STUDIES FROM THE NEUROLOGICAL LABORATORY OF DENISON UNIVERSITY.

X. THE NOSE AND JACOBSON'S ORGAN WITH ESPECIAL REFERENCE TO AMPHIBIA.

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I. Introductory.

It is the purpose of this introduction, first that we may become well-orientated ourselves in undertaking to carry on our original investigation; and further to assist those who may not be so familiar with this particular subject in taking in the full significance of any new facts which have recently been established. It is designed also to group together a few significant generalizations which seem important in this connection. If this sketch appears imperfect, it must be remembered that other points are elaborated below.

The olfactory organ as one of the five principal organs of sense takes an important place in the studies of the Morphologist. Offering, as it appears to, at first sight, greater simplicity of structure than either the optic or auditory apparatus, it has seemed to promise an easier field for investigation as well as a greater variety of results. But upon deeper and closer study the true complexity of the relations, both morphological and histological, is brought to light, and the more far-reaching the study, the greater the emphasis which is laid upon the fact. The only means therefore by which we can soon acquaint ourselves with the main facts is by viewing the whole question successively from different standpoints. The great diversity in the configuration of the peripheral organs allows great range for comparison, while the circuitous internal connections, though

but imperfectly made out, have not prevented the publication of certain psycho-genetic conclusions. But although there are many questions which arise in this study which seem as far as ever from an adequate answer, yet there are other questions which seem to require but persistent and thorough investigation to yield fruitful results. Perhaps this is not more true of the olfactory organs than of others, but certainly there is evidence of a simpler functioning than is the case in the eye and ear at least, whether the organs themselves are correspondingly more simple in structure or not.

Smell is one of the earliest senses phylogenetically. Hints of such a sense are found in the function of the processes and antennæ found in many invertebrates, (*star-fish, insects, etc.*) *Ants* communicate by means of their antennæ, and the fact that recognition is prevented by immersion in water, along with other experiments, suggests that such recognition is largely at least due to olfaction. An ant immersed as above described is immediately set upon and destroyed by its fellows, comrades in the same colony, after a short examination of the victim by means of those infallible sense-bearing feelers. The explanation is that the peculiar odor characteristic of each member of a given colony is lost by this submersion of the ant. The supra-oesophageal ganglia found in some types are supposed to be not a "brain" as often described but a mass of sensory organs among which is a more or less highly differentiated proton of an olfactory apparatus. This reference, however fanciful and perhaps unreliable, may assist in homologizing invertebrates in this respect with higher forms.

1. Perhaps the most probable theory as to the *origin of the primitive olfactory epithelium sacs* is that which postulates their origin from the lateral line system. This theory is supported by such authors as Beard, who is very explicit on this point. He says: "The nose and ear are in the same category of sense-organs as those of the lateral line (the branchial sense-organs), a system of sense-organs which vertebrates have inherited from their annelidan ancestors. The power to evolve new sense-organs from indifferent foundations must be absolutely refused

to vertebrates. They can form new sense-organs only by a further differentiation of the segmentally arranged sense organs which already exist and which have been inherited from the Annelida, their ancestors." That is, he maintains that the nose and ear are comparable in origin, not being modified gill-clefts as formerly supposed, but developed from these simple paired pits which (as in the fish) are found scattered about the head and arranged in a line along the lateral aspect of these lower types. Like the lens and labyrinth of the ear, they are formed from the external epithelium; unlike them they are never closed up. The nasal epithelium depression which so much resembles in early development the corresponding optic and auditory depressions, is developed a little later in the history of the individual (that is, in the development, or ontogeny) and like them, from the outer germ-layer. This *nasal area* lies on either side of the frontal process in the embryo. Early in the process of the differentiation the edges or rims of these depressions rise into folds or ridges. As these thicken there is a corresponding proliferation of neural cells from the brain-tube which come into connection with the cells of these thickened walls. This is what may be called the primitive olfactory ganglionic foundation. This evagination of the cerebral vesicle is undoubtedly the fundament of the olfactory lobe, while the fibrillæ which terminate in this thickened epithelium are later carried back to form the olfactory bulb and nerve bundles. Thus the nose is all developed, really, by the growth and differentiation of one small piece of sensory epithelium.

Embryonic development.—The olfactory is connected with and associated with the pituitary in the embryonic development, and as recently shown, they are really situated upon the dorsal surface. The olfactory nerve is supposed by some to be the supra-branchial branch which has every other element suppressed. The olfactory nerve is formed from the anterior cerebral as a secondary vesicle on its under surface. Professor Beard says, "In brief the olfactory nerve, or better, the olfactory ganglionic foundation, is derived from two sources, the lateral ganglion and

the neural ganlion, as is true for all true cranial segmental ganglia."

Naturally, next, would follow a rapid survey of the progressive differences in general configuration of the peripheral organs, but as this will necessarily be referred to under other topics we will not lengthen the review by introducing a full discussion here.

2. *Evolution of the external and internal nares.*—In lower vertebrates the olfactory opening is single. In *fishes* the olfactory sac divides and each comes to have two openings but neither is within the mouth. It would appear that in higher vertebrates the mouth becomes more extensive and envelopes the caudal opening of the nasal sac, producing the internal nares.

Ganoids and Teleosts have two external openings, anterior and posterior, through which the water passes.

In *Amphibians* it is said that the posterior nares are formed in a different manner. The groove closes completely behind and a new perforation is formed from the blind end of the original nasal groove. Balfour ("Comparative Embryology," from whom this is condensed) thinks this is a secondary process.

Both external and internal orifices are situated far forward near the edge of the mouth in *Dipnoi* and the *amphibian* stage.

In *Dipnoi*, says Le Conte, we have for the first time *nostrils*. These fishes completely combine gill-breathing with lung-breathing. The steps from these to the lowest amphibian reptiles is so small, that some have classed the *lepidosiren* among amphibians instead of fishes.

In *lizards* the method of formation of the internal nares is somewhat different. A groove connecting the nasal sac with the roof of the mouth is formed, but it forms on the inner aspect a great lateral diverticle clothed with a continuation of Schneider's epithelium, and forms the fundament of Jacobson's organ. Subsequently the groove is closed in and Jacobson's organ separates from the nasal passage and acquires a new opening into the

mouth at the front end of a groove running back to the posterior nares.

In *birds* the nasal sac is extended to form a groove. The hinder part becomes enclosed in the mouth and closes except at the posterior where it remains open, forming the posterior (or internal) nares.

3. An interesting field for further investigation is the *evolution of the respiratory regions* of the nose. The nose is one of the organs which serve a double purpose. It is not only the seat of the sense of smell, but was evidently intended to be also the principal organ through which an animal breathes. Its more or less circuitous passages, warm and moist, protect the lungs by taking the chill from the inspired air and arresting irritating dust. The cavity of the nostril in many types is extended by means of certain so-called turbinated bones, covered by the extremely sensitive olfactory membrane. This cavity is further separated into two parts, the respiratory passages of the nose, and the true olfactory centers. The latter are usually situated farther entad, so that in general it is not true that the entire olfactory epithelium is concerned in the act of smelling. In man, for example, the terminal nerve cells which alone take cognizance of odors are situated in the upper third of the nasal chambers out of the line of the ordinary inhalation. For this reason we do not usually notice odors except when we sniff—draw the air into the upper part of the nostrils and hold it there a moment—when we may become aware of even the faintest scent.

The fact that certain *Amphibia* during their aquatic life do not possess ciliated epithelium but when entering upon their terrestrial life acquire it, seems to indicate that the possession of such epithelium bears some relation to the necessary circulation of the air through the nasal passages during the land-life of these types. There certainly is some significance in the fact that as a class aquatic animals are not supplied, while as a class land animals are supplied with this ciliated olfactory epithelium. Some have suggested that the cilia serve to renew the medium bearing the odoriferous particles, but this perhaps would conflict

with the fact that in the olfactory region, in higher types—i. e. the region in which the terminal filaments from the olfactory bulb are distributed—the epithelium cells are columnar and non-ciliated (Ref. Handbk Med. Sciences, Lit. No. 28.) while in the respiratory portion of the nasal cavity the epithelium is columnar and ciliated.

