THE MORPHOLOGY OF THE ANTORBITAL PROCESS IN THE URODELES *

GEO. M. HIGGINS, UNIVERSITY OF ILLINOIS

In the development of the chondrocrania of almost all Urodeles a small process arises from the lower margin of the trabecula, just in front of the eye. In the early stages of Amblystoma punctatum, where the details of development have been followed more closely, this structure first appears in a larva about 25 mm. long, in which a small cartilage bar develops laterally from the trabecula, considerably back of the choana. This structure has usually been designated the antorbital process, a term most appropriate from the standpoint of its position, and one used throughout this discussion.

Before the antorbital process has appeared, a nasal capsule has begun to develop; first, by the indepedent chondrification of an ethmoidal column, which develops from in front backward, and comes to lie along the median dorsal surface of the nasal sac. Later this column unites to the cornu trabeculae in front and the crista trabeculae behind; and, at about the time that the antorbital process begins to develop from the trabecula, a cartilage bar chondrifies laterally from the posterior end of the columna ethmoidalis, partially covering the nasal sac at the choana. By a further growth, this bar expands laterally, anteriorly and posteriorly into a broad plate of cartilage, which, covering the nasal organ, forms the roof of the capsule. Earlier writers on the chondrocranium of the Ichthyopsida (Winslow, 1898; Terry 1906) speak of this plate as the lamina cribosa, a rather inappropriate term, for it is evident that this structure

* Contributions from the Zoological Laboratory of the University of Illinois, No. 163.

can not be the homologue of the cribiform plate of mammalian anatomy, since the olfactory nerve does not pass through any portion of it. Accordingly it would seem that the term planum tectale would more adequately express the function and the position of this cartilage.

In the younger stages of Amblystoma, the antorbital process and the planum tectale are far removed from each other, the former having no association whatsoever with the nasal region. During later development, however, the distal part of the antorbital grows forward, while the base of the tectale extends farther backward, so that in a larva 34 mm. long, these structures have come to lie very close to each other. During the later larval period, the cornu trabeculae, which supports the anterior parts of the nasal organ, extends backward toward the antorbital and the tectale; and, in a larva at the end of metamorphosis, these structures have all united to form the lateral and the posterior walls of the nasal capsule.

It is evident, therefore, that the antorbital process, although having its origin some distance back of the nasal region, is destined to become with the planum tectale, the posterior wall of the nasal capsule, which is pierced by a single opening, the foramen orbito-nasalis, through which the branches of the fifth nerve pass to the olfactory organ.

Considerable diversity of opinion has existed in the past, in regard to the homology of this cartilage bar, which arises from the trabecula considerably back of the nasal region, but later becomes a part of the posterior wall of the nasal capsule. Throughout the literature, the terms palatine cartilage and antorbital process are used interchangeably in its designation, the latter possibly being more commonly employed; while Parker, in a series of extensively illustrated papers on the skull of the Anura and Urodela has employed the term ethmo-palatine. Gaupp (1893), in his work on the chondrocranium of Rana fusca, held that the antorbital process of the Urodeles is homologous with the pterygoquadrate arch of the Anura; and he uses the terms "Antorbitalfort-

satz" and "Cartilago palatina" with reference to the same structure. It may be remarked parenthetically, that the terms palatine cartilage or palato-quadrate arch, frequently applied to the pterygoquadrate is incorrect, as it contains no palatal element, and no part of the palatine bone is derived from it.

In the development of the chondrocranium of Cryptobranchus alleghaniensis, possibly a more primitive Urodele, some light is shed upon the history of this antorbital process. In a larva, two weeks after hatching, when the cristae trabeculorum are already well-developed there is no evidence of a developing antorbital. Slightly posterior, however, to the position of its probable appearance, procartilage cells have formed in the surrounding tissue, lateral to the trabecula; and these cells continue posteriorly into the anterior end of the pterygoquadrate, extending forward from the hinge of the lower jaw. In a larva five weeks old, these procartilage cells have chondrified; the pterygoquadrate now reaches farther forward, and unites to the side of the trabecula in the position from which the antorbital process normally develops in other Urodeles. In this stage, there is no extension forward of a cartilage bar from the junction of the pterygoid with the trabecula; but in a larva three months after hatching, a small process reaches forward from the end of the pterygoquadrate toward the nasal capsule, and an antorbital process has assumed proportions similar to that in Amblystoma. My oldest larva of Cryptobranchus does not show any connection between the antorbital process and the nasal capsule; it is probable, however, that in a later stage these parts would be united, for the nervous supply and the associated cartilages are similar to those in Amblystoma.

In no other Urodele, as far as I have been able to discover, with the single exception of the Siberian genus Ranodon (Wiedersheim, 1876; fig. 69) is there a similar connection of the pterygoquadrate with the anterior part of the skull. In a larva of Spelerpes fuscus (Wiedersheim, 1876; fig. 108) there is a cartilage bar directed posteriorly from the nasal capsule toward the pterygo-

quadrate, which has been called the maxillary process; and the proximity of these two structures would suggest an earlier continuity between them. Elsewhere in all described Urodeles, the extent of the pterygoquadrate forward from the quadrate is variable throughout the order; and in the adult Cryptobranchus (and this holds true for the Japanese japonicus, as figured by Parker, 1876) the connection between the pterygoid and the structures farther forward is lost. In the chondrocranium of Epicrium glutinosum, the blind caecilian of the tropics, the pterygoid process reaches well forward toward the nasal region; and the proximity of the antorbital to the pterygoid suggests that here, as in some of the Urodeles, these structures may have been at one time more closely related.

