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THE OLFACTORY SYSTEM OF TAILED AMPHIBIA

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The nasal capsules of salamanders have rather large chambers more or less protected by cartilage and bone. In the Proteidæ and Sirenidæ there is no bone dorsally, but in varying degrees the other families have capsules largely covered over and above with bone as well as cartilage. Usually a small area about the external openings are free from cartilage. In many, especially members of all families but Proteidæ, Sirenidæ and Amphiumidæ, two rather distinct regions are found in each olfactory chamber; the main portion or *cavum nasi* and a lateral, the *sinus lateralis nasi*. In the last the *ductus naso-lateralis* opens. In many the sinus lateralis is lined with ciliated epithelium.

Seydel '95, named a gland mesial to the sinus lateralis and under the cavum nasi as Jacobson's gland. Mihalkovics '98, considered this absent from salamanders, but concludes that the sinus lateralis which he calls recessus maxillaris, has a similar function of testing the external air current, that is, the structures are analogous, but not homologous with a true Jacobson's organ. Hinsberg, 1901, in the development of Triton came to the conclusion that a patch of sensory epithelium homologous with Jacobson's organ, arises medially and moves to a position lateral to the internal nares before this opening is completed. In this way the lateral position is a specialization of Urodela. Zuckerkandl, 1910, agrees in general with the last, but because of the nerve supply does not believe in homology with higher vertebrates. Bruner, 1914, agrees with Seydel as to the location of Jacobson's organ and Herrick, 1914, from the nerve supply does believe that this organ is present in Urodela. Von Navratil, '26, does not agree with Seydel's homology of the lateralis nasi. Kurepina, '27, claims the existence of a primary oronasal groove between the nose and the mouth, therefore there can be no lateral shifting of Jacobson's organ.

In general then it is agreed that the sinus lateralis is the functional equivalent of Jacobson's organ, used for testing water currents.

The external nasal openings may differ in size as well as form. In adult Siren they are elongate slits and also to some degree in Necturus. In adult Amphiuma they may be a little more elongate, perhaps more oval than slit-like. In most of the others the openings are circular to oval, the appearance somewhat modified by their activity. In the Plethodontidæ the openings are from circular to oval, always with a groove reaching from the nasal opening through the upper lip.

The nares differ greatly in size; not always correlated with the size of the animal. Some small species of Plethodon, Batrachoseps or Desmognathus may have openings not more than .2 mm. across, but in some species of the genus, Thorius, even smaller than these other plethodonts, the size of the nostrils is comparatively and actually very great. A head 1 mm. long might have a nostril .5 mm. across, about as large as the eye area in the same animal. In Amphiuma, large adult, the opening was 2 mm.