The Dipnoi are the lowest types in which the nasal cavity begins to differentiate for the secondary function of a respiratory passage, from this stage onward the olfactory sac being in communication with the mouth.

4. *Psycho-genetic conclusions regarding the sense of smell.* This is an apparently unworked field. Such questions as the relation of the nasal apparatus to the habits of the animal; the psychogenesis of smell, etc., have but lately received any attention deserving notice.

Edinger's psychogenetic conclusions.—Although the olfactory sac is developed by invagination of the ectoderm, and hence the olfactory organ is developed later than the numerous tactile organs scattered over the whole epidermis, yet the sense of smell seems to be developed before the sense of touch. We must not regard those reflexes which are seen in the motions of the amœba and other low forms as indicating the possession of any true sense of touch, but only a susceptibility to stimulus, that is, mere irritability. Thus we see that although the organs of touch precede in development the organs of smell, yet because the latter form their central connection first, the sense corresponding is the first to be developed. That is, we may say that touch and smell existed, and touch existed before smell, but the sense of smell was the first to become conscious. (Properly speaking of course, the sense of smell or touch is not rightly called a sense until it becomes conscious.) Now the psychical processes which pertain to the sense of smell have been referred to (i. e. have their center in) the hippocampus. And if it is true as seems almost certain that the Ammon's horn which is the homologue of the hippocampus in lower types, is the first cortical center to develop, then it would seem to follow that the first psychical function to develop, corresponding to this most

primitive establishment of cerebral connections, is the sense of smell. As Edinger says: "We are today justified in assuming that the cortex is the bearer of the higher psychical functions. If then it is true that the olfactory tract connects with the higher centers first in phylogenetic development, then it follows that the earliest cortical activity is associated with the perceptions of smell." What the ultimate significance of the early development of the olfactory sense may be, is yet to be determined.

With regard to the *delicacy of the sense of smell* even in the higher types where it is not so fine a sense, it has been shown by experiment that $\frac{1}{400,000,000}$ part of a milligram of polycarpine, or $\frac{1}{300,000}$ part of a milligram of bromine, in one square centimeter of air is perceptible. Olfactory sensations are probably received from material emanations from the odoriferous substance, the emanations being absorbed by the fluid in which the end-cells are imbedded. This moisture is so essential to the proper action of these cells that its absence, as in certain stages of a cold and in certain diseases, may for the time quite destroy the sense of smell. For the same reason odors are less readily perceived in an uncommonly dry atmosphere. This blunting of the sense is brought about also by certain occupations which necessitate working in a dusty atmosphere.

The nerves of smell may become the seat of disease. An abnormal increase of the acuteness of the olfactory sense is *hyperosmia*; an abnormal decrease, *anosmia*. Complete *abolition* of the sense sometimes takes place. It seems that for the development of smell the odorous particles must be transmitted to the nasal mucous membrane in a *gaseous* medium as the simultaneous contact of fluids destroys all appreciation of odor. Section of the olfactory bulbs entirely destroys the sense of smell. Injury to the fifth nerve may also destroy smell even where the olfactory nerve remains intact. This is probably only an indirect cause, however. This may be plausibly explained as the result of a deficiency in the secretion which is controlled by this nerve branch.

The delicacy of the sense of smell is determined in experi-

mental work sometimes by an *Olfactometer*. For a description of this instrument as well as the process of using it see "Les Odeurs. Demonstrations avec l'olfactometre et le pésevapeur, par M. C. Henry," Paris, 1892. According to the writer of the above, most of the perfumes are of organic origin. There seems to be some relation between the odor and the atomic weight, more or less independent of chemical composition. It is further supposed that perfumes are propagated by the emission of solid, liquid or gaseous particles; hence the laws of diffusion and evaporation may largely control not only the degree of delicacy of the sense of smell, but perhaps also the apparent modalities. At any rate these are fruitful fields of research.

6. Ziehen says that the number of *modalities of smell* is very great as compared with the modalities of taste, although there is at present no good classification of the former. The specific names of odors almost always are taken from the odorous objects, or borrowed from the nomenclature of some other sense (as violet, rose, sweet, dry, etc.) With most persons the sensation of smell is exceedingly subjective, and any natural classification is made on this basis. This sense is always very closely associated with the well-being of the individual. The sense of smell is poorly localized in the higher animals, but is very closely associated with the cognitive powers and consequently is better localized in some lower animals. Indeed it almost takes the place of a natural language and takes the place of hearing in some cases. The word "taste" is often used when the word "smell" should be employed. We speak of tasting odoriferous substances such as onions, wine, etc., when in reality we only smell them as we hold them in the mouth. This is proved by the fact that the so-called taste of these things is lost when the nose is held or the nasal membrane rendered inert by catarrh.

7. *Central Olfactory Nerve Connections.* Methods of extirpation and subsequent histology have shown that the hippocampus is the olfactory region or centre in the brain. Moreover we find in aquatic animals (fish, dolphin, whale, sharks, rays, etc.) that the entire olfactory lobe is absent, and find in

semi-aquatic animals which frequent the water most that the hippocampus and radices are correspondingly reduced. The whole region in the limbic lobe below the rhinalic fissure is given up to the somatic senses in general, and to smell more especially.

The olfactory fibres probably do not develop from the olfactory lobe, but rather take their origin from the epithelium of the olfactory pits. It is likely that they originate primarily from the cells of the spinal ganglion as they bud out from the region of the neuro-pore. All evidence goes to show that they grow in from without rather than in the opposite manner. In the earliest stages the olfactory pits have no nerves. Later there is noticed a slight proliferation in the direction of the nerve tube. And it is just at this point that lack of decisive evidence makes it uncertain whether the olfactory nerve derives its fibres from the olfactory ganglion only or whether there is an interaction, fibres also growing out from the tuber. The former seems most likely. The tuber at its cephalic extremity, i. e. the bulb, in general, consists of two well-defined portions called the *pero*, the thick, outer, fibrous, buskin-shaped layer, and the *pes*, the inner, cellular layer. The *pero* is formed by the fibres of the olfactory nerve which diverge over the surface interlacing and commingling, thus forming the above-mentioned sheath-like cap enveloping the *pes*. The *pes* may be called the cerebral part of the bulb since no fibres pass from it without into connection with the olfactory epithelium. The adhesion of the *pero* to the *pes* is apparently of a secondary character, being probably mechanical, without any morphological connection. The internal structure of the *pero* would seem to show the same. The fact that the fibres lose their sheaths in their passage through the *pero*, but acquire them at their exit, would also attest it. (*Journ. Comp. Neurol.*, Vol. II, Feb., '92, pp. 2-7.)

The inner structure of the olfactory bulb may here be noted briefly. Passing entad we encounter successively the following layers: first, the fibrous outer layer consisting of apparently irregularly disposed fibre clusters, intercrossing confusedly, (i. e.,

fibres of the olfactory nerve); second, we come to the so-called glomerular layer where are probably manufactured the myeline sheaths of the nerve-fibres and where the terminal dendrids of the fibres of the olfactory nerves enter into relations with those of the protoplasmic processes of the cells of the next, or ganglionic layer; third is found the ganglionic layer of pyramidal cells whose axis cylinder processes unite to form the radices lateralis and mesalis. The fourth and last layer of the pero consists of dense stratified granules. The pes consists of small fusiform cells like those of the hippocampal lobe, which goes to prove its central origin. It is from this layer that the large and circular bundle of radix entalis arises.

