu trabeculae
EC Ethmoidal column
MPQ Muscularis process of the quadrate
NOR Nasal organ
OLF Olfactory nerve
PE Planum ethmoidalis
PB Planum basale
PP Pterygoid process
PPT Pons pterygoidei
PT Pons trabeculae
QEP Quadrato-ethmoidalis process
T Trabecula