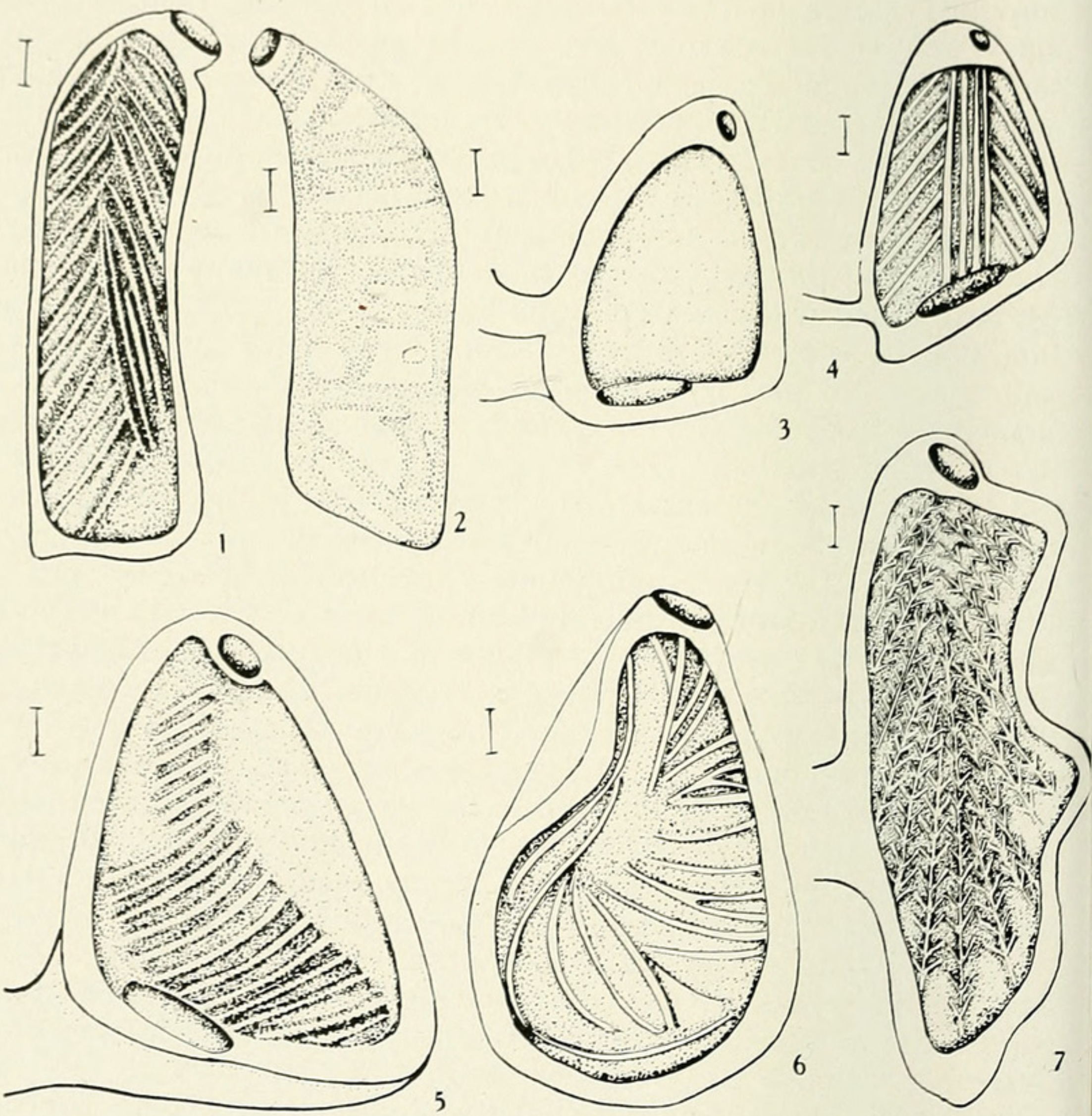

PLATE 36

Olfactory capsules of salamanders. Scale equals one mm. All but 2, views into the chamber after the removal of the dorsal wall, showing the surface of the ventral mucous membrane. Folds of the olfactory mucous membrane shown in all but 2 and 3.

1. Necturus. 2, Upper view of the olfactory capsule of Necturus, cartilage areas stippled. 3, Salamandella. 4, Triturus torosus. 5, Cryptobranchus. 6, Siren. 7, Amphiuma.

in its greatest diameter, but a large adult Dicamptodon where the nostril was circular or nearly so it was 2 mm. in diameter.

In all salamanders examined, but members of the Proteidæ, Sirenidæ and Amphiumidæ, where the nasal openings are circular to oval in outline, as far as examined in the living condition or suggested by preserved specimens of almost all species, the nostril seems to be closed largely from one side by the enlargement of an extensive lateral plug, due to the fact that the anterior rim is practically fixed in position, without movement when the opening is shut off from the exterior. This apparatus has been described in Salamandra by Bruner in 1896 and 1901. He describes three smooth muscles, one constrictor, two dilators. The *M. constrictor naris* bounds the caudal edge of the opening in little more than a semicircle, its ends being inserted on the anterior wall of the nasal fenestra on the cupullar cartilage portion of the nasal capsule. The *M. dilator naris* arises from the posterior border of the nasal fenestra, from the *cart. retro-narina* and passes forward to the caudal border of the nasal opening, being inserted into the constrictor muscle and the tissue binding it in the wall of the nasal opening. He also recognizes the *M. dilator accessorius* from the lateral border of the fenestra narina, from cartilage of the capsule and from the maxilla, to be inserted into the caudo-lateral margin of the nostril, deep in the fibers of the constrictor muscle, after taking an oblique course.