From these two portions of the olfactory bulb arise three bundles of fibres which pass backward, and in the case of two of them, at least, into certain definite relations with the hippocampus, and whose course is the occasion at present of so much discussion. The largest of these bundles, known as the *radix lateralis* from its position on the lateral aspect of the tuber, arises from the pero, or the outer layer. This bundle has been traced with comparative accuracy back to its cerebral connections in the hippocampus. The fibres of the radix lateralis gather in the granular layer of the pero, about the tip of the ventricle and on the ventral aspects of the tuber; pass ectad along the outer surface, spread out over and dip into the hippocampal region. They connect here with the ectal region of the hippocampal lobe. The *radix mesalis*, so called because it arises on the inner aspects of the tubers, and thus approximates the median line, has been traced into the indusium, the so-called striæ Lancisii, (Fish, No. 7.) It arises from the pero. This bundle is small as compared with the outer radix lateralis and is not so compact, being dispersed over the inner and ventral aspect. It has been found to pass to the gyrus fornicatus in the opossum, which is the cephalic part of the hippocampus. Beyond this its fibres have not been traced with any degree of certainty. The fact is here to be noted that the radix lateralis arising from the lateral aspect of the pero ends in the hippocampus without any morpholog-

ical deviation in its course, while the fibres of radix mesalis arising from the median aspect of the pero pass dorsad of the callosum when the latter is present as striæ Lancisii to the hippocampus, and in the absence of the callosum (opossum) directly dorsad to the gyrus fornicatus. Into and through the anterior commissure and thence possibly to the hippocampus pass also the fibres of the third bundle, the *radix entalis*. This is the bundle which arises from the pes proper and in no case appears to enter into connection with the olfactory cells.

In the lower types, as the fish, there is only a rudiment which can be homologized with hippocampus of the higher forms. This homology has been traced by following the course of the radix lateralis as it passes in the fish to this point. In the higher types this is seen to be more distinct, while in reptiles the typical folds of the hippocampal gyre begin to assume their characteristic complexity. In mammals this folding becomes exceedingly complex, thus making the tracing of the fibres from the olfactory lobe very difficult. The lobe in the occital region of the cerebrum in the brain of reptiles which contains the undoubted homologue of the hippocampus is called by Edinger the ammon cortex. A comparison of the reptiles with the opossum and rodents in general shows that the only difference lies in the extreme complexity of the relations in the higher types which obscures the homology. The problem now is to trace the three radices back to the hippocampal region in all these types and completely homologize these different parts; to explain the relative position of these bundles, accounting for their migration and perversion by determining, among other things, at just what point lies the evolutionary front of the head. Another point of interest is the fact that recent investigators have shown that the first centres of the olfactory nerve lie in the pero of the bulb, and that from this point there migrate inward nerve filaments which come into connection with out-going fibres from the cortical centres. Thus the fibres connecting the bulb with the cortex acquire a new significance and may be homologized with the projection or irradiation fibres of the optic centres which connect with the occipital cortex.

The olfactory nerves in *man* enter the nasal epithelium through some twenty openings in the bony arch and then branch into a perfect meshwork of fibrillæ, their extremities reaching to unite with the minute cells of the epithelial layer. Other accessory nerve-bundles which supply the olfactory organs are, a branch of the ophthalmic (V), filaments from the anterior dental branch of the superior maxillary, the vidian, naso-palatine, descending anterior palatine, and nasal branch of Meckel's ganglion.

8. *Function of Jacobson's Organ.* Notice that among animals which live more or less on, or near, or burrow in the earth, such as ruminants, rodents, lizards, snakes, amphibians, etc., *Jacobson's organ* is more or less developed, while the nose is simple and comparatively undeveloped; while among animals that live entirely or mostly in the water, and in general among those animals who do not bring the nose to the ground, and do not depend upon the sense of smell in the search for food, as in man, birds, fishes, crocodiles, chelonia, etc., we find Jacobson's organ undeveloped or only rudimentary, while the nose proper is often quite complicated in its structure.

Again, glands seem abundant in water-livers, and more scarce in land-livers. Compare the difference even between the groups of Reptilia where you would not expect so marked a difference. Chelonia and Crocodilia are well supplied, while there is a comparative paucity of glands in Lacertilia and Ophidia. The *function of Jacobson's organ* is to determine directions, perhaps. Others suggest that it may consist in bringing the food taken into the mouth under the direct control of the olfactory nerve. In Reptilia for example, the function of Jacobson's organ seems to be to perceive odors of food during mastication. In man these functions, whatever they are, are evidently assumed by the turbinal convolutions.

II. Cartilaginous Investment.

Born and Solger have given good accounts of the anatomical relationships of the olfactory organ, in its relation to the bones of the cranium, the skeletal parts of the

nose, etc. The olfactory cavity is first enclosed with a cartilaginous or bony investment in *Elasmobranchii*. *Polypterus*, the most highly developed of the fishes, has a complicated system of folds around a spindle. These compartments increase the surface of the cavity, a nerve passing to each fold. In *Dipnoi* and *Perennibranchiata* there is an external perforated cartilaginous capsule. In *Amphibia* true turbinals first appear, processes of the cranial skeleton which serve to increase the epithelium exposure. These spaces and cavities attain to considerable development in *Anura*.

Born has very fully dealt with the bony environment as found in adult *Anura*, taking *Rana esculenta* as an example. In *Crocodylia* and onwards, the olfactory organ is situated farther backwards, the posterior part lying immediately below the brain. In *birds* we have one true turbinal and two pseudo-turbinals, while in *mammals* the surface is increased by three methods; the formation of the hard and soft palate, the development of the turbinal bones, and the formation of the accessory cavities of the nose.

The type chosen in the present studies for delineating the nasal cartilaginous investment in *Amphibia* is a specimen of *Urodela*, *Amblystoma punctatum* taken at about the time of the metamorphosis. The description of the type before us is based on a close comparison of the specimen under investigation with the description of the investment of an adult *Axolotl*, and *Amblystoma opacum* which is a North American species developed from an *Axolotl* form. This description is found in "The Morphology of the Skull," by W. K. Parker, (No. 20.)

The broad flat *inter-nasal* tract of cartilage in Figs. 1-15, Plate V, occupies only about one-third of the longitudinal axis of the skull, while its breadth is approximately the width of the head. It has a concave margin behind, in which is lodged the fore part of the brain. The anterior margin is also concave where the two trabecular cornua separate. The olfactory crura pierce the shelving front wall of the cranium (in the internasal plate) just on the inner surface. The cartilaginous processes of the nasal plate nearly meet externally and in one case actually

connect on the lateral aspect of the olfactory cavity. (See Fig. 7, Plate V, *in*.) The external nares are bounded in front by the incurved anterior cornu, and above and below by the dorsal and ventral cornua of the internasal plate.

The *pre-maxillary*, seen in cross section (*in*, Figs. 1-10, Plate V), sends a process backward over the internasal and overlapping for a short distance the frontals, (see *px*, Figs. 5-10, Plate V). The nasal processes of the pre-maxillary meet in the middle line through almost their whole extent, in this type, so that the internasal cartilage is not visible from above, and the membranous space which in other examples exists in front of the cartilage, is reduced to a fissure. This bone does not, as in *Axolotl*, surround the olfactory cavity upon its external aspect, but seems to be pushed dorsad and above, its lateral investing function being usurped by the large maxillary seen at *mx*, Figs. 7-15, Plate V.

The premaxillaries do not develop a palatal plate, but the *maxillaries*, which are very much lengthened backwards toward the mandibular articulation, have an turned edge which Parker describes as a rudimentary palatal plate. The maxillaries have also a short nasal process extending dorsad and backwards. (See Figs. 9, 10, 11, Plate V.)

The *naso-lachrymal*, as seen in Fig. 19, Plate V, *nl*, just after it emerges from the general cavity of the nose, is found lying encased on three sides by the maxillary; and by two small processes of the nasal, forming for a short distance a slight groove in which it rests. This complete envelopment in the investing cartilages is well shown under a higher power in Fig. 5, Plate VI. This position it retains until it approximates the surface of the head, when it lies in a slight depression in the nasal. Finally as it bifurcates on its approach to the eye (Figs. 13-15, Plate V, *nl*) it lies entirely free just beneath the surface of the skin.

The *frontals* are seen in Figs. 5-15, Plate V, at *f*. Each frontal is overlapped by the nasal process of the pre-maxillary, (*px*, Figs. 5-10,) by the nasal (Figs. 13-15, *n*) and by the ectethmoid (not shown in figures, lying as it does farther caudad).

