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A STUDY OF THE DEVELOPMENT OF THE NOSE
AND ITS ACCESSORY CAVITIES.*

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This paper must be considered as only a preliminary one, for the field is so broad that the author has been unable to cover it exhaustively.

The primary origin of the olfactory organ is not well understood: possibly it may have arisen by a modification of primitive integumentary sense organs.

In its simplest form the olfactory organ consists of two pit-like depressions of the integument of the snout opening on the surface by external nostrils. It is lined by an epithelium which is connected with the brain by the olfactory nerves. The olfactory organs of all the true fishes consist of sack-like depressions which do not communicate with the mouth. In the course of development each external nostril is divided by a fold of skin into two openings, thus forming an anterior and posterior nostril.

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Dipnoi are fishes which resemble amphibia in several ways. They live in shallow streams and bury themselves in the mud during the dry season. The air bladder is converted into a functional lung and the nasal cavities communicate with the mouth as well as with the exterior. In consequence of this, anterior or external, and posterior or internal nostrils (choanae) can be distinguished and a free passage is thus formed through which air passes and the olfactory organ takes on an important relation to the respiratory apparatus.

In amphibia the structure of the olfactory organ becomes modified in correspondence with the change in the mode of respiration. The nasal chambers become differentiated into an olfactory and respiratory portion and an extension of the olfactory surface takes place by the formation of one or more prominences on the floor and side walls of the nasal cavities. These prominences correspond to the turbinals of higher forms

Glands, situated under the olfactory mucous membrane, can now be found, and the secretion from these glands moistens the mucous membrane of the nasal cavity.

In reptiles, owing to the growth of the brain and facial region and the formation of a secondary palate, the olfactory organs from reptiles onward gradually come to be situated more ventrally beneath the cranium.

The secondary palate is formed by the pterygopalatine arch and is well developed in all reptiles. In snakes and lizards this arch is more or less movable and free from the base of the skull, but in crocodiles it meets with its fellow in the median line, and the shelf-like palatine processes of the superior maxillary bones unite with the palatines. Thus a secondary roof is formed to the mouth, distinct from the true (sphenoidal) base of the skull. The cavity thus formed closes in the posterior prolongation of the nasal chambers which consequently becomes sharply differentiated from the mouth and the posterior nares open farther back into the pharynx or nasopharynx instead of the mouth.

In birds there is an anterior nasal chamber, lined by stratified epithelium, and an olfactory chamber situated above and posterior to the former. The olfactory chamber contains the ethmoidal turbinal, the form of which varies greatly. It

may be simply a prominence or more or less rolled upon itself.

Corresponding to the much more marked development of the facial portion of the skull, the nasal cavity of mammals is much larger and there is a more extensive development of the turbinals.

The turbinals become very complicated and form a sponge-like labyrinth, the cell-like compartments of which are lined throughout with mucous membrane. The number of olfactory turbinals varies considerably, but in most mammals there are at least five. These olfactory turbinals are generally described as ethmoidal turbinals because they are usually supported by the ethmoid bone. The turbinal of lower vertebrates corresponds to the maxillary turbinal in mammals situated in the lower or anterior part of each nasal chamber and supported by the superior maxillary bone.

The maxillary turbinal in mammals no longer possesses an olfactory epithelium and in microsmatic mammals (seals, whales, monkeys and man), the lower portion of the ethmoidal turbinal also loses its olfactory epithelium. This change in the mucous membrane of this portion of the nose corresponds to the change in function, for its principal function now is to clean, warm and moisten the inspired air.

The author wishes here to acknowledge his indebtedness to Dr. Robert Wiedersheim's book "Comparative Anatomy of Vertebrates," from which the statements above have been compiled. With this description of the development of the olfactory organ as a guide, let us study some members of the different classes of vertebrates more carefully.

FISH. The olfactory organ in the Lake Erie white fish is composed of two symmetrical cavities situated in the anterior part of the head and separated from each other by a thick septum.

Each cavity is somewhat hemispherical in shape and communicates with the exterior by two small round openings in the roof of the cavity. These openings are situated one behind the other and so may be designated as anterior and posterior nostrils.

The external wall and floor of each cavity is smooth, but the median wall (septum) supports a rounded prominence.

from which radiating processes extend into the nasal cavity (Plate I, 3). These processes correspond to the turbinals in higher vertebrates. The two nostrils open just above these processes and thus allow a free circulation of water through the cavity (Plate I, 1 and 2).

The nasal cavity is separated from the mouth by a rather thick wall, but in the posterior inferior part of the cavity there is a slight depression extending downward toward the mouth (Plate I, 5).