After the examination of this structure in a number of examples from all families, I can confirm these results in general, especially in these salamanders with circular or nearly circular openings and with the lateral nasal plug or operculum which closes the opening. This includes in general all families but Proteidæ, Amphiumidæ and Sirenidæ where the nostrils are more slit-like. In these last I did not find a lateral plug clearly indicated and the constrictor muscle was nearly if not entirely about the nasal opening with many fine fibers of a retractor function not limited to one side of the slit-like opening. Also in all those which I examined with a well-marked nasal plug I failed to convince myself that there was a distinct accessory oblique muscle.

The glands of the nasal region differ somewhat in various species. In almost all, in the mid-dorsal area between the olfactory sacs there is a large median gland which in some cases seems to have communication with the olfactory area. In some salamanders, especially members of the Plethodontidæ there are large glands either side of the nasal areas on top of the bone, with one or more ducts leading to the margin of the nostrils. Sometimes these extend back to the orbit and may have openings there but of that I could not be certain. Sometimes this gland or group of glands just under the skin and above the skull extend out laterally as part of the gland described or as more or less separate structure with its secretions also passed to the margin of the nasal opening. In addition to these there are glands in the nasal capsule in many forms. They were seen in almost every species that I have examined. Francis '34 gives them for Salamandra, which might be considered typical, as follows:

The *glandula nasalis externa* situated above the sinus lateralis nasi within the fenestra narina very near the opening of the *ductus naso-lacrimalis* into the nasal capsule.

The *glandula nasalis interna,* practically surrounding the cavum nasi within the nasal capsule. It keeps the olfactory epithelium moist.

According to Bruner '01, the muscles of the nostril are related to the glandula nasalis externus in such a way as to force the secretion out with the closing of the nasal opening.

It is possible that a poorer development of this last gland is correlated with the development of the external skull gland which supplies secretion to the nasal opening in Plethodontidæ. I have not seen this gland described before and so far have not seen it except in several but not all the genera, but especially in Plethodon, Eurecea, Batrachoseps and a few others of the family. As the word external is used in connection with another structure, the term *superficial* gland might be applied to it.

The inner surface of the nasal chamber has the mucous membrane sometimes smooth, in others quite complexly folded. Although there is much individual variation and some differences of appearance depending upon the method of preparation for examination the following is true:

The mucous membrane of the interior of Necturus is usually complexly folded with long high, diagonal folds. In Cryptobranchus nearly cross folds are found on the ventral surface. In Siren the folds are irregularly cross and longitudinal. In Amphiuma the folds quite well fill all the ventral surface of the mucous membrane, diagonal to longitudinally disposed with small lateral branches from the folds. In some Salamandridæ both longitudinal and diagonal folds may be found, but in all cases examined they were not prominent and in some the lining of the chamber was almost smooth. In the other specimens examined representing four families the mucous membrane was quite smooth.

In this description the lower surface has been described; the inner side of the upper side of the chamber is usually similar but not so marked as to ridges and folds.

The olfactory epithelium in many cases is very thick with many layers of nuclei. In certain especially prepared specimens long bipolar nerve cells were found scattered among the other long slender cells.

In general the development of the nasal capsule is as follows, following the condition in Ambystoma more closely than any other. This is based upon the study of dissections and serial sections of different stages and upon the work of Higgins 1920, who made wax plate reconstructions of various early stages.

The skeleton of the nasal area is a little later in the formation of a cartilagenous capsule than the development of the otic capsules. The first indication of nasal pits is also well after the eyes are conspicuous with lens and cup. The olfactory pits develop rather slowly in stages before hatching and are at first mere shallow depressions in little flattened discs of thickened epithelium. The cavity slowly enlarges and extends out laterally and caudally. The penetration into the oral chamber comes about the time the cartilagenous trabeculæ are in evidence; a little before or a little after depending upon the species. At first the ends of these trabeculæ are not enlarged but before long they flatten out and form lateral parts, the *crista trabeculæ*. Sometime later these ends of the trabeclæ unite across the middle line to form a flat plate, the *planum basale*. At about this time isolated dorsal cartilages on each side, the *columna ethmoidalis* are formed as longitudinal rods dorsal to the basal plate. With later growth of these isolated rods they become fused with the trabeculæ on each side in the *crista trabeculæ* while the ethmoid columnæ are also united across the midlle line in the narrow *pons ethmoidalis*. In a later stage, almost all parts become broader, the region of the bridge