The frontals appear to be larger than the parietals which they partially overlap; the parietals lying just in front of the auditory capsule are not represented in the figures.

The *nasals* (Figs. 6-15, *n*) are wedged in between the nasal process of the premaxillary in front, and the ectethmoid behind, meeting the maxillary at different points laterally. The nasal, like the frontal bones, is closely applied to the cartilaginous plate and olfactory capsule, but does not graft itself upon the cartilage so as to ossify it. A general knowledge of the relations of the investment in the different types of Amphibia under discussion may be gained by a comparison of the various drawings of models and sections; especially see Plates X-XII.

III. *Naso-lachrymal and Glands.*

The general relations of the *naso-lachrymal* in Amphibia, to the apparatus which corresponds to it in higher vertebrates has been amply discussed by Born (No. 4.) We here briefly describe it as we have found it in different types, and from drawings of our own.

The *Naso-lachrymal* duct conducts the lachrymal secretion from the conjunctival sac of the eye into the nasal cavity. This duct is found in some cases as a shallow furrow which runs downward to the upper margin of the mouth. This stage is the permanent condition in many *Selachians*, and is found in the embryonic stages of some higher types. (See European salamander, below.)

The *naso-lachrymal* duct in *Salamandra atra*, European salamander, at first where it has its origin in connection with the eye, (within the inner lower lid of the eye) passes as a *naso-lachrymal* sinus for most of the way until it comes into the vicinity of the olfactory cavity where it dips beneath the surface passing for a short distance as a closed duct. See model, Fig. 1, Plate XI, *nl, or, op, ey*; dorsal view, as also of *Amblystoma*, Fig. 3, Plate XII. This duct then suddenly drops ventrally ending in a ventro-lateral diverticle of the cavity at *or*. This is seen in Fig. 1, *nl*, Plate VI and Fig. 2, Plate XI, *or*, and Fig. 1, Plate XI, *or*.

This tube appears in cross-section also as a mere group of cells arranged as seen in Fig. 2, Plate VI, *nl*, *epit* etc. A series of cross-sections shows this tube to consist of a mere grouping of cells with an ill-defined duct within. The cells are arranged in a circular manner leaving this space within which opens above into the groove and below into the lumen of the diverticle. This is shown at a later stage in *Amblystoma*, Fig. 5, Plate VI, *nl*. From the general cavity of the nose there projects a lumen into this diverticle, which is continuous with the tube of the above mentioned duct. This duct then passes laterad, dorsad, and caudad as above described. The eye-ball, *ey*, is much reduced comparatively, and shows roughly the reconstruction of the bifurcated opening of the naso-lachrymal upon the lower eye-lid. In this figure (Fig. 1, 2, Plate VI) the tube is situated just below the epidermis and can be followed for several sections quite distinctly until it emerges upon the surface as a groove or furrow. See Fig. 1, *nl* and *op*, Plate XI.

Under a high power the cell-walls may be discovered of these epithelium cells as well as of the characteristic connective-tissue cells with which they are surrounded (Fig. 2, *epit* and *con*, Plate VI). An outer layer of epithelium cells intervening between the true epithelium and connective-tissue cells have become flattened and adhere to the outer sides of this tube. See also Fig. 5, *epit* and *con*, Plate VI. Surrounding it is, further, the fibrous tissue which binds the tubular structure somewhat to the skin beneath which it lies. Chromatophores line the skin here very abundantly. See *fig*, Figs. 1, 2, Plate VI. This abrupt change in the course of this duct appears almost entirely within three or four sections (which are not more than 15-20 micromillimeters thick.) At this stage the lachrymal glands are not developed to any extent, which accounts for, or correlates with the undeveloped condition of the duct. As seen in the other types the duct here also divides into two tubes for a short distance before entering upon the open surface of the lower lid (*op*, shown also in Figs. 3, 4, Plate XI.)

This diverticle, out of which the naso-lachrymal leads, may be homologized with the smaller outer, upper diverticle found in

tadpoles (*od*, Fig. 5, Plate X; also Fig. 5, Plate XI.) A close homology will be seen to exist between this type and other Urodela. See Figs. 3, 4, *nl*, *or*, *op*, *ey*, etc., Plate XII.

A very similar condition and relative position for this duct is seen to exist in *Amblystoma punctatum*. Its entire course from the point where it originates upon the lateral aspect of the cavity from its peculiar diverticle (see *or*, Figs. 3 and 4, Plate XII) to its opening upon the lower lid of the eye (*op*, Fig. 3, Plate XII) is seen in Fig. 3, Plate XII. Its course, as in *Salamandra atra*, is in general parallel to the longitudinal axis of the nasal cavity. Having its origin just behind and a little mesad of the exterior nares it courses backward, ending just dorsad and a little laterad of the internal nares.

Fig. 3, Plate VI is a transverse section showing the origin of the naso-lachrymal, *nl*, from the general cavity of the nose, *gen*. In this figure is seen the opening of the cartilaginous investment through which this duct makes its exit between the two internal processes, *in*. The real tube of this duct can only be distinguished from the many gland ducts with which it is associated by this internal connection with the general cavity, *gen*. The structure of this duct, and the epithelium membrane which lines it is nicely shown in Fig. 5, Plate VI where it is revealed under a high power. In *Amblystoma* this duct appears at one point to be completely enclosed within the bony investment, but for only a short distance. See Fig. 5, Plate VI, *n* and *mx*. *Ey*, Figs. 3 and 4, Plate XII, as in *S. atra*, shows the eye much reduced, to illustrate the method of termination of the duct.

In adult Anura, *Hyla versicolor*, *Bufo lentiginosus*, *Rana virescens* etc., the outer tip of the lateral cul-de-sac breaks through the investment (see Figs. 3 and 4, Plate VIII, *nl* and *or*) and makes its way through the bony environment in the form of a tube extending outward and backward toward the eye (*nl*, fig. 5, Plate VIII). In *Pelobates fuscus*, says Born (No. 4), the canal passes backward, as mentioned, only in this case enclosed in a tubular extension of the bone. In other Anura it lies in a mere hollow in the bone. From this point, as in the other cases, it passes in the direction of the under eyelid where

it ends in two grooves which separately open upon the free margin of the inner half of the lid. In the larvæ they end on the inner side, while in the adult, as a rule, they end nearer the outer side of the lid.

"If in an adult frog you expose the three nasal cavities" says Born (No. 4), "it is easily possible to see in the section of the lateral sac a fine tubular connection" which may be recognized as the naso-lachrymal duct. How this tube closes up from its original position as a mere groove is not yet clear, but it is always so seen. The canal never appears in the adult as a groove but always as a closed cavity. It appears, on section, in connection with a black band, in the larvæ, which in *Rana esculenta* stretches from the eye to the nose. The canal passes out through the upper nasal glands, *up* (Fig. 3, Plate VIII), is widest nearest the nasal end and narrows on approaching the lid. This is nicely shown in *Bufo lentiginosus*, Fig. 1, Plate XII, *up*, *or*, *nl*. Its epithelium is, in general, of the same character as that of the lateral cul-de-sac.

The general relations of the naso-lachrymal in the adult *Rana virescens* were so nearly identical with those in *Hyla versicolor*, that the conditions as found in the latter only were modelled. It is essentially such as described by Born in his work entitled "Ueber die Nasenhöhlen und den Thränenasengang der Amphibien" (No. 4). These relations are modelled in Figs. 3, 4, Plate XI, at *nl*, *or*, *bi*, *up*, etc. Figs. 3-6, Plate VIII, *nl* and *or* are four camera-drawings which illustrate the methods of origin of the duct in both these types.

In *Bufo lentiginosus* modelled in Figs. 1 and 2, Plate XII, we find the naso-lachrymal originating as in all Anura from its own special diverticle, *lc*, upon the external aspect just behind the external nares, *extl*. In spite of the marked difference in the general configuration of the nasal cavity in this type as compared with other adult Anura, it is not difficult to homologize it with other types in this respect. See *nl*, *or*, *up*, etc., figs. 1, 2, Plate XII.