TURTLE. The olfactory organ in the turtle consists of two symmetrical cavities separated from each other by a thick septum. The respiratory part of each nasal fossa is a tube-like structure extending downward and backward and opening into the anterior part of the mouth (Plate II., Figure A, 1 and 4). The olfactory region is a spherical chamber situated above the respiratory region with which it communicates by an oval opening in its floor. (Plate II. and IV., Fig. A and D, 3). Projecting into each fossa, from the lateral walls, there are two prominences (Plate II. and IV., Fig. A and D, 11) which correspond to the turbinals in higher forms. These prominences form the anterior and inferior boundaries of the olfactory region. The anterior prominence extends downward across the nasal fossa and unites with the septum, thus partially subdividing the respiratory region into an anterior and posterior portion.

DUCK. The nasal fossae in the duck are two symmetrical cavities which communicate with each other at their anterior and posterior extremities, the septum being incomplete at these points.

The maxillary turbinal is shaped like an inverted T, attached to the roof of the nasal chamber and is suggestive of the turbinal with a double coil seen in higher forms of vertebrates (Plate V. and VI., Fig. A, B and C, 1).

There are two ethmoidal turbinals. The anterior inferior one (Plate V. and VI., Fig. A, E, F. and G, 2) is a double coil of which the superior coil curves upward describing nearly a complete circle; the inferior coil is scroll-shaped making two turns within itself (Plate V. and VI., Fig. G, 2).

The superior ethmoidal turbinal is a simple structure (Plate III, Figures A and G, 3), consisting of a rounded prominence from which two irregular processes extend downward into the nasal fossa.

There are no accessory sinuses of the nose but in addition to the numerous small air cells the greater part of each superior maxillary bone is occupied by a large air cell (Plate V. and VI, Figures F and G, 10). These air cells, like the

other pneumatic cells in the bird's skeleton, make the bones lighter in weight.

Dog. The dog's nose is a very complicated structure. The maxillary turbinal is attached to the superior maxillary bone by a single shelf-like process which is much broader at its posterior than at its anterior end. From this process, numerous curved branches are given off, which form an intricate labyrinth almost completely filling the anterior part of each nasal fossa. (Plates VII, VIII, IX and X, Fig. A, B, C, D, and E, 1).

The ethmoidal turbinal is an exceedingly complex structure. It consists of a mass of thin delicate scrolls of which at least five radiate from the convex surface of the cribriform plate. It articulates with and is supported by the sphenoidal, frontal, nasal and superior maxillary bones and *some of its numerous branches extend into all the accessory cavities of the nose.* (Plates VI. to X. Fig. A, B, C, D, E, F, G and H, 2). One scroll extends forward over the maxillary turbinal and anteriorly it is supported by *a process which is attached to the external lateral wall of the maxillary sinus.* (Plates VII. to X., Fig. B, C, D, F and G, 12).

The ethmoidal cells are cavities in the scrolls of the ethmoidal turbinals or cavities between the scrolls and the surrounding bones of the skull. (Plates VII, VIII, IX and X, Fig. B, C, D, H, J and K, 4).

The maxillary sinus is hollowed out of the superior maxillary bone and is only partially separated from the nasal fossa by the ethmoid bone. (Plates VI to X, Figures B, C, F and G, 11). The ostium maxillare is large and extends downward to the floor of the cavity, opening into the nasal fossa in the inferior meatus just posterior to the maxillary turbinal. (Plate VI and IX, Fig. A, C and D, 3). The hiatus semilunaris is a groove formed in one of the processes of the ethmoidal turbinal and leads directly from the frontal and ethmoidal cells into the maxillary sinus so that these cells all drain into the maxillary sinus and thence into the inferior meatus (Plates VII and IX, Figures C and F, 14). The frontal sinus is situated between the two plates of the frontal bone and *its anterior inferior part is occupied by a double coil of the ethmoidal turbinal which is attached to the external wall of the sinus* (Plates VII, VIII, X. and XI, Fig. A, B, C, D, H, I and K, 5 and 6).

The sphenoidal sinuses (two in number) are separated from each other by a rather thick septum in the median line and *are nearly filled by scrolls of the ethmoidal turbinal* (Plate XI, Fig. I and K, 8).

The posterior part of the vomer is expanded into two lateral wings which unite with the ethmoidal bone and thus divide the posterior part of each nasal fossa into two superimposed cavities (Plates VII to X, Figures D, F, G and H, 18). The superior cavity contains most of the ethmoidal turbinal and is distinctly an olfactory chamber. The inferior cavity is simply a tube-like structure forming a direct communication between the anterior half of the nasal fossa and the nasopharynx, (Plates VII to X, Figures A, D, F and G, 21).

The function of the accessory cavities of the nose in the dog, seems to be to provide space for the tremendous development of the olfactory turbinals, to conduct air over the external surface of these structures and to furnish a system of drainage for them.

MONKEY. The olfactory organ in monkeys varies considerably in different species, but there are certain characteristics which are constant.

The maxillary turbinal is a comparatively simple structure and consists of a single or double coil. The superior coil is usually smaller than the inferior coil and is frequently only rudimentary or absent entirely. The turbinal is supported by the superior maxillary bone and its base forms a large part of the internal wall of the maxillary sinus.