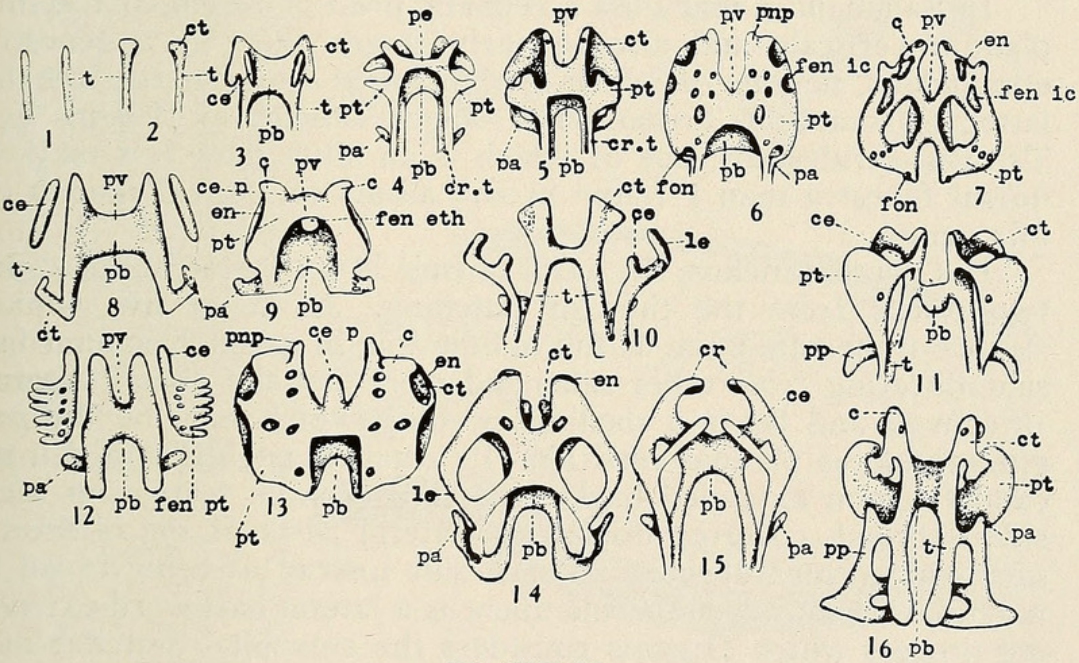

PLATE 37

Olfactory, cartilagenous skeleton of immature salamanders, largely after Higgins. All from above but 16; c, cupula; ce, columna ethmoidalis; cr t, crista trabeculæ; ct, cornu trabeculæ; ce p, cephalic processes; cr, circumnaral ring; en, external nares; fen pt, fenestrated process; fon, foramen orbito-nasalis; pa, processus antrorbitalis; pb, planum basale; pe, pons ethmoidalis; pt, planum tectale; pv, planum verticale; pp, ptergoid processes; t, trabecula; le, lamina externa.

1-7. Stages in the development of Ambystoma. 1, about 10 mm. 2, 11 mm. 3, 20 mm. 4, 25 mm. 6, 55 mm. 7, Young adult.

8 and 12, Necturus, 30 and 45 mm. 9 and 13, Salamandra, 38 mm. and young adult. 10, 15 and 14, Amphiuma. 11 and 16, Cryptobranchus, 5 weeks, and three months. 16 from below.

becomes the *platum verticale* with the *foramen nasalis internus* formed at the apex of the median part on each side near the median nasal incision. The *platum tectale* is a narrow lateral extension of the columna ethmoidalis and is now quite broad. There is also a lateral projection from the trabeculæ, in front of the eyes, of the *process antrorbitalis* which at first is somewhat by itself, one on each side, but later joined in with the olfactory cartilage. At such a stage the olfactory capsules are nearly inclosed dorsally and ventrally; dorsally by the *platum verticale* and ventrally by the broader *platum basale*. Very soon the capsule is quite complete and the internasal space between the two capsules becomes more marked with the narrowing of the platum verticale. In an early stage a number of foramina and frontinelles are found, some remains of older ones, some new. The external nares are marked on each side and near the *fenestra infraconchalis,* at the caudal end on each side dorsally. In a later stage, much like the adult, large characteristic dorsal and ventral fontanelles are evident.