Born (No. 18) further has shown in the *lizard* and *chick*, at the base of the groove separating the nasal passage from the

folds which represents the eyelids, a rod-like thickening of the epidermis which seems to be distinct from its mesodermic surroundings, and to resemble the naso-lachrymal duct; ending, as it does, in the lower eyelid, where as usual it splits in two, the outer branch not quite reaching the epidermis while the inner one does.

Glands.—Bowman's glands (in *Gymnophiona*) are grouped on the dorsal transition area of the olfactory organ where it bulges out to form what has been homologized with the Jacobson's diverticle. Burckhardt further distinguishes in this group what he calls Jacobson's gland which forms a richly branched mesh-work at the base of the olfactory sac where it opens into the external nares, the structure being the same as the dorsal nasal glands.

These glands as seen in *Urodela* are well exhibited in Fig. 4, *gla*, Plate VI, *Diemyctylus viridescens*, where they are seen in connection with the diverticle *jd*, which is characteristic of this group. See also fig. 3, Plate VI, *gla*, *Amblystoma punctatum*. They are further shown in the different models lying, as they do, in their different relative positions in the different types.

In *Salamandra atra* they are seen in Fig. 1, Plate XI, *gla*, dorsal view of cavity, just a glimpse of them being obtained in this figure as they are hidden by the overarching projection of the premaxillary. In fig. 2, Plate XI, *gla*, which represents a ventral view of the same they are seen lying on the inner ventral aspect of the cavity at about the center of its longitudinal axis.

In *Amblystoma punctatum* they lie scattered more promiscuously along almost the whole ventral median aspect of the cavity as seen modelled at *gla*, Fig. 4, Plate XII. They are represented in the model by ridges or furrows. See also *gla*, fig. 1, Plate VII, also *gla*, Fig. 1, Plate IX and figs. 3-5, Plate V.

Born distinguishes in *Anura* four different groups of glands: two opening into the nasal cavity and two emptying into the mouth and throat respectively. The two latter, the intermaxillary and choanal, on account of their position, are not shown

in the models. The former two are the upper and lower nasal glands. Born has fully discussed the position and structure of these different groups, we will here only indicate upon the model their position as found in several different types of Anura.

Figs. 6 and 7, Plate X, which are pen-drawings of wax models of right cavity of tadpole of leopard frog, *Rana virescens* show the glandular formation even at this stage, *gla*. It is observed that in this case as in most of the larval Anura the glands lie in close connection with the inner diverticle, *id* or *jd*.

Fig. 7, Plate XI, which shows the dorsal view of an older tadpole shows these glands lying upon the median aspect of the cavity supported below by the fundament of the internasal tract of cartilage, *in*. In this stage they have attained to larger dimensions than in those before referred to.

Figs. 3 and 4, Plate XI, are dorsal and ventral views respectively of model of nasal cavity of an adult tree-toad *Hyla versicolor*. In this stage both groups of glands are developed. The upper nasal glands are seen at *up*, fig. 3, Plate XI, the lower at *lo* in both figures. The latter are situated as in the larvæ upon the median aspect of the cavity but farther forward, relatively, in the adult. The former lie upon the latero-dorsal aspect just behind the anterior (or external) nares, *extl*. They are much smaller than the lower nasal glands.

In *Bufo lentiginosus* which is modelled in Figs. 1 and 2, Plate XII, are also seen the upper and lower groups of nasal glands, *up* and *lo*, situated relatively in the same positions as above described. They are modelled as adhering to the respective diverticles of the olfactory cavity for convenience and durability of the models.

The paucity of glands in *Lacertila* and *Ophidia* as compared with the other reptilia seems to be compensated by the greater development of Jacobson's organ, which being a smaller organ would not require such a profusion of glands. See Figs. 2, 3, 4, 5, 6, Plate IX, *gla* and *jo*. In mammals the Bowman's glands are diffuse.

IV. Innervation and Histology of the Epithelium of the Nose and Jacobson's Organ.

Histology of the Epithelium.—The olfactory epithelium is usually the simplest form of neuro-epithelium found in animals.

The single olfactory cells which are the first indications of a specialized sense-organ for smell, are the phylogenetic derivatives of the olfactory buds seen in the olfactory crypts in the adult higher forms. In almost all cases the olfactory epithelium is more highly developed on the side toward the brain, the thinner walls of neuro-epithelium lying upon the ventral and lateral surfaces. It is often lobed or corrugated also on the side nearest the olfactory bulb, where then nerves enter. See Fig. 3, *cor*, Plate VII.

The uncertainty formerly existing in the minds of many investigators as to the exact nature of the termini of the olfactory nerve in the nasal cavity and in Jacobson's organ seems now to be quite satisfactorily removed. The concurrent testimony of so skillful investigators as Cajal, Van Gehuchten, Lenhossék, Brunn and Retzius, leaves but little doubt that the so-called olfactory cells of the olfactory epithelium and of Jacobson's organ are real nerve cells and that there is actual nervous continuity between the cilia at one pole and the fibre of the olfactory nerve springing from the other pole of these cells. Preparations recently made in our laboratory both by the Golgi method and by the hæmatoxylin process (and figured in Plate XIX, Figs. 1, 2, and 3; plate XX, Fig. 3, *Journal of Comparative Neurology*, September, 1893) prove conclusively, if additional proof were necessary, that the fibres of the olfactory nerve as they pass into the olfactory tuber break up into terminal brushes ("end-bäumchen") in the glomerules without coming into relation with any cells at this end of their course. In accordance, then, with the current morphological ideas of nervous structure, the peripheral neuron of the olfactory system would consist of the olfactory ganglion cell in the nasal membrane, its axis-cylinder process which forms one of the constituent parts of the olfactory nerve, and its terminal brush in the

glomerule. See Current Views of the Structure of Olfactory Organs and Taste-bulbs, Journ. Compar. Neurol., III, Sept, 1893.

Previous investigators have discovered a difference in the nerve end-filaments as found in olfactory epithelium, as compared with the epidermal, optic, auditory and gustatory. They have claimed that in the former case the nerve filaments enter into immediate connection with the cells. Recently some authors have endeavored to show that filaments enter the cells of Corti in the ear, and the cells of the corium of the skin. But these investigators (notably Ayers and Pfitzner) have not made good their claims to the satisfaction of many, so that the olfactory epithelium still appears to hold its peculiar position in this respect.

Our own studies of the olfactory epithelium of trout, salamander and frog, confirm the general belief that there are two kinds of cells, the smaller sensory type, and the larger moniliform supporting type. (Fig. 6, Plate VII; Fig. 2, 4, 5, 7, *Frog*, *a*, Plate VII). The smaller cells (Trout) are probably as Max Schultze calls them, "the true olfactory cells." They consist of a nucleus and two long processes, the one ending upon the surface of the mucous membrane and ciliated, and the other passing back through the ganglionic nutritive layer and terminating in connection with a filament from the nerve-bundle. The larger supportive cells (Figs. 2-7, *b*, Plate VII) are also ciliated upon their free ends and as indicated by the term, moniliform, seem to consist of several cells superimposed upon one another, forming a bi- or tri-nucleated rod, as it were. That these are really several cells successively impinged one upon another, and not, as some seem to think, poly-nucleated single cells seems to be quite clearly demonstrated by a careful drawing of a portion of the olfactory epithelium in *Amblystoma punctatum*. See Fig. 2, *a*, *b*, Plate VII.

A peculiarity of the olfactory cavity of *Amblystoma* is the presence and marked development of numerous crypts formed by the deep folds in the olfactory epithelium (Fig. 1, Plate VII, *Cry.*) Between these and lying about and among them are the

numerous small glands which seem to have their openings in the interspaces of the crypts. (Fig. 1, *gla*, Plate IX). This arrangement is seen in Fig. 6, Plate VI, in cross section, and in Fig. 1, Plate VII, longitudinal section. See also Fig. 2, Plate VII, *epi*.