The ethmoidal turbinals vary in number from two to five and are situated above the maxillary turbinal. They are also comparatively simple structures. *In some species they extend into the posterior superior part of the maxillary sinus.* The maxillary sinus is always present and opens into the middle meatus. *On its outer wall there is a bony ridge, in some species slight, in others very prominent, which partially subdivides the sinus.* (Plate XIII, 7.) This ridge is, I think, a rudiment of the ethmoid turbinal and probably accounts for the bony partition frequently seen in the maxillary sinus of man.

The ethmoidal cells vary greatly in size and number. In some species there are none, in some a single group opening into the middle or superior meatus, according to their location, and in others two groups, the anterior cells opening into the middle meatus and the posterior cells into the superior meatus. (Plate XII, 3.)

There are no frontal sinuses in most of the monkeys' skulls which I have examined but the frontal bone in this region is composed of cancellous tissue, and in some of the higher orders of monkeys the most anterior ethmoidal cells extend up between the two plates of the frontal bone. (Plate

XII, 1.) In the chimpanzee there is a well developed frontal sinus in each frontal bone with a thin bony septum in the median line. This sinus communicates directly with the anterior ethmoidal cell. (Plate XIII, 1.)

In those specimens in which there are no frontal sinuses and the ethmoidal cells are small or absent also, the orbits are situated very close together and this juxtaposition of the orbits may account for the disappearance of the frontal and ethmoidal sinuses, these sinuses having been crowded out by the orbits.

The sphenoidal sinuses vary greatly. In those monkeys in which the turbinal structures are simple and rudimentary, the sphenoidal sinuses are small or have disappeared entirely, but where the turbinals are less rudimentary, one or more sphenoidal sinuses are present in each lateral half of the sphenoidal bone and some show distinct evidences of turbinals extending into them, (Plates XII and XIII, 5 and 6.)

MAN. The general characteristics of the nose and its accessory sinuses in man are too well known to need a detailed description here. There are, however, certain structures which occur frequently enough to be considered fairly constant, and are of importance when studied in relation to the development of the nose. A third ethmoidal turbinal, and more rarely a fourth one, may be present. These structures are evidently rudiment of the more extensive development of the ethmoidal turbinal in lower forms and as is usual with such structures, they occur more frequently in the embryo than in the adult.

The maxillary sinus is sometimes partially divided into an anterior and posterior chamber by a bony partition extending across its floor (Plate XV., Figure B, 5), or up on its external lateral wall. Such partitions are, I think, rudiments of the ethmoidal turbinal which, in the dog, extends down into the maxillary sinus.

The frontal sinus sometimes communicates with an anterior ethmoidal cell (Plate XIV, Figure A 1), or the posterior inferior part of the sinus is encroached upon by the ethmoidal cells, or there are two sinuses in one lateral half of the skull, or the frontal sinus is absent.

The sphenoidal sinus sometimes communicates with a posterior ethmoidal cell or the sinus is divided into two sinuses, one of which opens directly into the nasal fossa and the other into an ethmoidal cell or both open into the superior meatus. (Plate XVII, Figure D, 6 and 7.) These variations are all easily explainable, I think, when they are compared with similar structures in lower vertebrates and are probably reversions to more primitive types.

The variations in the frontal sinuses correspond to the structure of these sinuses as seen in such animals as the dog and the monkey. The division of a sphenoidal sinus into two chambers is caused by a plate of the ethmoidal (or sphenoidal) turbinal extending across the sinus as it does in some monkeys.

Summarizing briefly, we find that the olfactory organ in fishes consists of two sack-like structures, each of which communicates with the exterior by two openings, but the nasal cavities do not communicate with the mouth. The turbinals are represented by prominences on the median wall. In dipnoi the nasal cavities open into the mouth and the nose then becomes a part of the respiratory system.

In reptiles the nasal cavities are subdivided into olfactory and respiratory regions and the turbinal structures are more highly developed. The secondary palate separates the posterior nares from the mouth and the nasal fossae are thus prolonged and open farther back into the nasopharynx.

In birds, the turbinal structures are all more complicated and the ethmoidal turbinals especially show a still higher degree of development.

In macrosomatic mammals (animals which have an acute sense of smell), the turbinal structures are exceedingly complicated scrolls forming intricate labyrinths which occupy the greater part of the nasal cavities. The accessory cavities of the nose all contain olfactory turbinals and are in intimate relation with these structures.

In microsmatic mammals (animals which do not have an acute sense of smell), the turbinals all show evidences of degeneration or reversion, and are comparatively simple structures. The accessory cavities contain little or no true turbinal tissue and their functional activity is lost.

It seems probable, therefore, that in man the accessory cavities of the nose are rudimentary structures.

The foregoing statements are based upon the study of the nose in fishes, frogs, alligators, turtles, birds, dogs, cats, wolves, foxes, bears, beavers, seals, rabbits, guinea pigs, lions, deer, sheep, cows, pigs, buffaloes, horses, elephants, monkeys and man.

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