On the dorsal side in addition to the external nares are the fenestra infra-conchalis, the foramen orbito-nasalis on each side.

In Salamandra maculosa a cephalic process develops from the planum verticale and also in early stages there is a fenestra ethmoidalis, neither of which are shown in Ambystoma, but the latter is found in Triton. The stages shown by Higgins for Triturus viridescens, one of which is an adult have less marked dorsal fenestra than I found in any adults of several species of this genus.

In Cryptobranchus, the nasal capsule is not formed until about two weeks from the time of hatching. At about five weeks, slender trabeculæ unite at the middle line in a small planum basale, differing from other salamanders in that the dorsal surface is convex and bears a median swelling which may be the beginning of the planum verticale. Its cephalic edge is straight, its caudal region extended backward. The planum tectale on each side is broad, covering dorsal and lateral parts of the olfactory sac. The cornu trabeculæ on each side instead of being broad is narrow. From each trabeculæ there is a lateral backward extending process which Higgins considers the antrobital, but it bends backwards without anterior projection to the pterygoquadrate. In a later stage the planum basale and verticale support the olfactory lobes with the capsules united by a broad planum basale without a median caudal lobe. The cornu trabeculæ is now united to the anterior extension of the broad *planum tectale.* The bar of cartilage extending from the trabeculæ backwards has extended back to unite with the anterior end of the pterygo-quadrate bar which extends back to the otic region. This unique condition recognized by Higgins in Cryptobranchus is similar to that found by Wiedersheim in Ranodon, but according to Higgins is lost in adult Cryptobranchus and Megalobatricus.