The model of *Amblystoma* shows also transverse and longitudinal sections of the nerve-bundles supplying the olfactory cavity. They are shown on the model cut off obliquely as they enter the olfactory bulb. (Fig. 4, Plate XII, and in section, Fig. 6, Plate VI, *cn* and *ln*.) Fig. 1, Plate X, *oln*, represents the innervation of the nasal epithelium of the tadpole showing the nerve-bundle as it originates in the olfactory bulb.

The innervation and histology of Jacobson's organ is in general comparable to that of the nose proper. With regard to the innervation of Jacobson's organ it is probable that the division of the olfactory nerve into two branches is not as Wiedersheim and Marshall formerly believed, homologous with the two branches of a cranial nerve to each side of a gill-cleft, but a division into two bundles passing respectively to the nose proper and Jacobson's organ, and where no diverticle is present, completely homologous with the similar division where it is present (as in the Reptilia).

The sensory epithelium of Jacobson's diverticle in *Gymnophiona*, says Burkhardt, remains as in the embryonic condition without any tendency to form sensory buds as in the olfactory proper, which indicates a retardation as compared with the nasal epithelium.

In *Amphibia* in general the nerve-bundle for Jacobson diverticle passes to a little pit (the olfactory fossa) on the olfactory tuber with connections to the radix lateralis, as in Reptilia. The olfactory nerve of *tailed Amphibia* (salamander) corresponds in its relations to the cerebrum, decidedly, to the lower branches of the olfactory nerve of frog larvæ and *Gymnophiona*.

Beard, speaking of its histology in *Reptilia*, finds the nerve-fibres ending in the bases of the ganglionic columns which lie just within the true epithelium cells. He says distinctly that the nerve-fibres do not pass between the columns or crypts, but

end at their base. In this he finds a close resemblance as in other respects to the olfactory epithelium proper. This crypt-like arrangement of the ganglionic columns of the olfactory epithelium as found in the Ophidia Beard also points out in an obscured situation in Lacertilia, and we have found it present also in several species of Amphibia. His conclusion in general is that Jacobson's organ in Lacertilia and Ophidia is a very highly specialized portion of the epithelium, and says that it, in these cases, at least, must be an incomparably finer sense-organ than their nose proper (No. 1.) On the structure of Jacobson's organ we have investigations by Klein, Leydig, Wright, Born and Solger, but as to the important question of its real nature and origin these are sadly deficient.

V. Evolution and Development of Jacobson's Organ in Particular.

Jacobson's Organ is without doubt as Beard says, "a specially differentiated part of the nose." It was discovered by Jacobson, the Danish anatomist, at the beginning of the present century. We will here endeavor to make a comparison of the different types possessing what we think to be the fundament or proton (Anlage) of a Jacobson's organ. In general it is safe to assert that no Jacobson's organ appears in any type lower than fishes, if indeed in fishes there can be found any true homologue of Jacobson's organ. In *Polypterus*, indeed (the most highly developed of fishes) there is a short distinct oval sac in the median line which has no connection with the rest of the olfactory, and which receives a special branch of the olfactory nerve, but it is doubtful if this is to be homologized in any sense with the true Jacobson's organ as found in the higher types.

In *Caecilians* there is a sac having a separate opening in the mouth, but this is to be homologized with the maxillary sinus (air-chamber) of higher vertebrates. Jacobson's organ is described by one author as a paired accessory nasal cavity, which in an early embryonic stage becomes entirely separated off from the nasal chamber, and which is supplied by the olfactory

and trigeminal nerves; it communicates with the mouth by a special aperture. This definition applies accurately to the accessory nasal chamber of *Caecilians*, already mentioned; in no other vertebrates, however, does it retain the character of a kind of separate nasal chamber, but on the contrary, the higher we pass in the vertebrate series, the more does the maxillary cavity become separated physiologically from the olfactory organ; it loses its olfactory epithelium and finally degenerates into a simple air-sinus.

Beard says that the so-called Jacobson's organ of *Gymnophiona* is not homologous with that of Reptilia but only a secondary olfactory organ, while the two-fold division of the olfactory nerve, though comparable, is yet not homologous with the condition found in Reptilia. Again Wiedersheim in his attempt to homologize the outer diverticle which he found in *Gymnophiona* (*Ichthyophis*) with the Jacobson's organ of Reptilia, found the difficulty confronting him that this diverticle appeared upon the outer side whereas in every case the true Jacobson's organ has been found lying on the inside of the nasal cavity proper. He therefore concludes that there is no homology or if there is he confesses the difficulty, while Beard denies the possibility, calling it a secondary olfactory organ, to prevent confusion.

Our studies lead us to an entirely different conclusion. We believe that this diverticle which Wiedersheim found, is in the original position of the primitive Jacobson's organ as an outer diverticle, and that in the course of its evolution it revolves from without, inward (i. e. from laterad, entad) until it holds the position seen in other Amphibia and Reptilia: viz. on the median aspect of the olfactory cavity proper. This, of course, would place *Gymnophiona* in this respect lower than *Anura* and possibly lower than *Urodela* in the phylogenetic series. There is some evidence, indeed, for believing that *Urodela* are but an arrested stage of a higher type—a higher amphibian arrested permanently in its larval condition. At any rate the adult conditions as found in *Urodela* are undoubtedly a transition stage from *Gymnophiona* and *Caecilians* and other lower types of Amphibia to *Anura* and the higher types.

The Sarasin brothers have some time since suggested that a diverticle of the nasal cavity of the salamander larva and newt may be homologous with this so-called Jacobson's organ of Gymnophiona, but no researches had yet been made. Burckhardt suggests that possibly the salamander is derived from forms which originally possessed a Jacobson's organ. We think it more likely that the salamander is a transition stage, as above suggested, in which the diverticle, which is the fundment or proton of Jacobson's organ, is not yet separated to act as a distinct organ.

Figs. 3 and 4, Plate XII, represent dorsal and ventral views of the model of the right nasal cavity of the American salamander, *Amblystoma punctatum*. Contrary to the general configuration of the nasal cavity of the frog, tadpole, etc., the curvature presents its convex surface toward the median line, or vice versa, its concave aspect is laterad. This peculiarity of curvature is constant among salamanders: see the model of European *Salamandra atra*, Figs. 1 and 2, Plate XI, drawings, etc. This curvature brings the external and internal nares toward the lateral line, whereas in the tadpole the internal nares are further toward the median line. The relative position of the nares in the *adult* frog or tree-toad is more nearly comparable to the condition in *Salamandra* both larval and adult. In following through a series of transverse sections of the nasal cavity of this type, we find the diverticle, which we attempt to homologize with the Jacobson's organ of higher types, lying quite laterad: see Figs. 3 and 4, Plate XII, *jd*; and Figs. 8, 9, 10, Plate V.

In *Salamandra atra* this diverticle lies more ventrad: see Fig. 2, Plate XI, *jd*; while in larval Anura it lies on the ventral median aspect: see Figs. 7 and 8, Plate XI, *jd*; and Fig. 5, Plate XI, *id*. In adult Anura it seems to become partly obscured by the change in external configuration;—the crowding forward and shortening of the longitudinal axis of the whole cavity. But even there it remains discoverable in the light of this homology, being confused by some authors with the so-called maxillary sinus which does not occur in its true form in the amphibian nasal apparatus.

Fig. 1, Plate XI, is a representation of a directly dorsal view of the right nasal cavity of a larval European salamander (*Salamandra atra*). Essential points of resemblance are immediately observed to exist between this European type and Amblystoma. The model as above figured is enclosed in its cartilaginous investment and so the complete homology is partially obscured; but in fig. 2, Plate XI, which shows the same model from a ventral view the points of resemblance are more fully brought out. Although the exterior shows some difference in general configuration, the European being narrow and thick and rounded, broad and flat and much thinner in comparison; yet the relative situations of the different parts are the same. It must also be taken into account that the former is a model of the larval cavity while the latter is a model of the cavity of an adult Amblystoma. The comparison of the investmental relations brings out still more markedly the difference in the comparative age of the two specimens (compare Figs. 1-15, Plate V, with *in* and *px*, Figs. 1, 2, Plate XI). The model of the European salamander is much more highly magnified, absolutely, than that of Amblystoma. The internasal plate is not as yet completely united along the median line, while the only one of the external cartilaginous plates which was sufficiently differentiated to be modelled was the pre-maxillary which sends back its overarching process as seen in Fig. 1, Plate XI, *px*.