In all of the Anura, on the other hand, the pterygoquadrate arch is connected throughout life with the posterior wall of the nasal capsule. In this respect, Ranodon and Cryptobranchus more closely approach the Anura than any other Urodele; for in the remainder of the group, there is no connection of the pterygoquadrate with the anterior part of the cranium.

It is usual to regard the pterygoquadrate arch of the Anura as the homologue of the upper jaw of the Elasmobranch, which, with the development of the osseous upper jaw of the higher groups has lost its original function as part of the feeding apparatus, and has fused with the cranium, thus contributing toward the posterior wall of the nasal capsule. In the chondrocranium of the Elasmobranch, there is no anterior extension of the pterygoquadrate beyond the curve of the upper jaw, to form any integral part of the nasal capsule; but in all of the Anura, as far as I know, the side wall of the capsule is apparently a continuation forward of the pterygoid, beyond its connection with the cranium. In Pipa americana, a small triangular cartilage plate, the ethmo-palatine of Parker, continues forward from the pterygoid and partially covvers the caudal parts of the nasal organ; while in Bufo and Rana, the side wall of the capsule, better designated

the lamina externa, is likewise continuous with the anterior end of the pterygoquadrate.

In Cryptobranchus, then, these relationships between the pterygoid and the nasal capsule, as found in the Anura, are carried over into the Urodela; and it would seem that the antorbital process, the pterygoid and the planum tectale of the Urodela may be readily homologized with these structures in the Anura. That being true, it would apparently follow that the antorbital process in Cryptobranchus and perhaps in all Urodeles, is, at least in its basal part, derived from the anterior part of the pterygoquadrate arch; while the more distal portion which must be the homologue of the lamina externa of the Anura, may be a new formation. It may be remarked, that in both the Anura and the Urodeles, the antorbital process unites with the cornu trabeculae, a structure clearly homologous throughout the class Amphibia, thus furnishing a further clue to its relationships.

In the early stages of the chondrocranium of Salamandra maculata, a Urodele in which the pterygoquadrate does not reach forward into the nasal region, the antorbital process arises from the trabecula much as in Amblystoma. During its development, the planum tectale, which forms the roof of the nasal capsule, develops laterally from the posterior end of the columna ethmoidalis; and, curving ventrally, covers the posterior and lateral parts of the nasal organ. In a larva, 38 mm. long, the anterior end of the distal part of the antorbital, which has developed forward toward the capsule, has come to lie just beneath and slightly posterior to the lateral margin of the planum tectale; so that these two structures are separated by a wide gap, through which the ophthalmicus and the superficialis branches of the fifth nerve pass to the nasal organ. Thus the antorbital process is ventral to these nerves. In all Urodeles, with the exception of Necturus and Amphiuma, in which the antorbital process does not unite to the structures farther forward, and probably in the later stages of Salamandra, this wide gap is reduced to an orbito-nasal foramen, which

pierces the posterior wall of the nasal capsule and conducts the rami of the fifth nerve into the nasal cavity. In the chondrocranium of Bufo americana, these same nerves pierce the posterior wall of the capsule just above the pterygoquadrate, where it joins the cranium; the same is true in Rana and Pipa, although in the latter, some modifications in the capsule have occurred, making the comparisons to the Phaneroglossa more remote. Since it is customary to regard nerves and their distribution as sufficient criteria for the determination of homologous structures, it would apparently follow that the orbito-nasalis foramen has been reduced from the large gap between the planum tectale and the antorbital process; and that these foramina in the Urodeles and the Anura occur in homologous parts. Accordingly that portion of the posterior wall of the nasal capsule dorsal to these nerves must be a derivative from the planum tectale, while the cartilage immediately beneath them is as clearly antorbital in origin, or in the Anura and Cryptobranchus clearly pterygoidal.

SUMMARY

The antorbital process of the Urodela arises from the lower margin of the trabecula, considerably back of the choana; during the later stages it unites with the structures farther forward, and forms a part of the posterior wall of the nasal capsule. In Cryptobranchus alleghaniensis the pterygoquadrate arch joins the side of the trabecula in the position from which the antorbital normally develops in other Urodela; and in this respect Cryptobranchus more closely approaches the Anura, in which the junction of the pterygoquadrate to the cranium is the characteristic condition.

The rami of the fifth nerve pass into the nasal capsules of the Urodela through an orbito-nasal foramen, dorsal to the antorbital process; while in the Anura, these same nerves pass through a foramen just above the pterygoid process, where it joins the cranium. That part of the posterior wall of the nasal capsule in the Urodela, ventral to these nerves is clearly antorbital;

while in the Anura, this ventral portion is as clearly pterygoid.

The basal part of the antorbital process in Cryptobranchus, and possibly in all Urodeles is derived from the pterygoquadrate arch, and is homologous with the anterior part of this arch in the Anura.

BIBLIOGRAPHY

Gaupp, E.

1893. Beitrage zur Morphologie des Schadels. Primordial-cranium und Kieferbogen von Rana fusca. Morph. Arbeiten, 2:275-480, 4pl.

Parker, W. K.

1876. On the structure and development of the skull in the Urodelous Amphibia. Trans. Zool. Soc., London, 11:171-214.

1881. On the structure and development of the skull in the Batrachia. Phil. Trans. Roy. Soc. London, 172:266, 44pl.

Terry, R. J.

1906. The nasal skeleton of Amblystoma punctatum. Trans. Acad. Science, St. Louis, 16:95-124, 4pl.

Wiedersheim, R.

1877. Das Kopfskelet der Urodelen. Morph. Jahrb., 3:352-448; 459-548.

Winslow, Guy M.

1898. The chondrocranium in the Ichthyopsida. Tufts Coll. Studies, 1:147-201, 4pl.