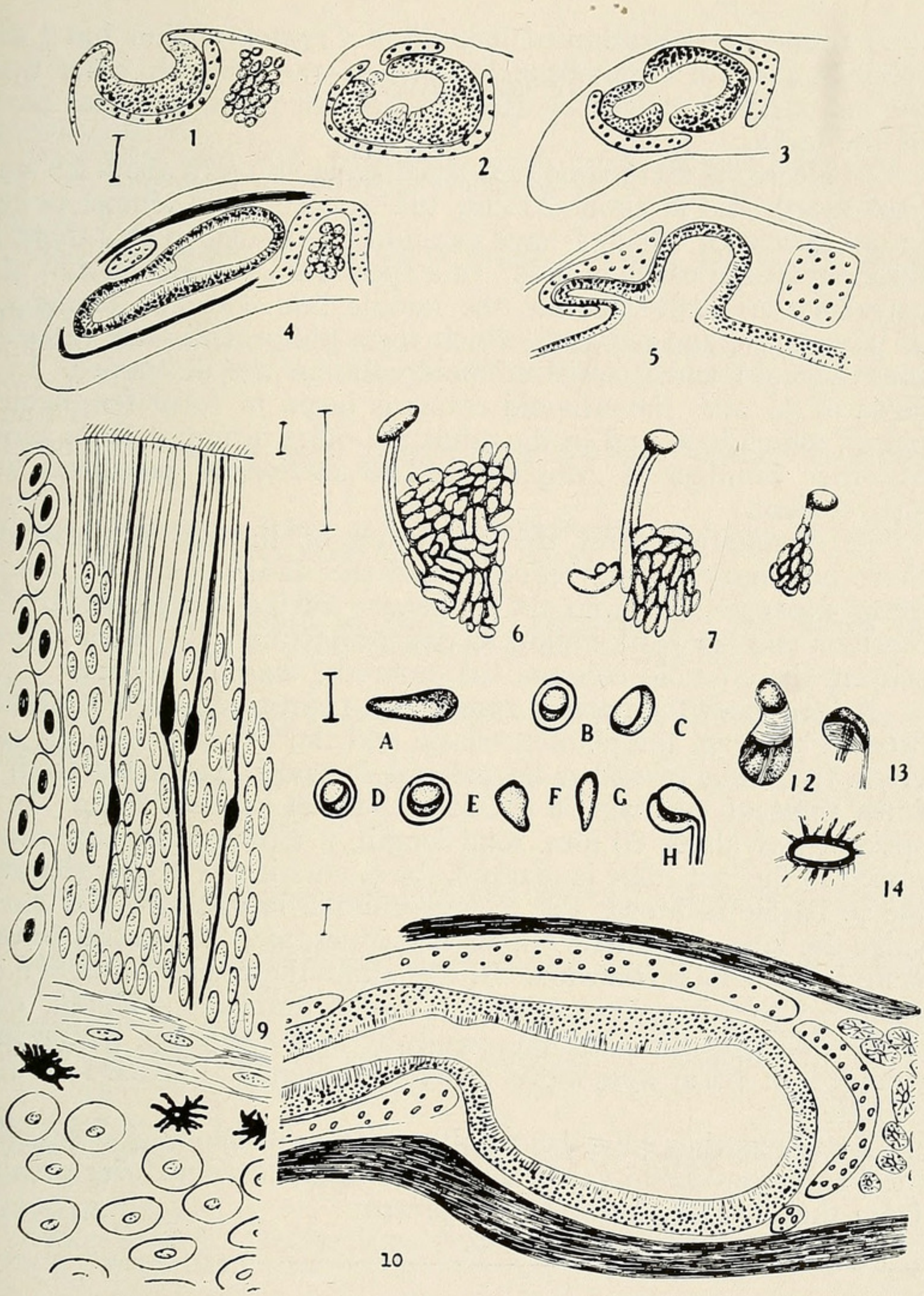

PLATE 38

Olfactory parts of salamanders. Scale equals 1 mm. in 6, 7, 8, 12, 13, 14 and A-H. Scale equals one-tenth mm. in 1-5. Scale equals one micron in 9 and one hundredth mm. in 10.

1-5. Various sections of the olfactory region on one side of Desmognathus fuscus of 30 mm. total length. Mucous membrane fine stippling; cartilage wider stippling; bone darker.

6. Superficial gland of Plethodon glutinosus, larger opening.
7. Same of Eurecea gutolineata.
8. Same of Batrachoseps.
9. Olfactory mucous membrane from Necturus, showing epithelium,

I found no indication of it in adult Cryptobranchus but I did see it in a larval Cryptobranchus which was probably older than the last stage described by Higgins, judged from the other parts of the larva.

In Necturus there is no true nasal skeleton up to about 25 mm. total length, but at about 20 mm. the trabeculæ are almost united in one specimen which I have examined although in this there is little expansion of their ends. In a specimen of about 30 mm. the trabeculæ are united across the middle line with the formation of p. verticale and p. basale which form the central plate between the trabeculæ and isolated ethmoid columns are developed. In a larva of 45 mm. the ethmoid columns begin to form fenestrated plates, which here and in the adult are quite different from those of other families of Amphibia. The antrorbital processes are also evident.

In Amphiuma after the expansion of the cornu trabeculæ there is a narrow connection across the middle line just below these expansions. From the trabeculæ farther back lateral extensions run forward ending in two projections, the inner representing the ethmoid column, the outer the *lamina externa.*

A little later the narrow connection from side to side becomes broader to form the planum basale and the forward ends of the crista trabeculæ or rather lateral and forward extensions from it form rings of cartilage, a special condition in Amphiuma. In a specimen of about 80 mm. total length, a circumnasal ring mentioned in the last stage is marked, the c. etmoidalis is very slender, the p. basale is broad, the p. antrorbitalis larger. At this early stage the large dorsal fontanelle is evident, and the ventral fontanelle is even more marked. In the adult there are a number of changes: the dorsal surface has two fontanelles dorsally, one quite small and the large one ventrally located; the p. basale has changed in form and more slender elements are fused in the capsule.

So far as they have been followed the olfactory skeletons of the Plethodontidæ in young and older stages do not differ greatly from the general plan of development.

EXPLANATION OF PLATE 38

blood vessel at the side, connective tissue below and cartilage below this. Cells in dark olfactory nerve cells.

10. Cross section of olfactory region of a small Siren. This shows cartilage, bone, mucous membrane with inner glands at the right.

12. Diagram of olfactory muscles, after Bruner from Salamandra. Deep shading nasal cavity.

13. Nasal muscles of Desmognathus.

14. Diagram of the probable muscular arrangement in Amphiuma, Siren and Necturus. Nasal opening light.

A-H. Nasal openings of various forms, scale 1 mm. for all. A, Siren. B, Ambysytoma. C. Cryptobranchus. D, Hynobius. E, Triturus. F Amphiuma. G, Necturus. H, Plethodon, more enlarged than the rest.

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