There remains to be remarked the correspondence in the position of the curious *diverticles* which are present in each case. One of these, the nasolachrymal, *or*, is discussed elsewhere. The other is seen in section, Fig. 1, Plate IX, *jd*, and is figured upon the model at *jd*, Fig. 2, Plate XI.

From camera drawings upon sheets of wax (the same method has been followed in all) the model figured in Fig. 6, Plate XI, was constructed to show the right olfactory cavity of a young tadpole, larval, body length 5 mm, leopard frog, *Rana virescens*. At this early stage the nasal sac consists of a general cavity with its two diverticles and its external and internal nares, *od*, *id*, *extl* and *intl*, Fig. 6, Plate XI, and Fig. 5, Plate X. The general curvature of the organ from its external to its internal

terminus is with its concavity mesad. In the proximity of the internal opening it is characterized by a great thickening of the epithelial wall (Fig. 3, Plate X, *t*). On the outer aspect of the cavity among the rather irregular modifications of the epithelium wall, an outer small diverticle is apparent which is quite distinct from the mere corrugations of its surface. See *od*, Figs. 1, 2, Plate VIII, 2 and 5, Plate X, and Fig. 6, Plate XI. This diverticle is evidently transitory as it does not appear in either of the older specimens (Figs. 6 and 7, Plate X, and Figs. 7, 8, Plate XI). On the inner aspect midway between the nares, rather ventral than dorsal, and somewhat lower and further forward than the smaller outer diverticle, is situated another and larger diverticle which, as has been hinted, may be homologized with Jacobson's organ in higher types (Reptilia etc.) See Figs. 2, 3, 5, 6, 7, Plate X, and Figs. 5, 6, 7, 8, Plate XI, *id* and *jd*. Large and apparently active glands lie immediately dorsad and in close connection with the diverticle, having also close connection with the general cavity, in the epithelial interspaces. See Figs. 6, 7, Plate X, Figs. 6, 7, Plate XI, *gla*, *epi*.

Fig. 6, Plate X, represents the inner aspect of a model of an older tadpole, over a centimeter in length, of the same species; *jd* represents in this figure the inner larger diverticle homologous, as we believe, with Jacobson's organ in Reptilia. Fig. 7, Plate X, shows a view of the same model looking down from above as it would be situated in its place within the right side of the head of the tadpole. The marked difference between the model figured in Fig. 5, Plate X, and Fig. 6, Plate XI, and this one, lies in the disappearance of the outer smaller diverticle, and in the comparative enlargement of this inner larger one with its glands (Figs. 6 and 7, Plate X, *gla*). The difference in the absolute size of the models, as in the other cases is due partly to the fact that lenses of different degrees of magnification were used to make the camera drawings in the different cases, and partly to the real differences in the sizes of the specimens under investigation.

In Fig. 1, Plate X, we have a camera sketch of a horizontal section through the right cavity of the tadpole modelled in Fig.

5, Plate X, and Fig. 6, Plate XI, revealing the entrance of the olfactory nerve-bundles from the olfactory tuber, *oln*. This view corresponds to a section of the model taken at D, Fig. 5, Plate X. In this section the opening in the cartilaginous fossa, *in*, shows the bundles in their connections with the *bulb*. Fig. 2, Plate X, is a section taken more ventrad, represented on the model as a section at E, Fig. 5, Plate X. This horizontal section shows the opening from the general nasal cavity, *gen*, into the outer smaller diverticle *od*, also the external nares *extl*, and the upper wall and very small beginning of the lumen of the cavity of the larger inner diverticle, *id*. In Fig. 3, Plate X, represented by a section of the model taken at B, Fig. 5, Plate X, we see the opening of the general cavity *gen*, into that of the inner diverticle, *id*. Also we see the great thickening of the inner wall, *t*, in the vicinity of the internal nares. It seems to be constant throughout that the wall becomes thickened on the inner, median side probably due the fact that it is on this side that the nerve termini make their closest connections. It is also on this inner aspect of the nasal cavity that corrugations generally appear, due perhaps to the entering, at different points, of distinct nerve-bundles. Fig. 4, Plate X, shows the internal nares, *intl*, and is represented by a section of the model in the plane indicated at C, Fig. 5, Plate X. Here again we notice the thickened inner epithelium wall, *t*. In Fig. 1, Plate VIII, we have a horizontal section of another specimen than the one modelled, from which the previous drawings were taken. This tadpole was also somewhat younger, but sufficiently similar to make comparisons with the same model. Here is seen the outer diverticle in a slightly different plane upon each side of the head, *od*, and also the external nostril, *extl*, upon the right side. A section taken at A, Fig. 5, Plate X, would show such a view as this. Fig. 2, Plate VIII, is a drawing of a transverse section also of a younger specimen, showing the opening into the lumen of the outer diverticle, *od*, and also showing a nerve-bundle entering upon its median-dorsal aspect, *oln*. Such a view would appear in a section of the model taken in the plane indicated at F, Fig. 5, Plate X.

The amphibian *Anura* during embryonic life are, as we have said, possessed of two diverticles, an outer upper lateral and an inner lower mesal one. Says Balfour (Compar. Embryology, No. 8), "a diverticle of the cephalic portion of the nasal cavity of *Anura* (frogs) is probably a rudiment (proton) of Jacobson's organ." Fleischer finds the likeness between the lower diverticulum of *Anura* (embryos) to the Jacobson's organ in reptiles and describes its subsequent probable development in the following words: "In the course of further development, (after the diverticulum stage), it passes further downwards and in doing so gets turned about its axis, so that the canal by means of which it was still connected with the nasal cavity comes now to open into the mouth cavity." We think it probable as before suggested that not only is this true, but that there has taken place a previous revolution from its external (lateral) position ventrad and mesad from the position which it occupies in *Gymnophiona* and some salamanders until it reaches the position as found in tadpoles, and further that this process is carried on beyond the stage mentioned by Fleischer until the diverticle comes to lie entirely mesad and as a separate organ (now known as Jacobson's organ). These remarkable changes in relative position are made strongly probable moreover by the corresponding shortening of the head, seen in its progressive stages corresponding to the advancing revolution of the diverticle. Beard is inclined to doubt the complete homology throughout, but our own researches in these various types seem to confirm the suggestions of Götte, Fleischer, Born, and Kölliker who have hinted at this homology.

A cross section through the nasal sac in an adult frog, in front of the internal nares, reveals three cul-de-sacs. The first is an upper wide and rounded cavity, the second a smaller lateral sac opening into the naso-lachrymal duct, and the third a lower smaller cavity communicating with the mouth by the internal nares and with the so-called maxillary sinus by an oblique cleft. The inner nares open into the mouth from the most lateral point of this maxillary cavity. In the higher types we find that this maxillary sinus, by the elongating of the palate, opens

not directly as here, into the oral cavity, but into the general cavity of the nose proper. These relations are well shown in the model of *Hyla versicolor*, Fig. 4, Plate XI, and Fig. 5, Plate VIII.

In the *lizards* Jacobson's organ is described as a small paired cavity lined by olfactory epithelium from the floor of which a papilla arises. This papilla is shown in Fig. 6, Plate IX, in *Eutænia*, and in Fig. 3, Plate IX, *pap.* It communicates with the mouth by a special aperture in front of the internal nares. See *Eutænia*, Figs. 3 and 4, Plate IX, *ap.* Beard (No. 1) says "It is now a fact that Jacobson's organ of reptiles is a specially differentiated part of the nose" but that "it must be an incomparably finer sense-organ than their nose proper." It is best developed and most functional in *Lizards*, Figs. 2-6. Plate IX shows these general relations in Reptilia, in *Eutænia* and black snake embryos. It is noticeable that in Lacertilia the parietal eye and Jacobson's organ are both functional, whereas in Anura and Urodela (Amphibia in general) both are degenerated or undeveloped. The question arises whether the diverticle is a degenerated Jacobson's organ, or Jacobson's organ a developed and perfected diverticle. We incline to believe the latter to be the true statement of the case. There is a remarkable gap in this respect between the two groups of Reptilia, Ophidia and Lacertilia on the one hand and Chelonia and Crocodilia on the other hand; the former possessing a Jacobson's organ so highly differentiated and the latter possessing only a rudimentary organ which until recently has defied detection in *Crocodilia*. This discovery was made by C. Rose, "Ueber das rudimentäre Jacobson'sche Organ der Crocodile und des Menschen." Anat. Anz. VIII, 14, 15, June, 1893. (No. 22.)

Further the two groups in which Jacobson's organ is well developed are, aside from its development, endowed with a very simple nose proper as compared with the conditions as found in Crocodilia and Chelonia. It appears that these two things were related in some way. Perhaps the nose proper of these two groups has a simple structure because of the high development and extreme delicacy of their Jacobson's organ, and Crocodilia

and Chelonia on the other hand are recompensed for the absence of any functional Jacobson's organ by the much greater complexity of their nose proper.

Jacobson's organ is very general in *mammals* especially rodents, ruminants, perissodactyles, where it exists as a mere tube ending blindly posteriorly and opening anteriorly into the mouth by the ducts of Stenson (or naso-palatine canals). A small depression on the median wall of the nasal pit in mammalian embryos is the proton of Jacobson's organ. The external nose of mammals is derivative of the outer chamber mentioned in Caecilia. The Jacobson's organ of *man* lies high up, far above the basales narium cartilage, which has its usual position.

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TABLE OF REFERENCE.

<i>a.</i> —true olfactory cells.	<i>jo.</i> —Jacobson's organ.
<i>ap.</i> —aperture of Jacobson's organ communicating with the mouth.	<i>lc.</i> —lateral cul-de-sac in adult Anura.
<i>b.</i> —supportive olfactory cells.	<i>ln.</i> —longitudinal section of nerve-bundle.
<i>bc.</i> —blood corpuscles.	<i>lo.</i> —lower nasal glands in Anura.
<i>bi.</i> —bifurcation of nasolachrymal duct.	<i>loc.</i> —lower cul-de-sac in adult Anura.
<i>c.</i> —olfactory terminal cilia.	<i>mc.</i> —mouth (oral) cavity.
<i>cn.</i> —transverse section of nerve-bundle.	<i>mx.</i> —maxillary plate.
<i>con.</i> —connective tissue cells.	<i>mx.</i> —maxillary cavity.
<i>cor.</i> —corrugations of olfactory epithelium.	<i>n.</i> —nasal plate.
<i>cry.</i> —crypts in olfactory epithelium	<i>ncc.</i> —nasal capsular cartilage.
<i>ep.</i> —epidermis.	<i>nl.</i> —naso-lachrymal duct.
<i>epi.</i> —epithelial interspaces.	<i>od.</i> —outer smaller diverticle in larval Anura.

<i>epit.</i> —epithelial cells.	<i>oln.</i> —olfactory nerve.
<i>extl.</i> —external nares.	<i>olnb.</i> —olfactory branch from V nerve.
<i>ey.</i> —eye.	<i>op.</i> —opening of naso-lachrymal duct upon lower eyelid.
<i>f.</i> —frontal plate.	<i>or.</i> —origin of naso-lachrymal duct.
<i>gen.</i> —general cavity of nose.	<i>pap.</i> —papilla of Jacobson's Organ.
<i>gla.</i> —glands.	<i>pig.</i> —pigment cells.
<i>id.</i> —inner larger diverticle, in larval Anura same as <i>jd.</i>	<i>px.</i> —premaxillary plate.
<i>in.</i> —internasal cartilaginous plate.	<i>t.</i> —thickened part of epithelium.
<i>intl.</i> —internal nares.	<i>up.</i> —upper nasal glands in Anura.
<i>d.</i> —homologue of Jacobson's organ, same as <i>id.</i>	<i>upb.</i> —upper cul-de-sac in adult Anura.

DESCRIPTION OF PLATES V-XII.

PLATE V, FIGS. 1 TO 15.

Series of camera drawings of cross-sections of the investmental cartilages in head of adult *Amblystoma punctatum*.

PLATE VI, FIGS. 1-6.

Fig. 1. Transverse section of embryo *Salamandra atra*, showing nasolachrymal in its origin and dorsal passage toward its emergence upon the epidermis.

Fig. 2. Camera drawing of the same, further caudad, showing the nasolachrymal duct in cross-section as it lies just beneath the epidermis.

Fig. 3. Camera drawing of nasal cavity of *Amblystoma punctatum*, showing entrance of naso-lachrymal duct, glands, etc.

Fig. 4. Camera drawing of olfactory cavity of *Diemyctylus viridescens*, showing glands and their connection with the olfactory cavity.

Fig. 5. Camera drawing of naso-lachrymal duct of *Amblystoma punctatum*, showing its position in the cartilaginous investment, also the histology of its epithelial lining.

Fig. 6. Camera sketch showing a portion of nasal cavity of *Amblystoma punctatum*, showing nerve bundles in cross-section, also in longitudinal section; and showing the crypts in the olfactory ganglionic layers.

PLATE VII, FIGS. 1-7.

Fig. 1. Camera drawing of longitudinal section of nasal cavity of *Amblystoma punctatum*, showing crypts, glands, external nares, etc.

Fig. 2. End-cells, *Amblystoma punctatum*, illustrating the formation of the so-called moniliform supportive cells; *a*, true olfactory (sensory) cells. *b*, supportive cells.

Fig. 3. Camera drawing of longitudinal section of nasal cavity of *Diemyctylus viridescens*, illustrating the corrugations and crypt-like involutions of the olfactory epithelium.

Fig. 4. Olfactory end-cells of *Rana virescens*; *a* and *b*, as above.

Fig. 5. Same, showing connection with nerve filaments.

Fig. 6. Sensory end-cells of olfactory epithelium of *Trutta fario*.

Fig. 7. Same as Figs. 4 and 5.

PLATE VIII, FIGS. 1-6.

Fig. 1. Camera drawing of horizontal section of right and left nasal cavities of tadpole, younger than the one figured in Fig. 5, Plate X, as young as that figured in Fig. 5, Plate XI. This section is indicated for convenience upon the same model as the above. See at A, Fig. 5, Plate X.

Fig. 2. Camera drawing of transverse section of right cavity of younger tadpole, as young as that figured in Fig. 5, Plate XI; plane of section indicated as above in Fig. 5, Plate X, at F.

Fig. 3. Camera drawing of transverse section of right olfactory cavity of *Hyla versicolor*, showing origin of nasolachrymal.

Fig. 4. Camera drawing of same, showing nasolachrymal as a duct in cross-section.

Fig. 5. Same, showing inner ventral diverticle, also nasolachrymal.

Fig. 6. Same, showing internal nares.

PLATE IX, FIGS. 1-6.

Fig. 1. Camera drawing of a portion of nasal cavity of *Amblystoma punctatum*, showing Jacobson's diverticle, the nasolachrymal duct in cross-section and a portion of the general nasal cavity.

Fig. 2. Camera drawing of transverse section of nasal sac and Jacobson's organ of *black-snake* embryo.

Fig. 3. Camera drawing of longitudinal section of *black-snake* embryo, showing nasal sac and Jacobson's organ opening into the mouth cavity.

Fig. 4. Same, showing Jacobson's organ opening into mouth cavity.

Fig. 5. Same, showing nasal sac completely enveloping Jacobson's organ.

Fig. 6. Camera drawing of horizontal section of nasal sac and Jacobson's organ of *Eutenia*, showing papilla projecting into the lumen of Jacobson's organ.

PLATE X, FIGS. 1-7.

Fig. 1. Camera drawing of horizontal section of right nasal cavity of tadpole, *Rana virescens*, modelled in Fig. 6, Plate XI, and Fig. 5, in this plate. The plane of this section is indicated on the model in Fig. 5, at D.

Fig. 2. Camera drawing of horizontal section of same. Plane of section seen at E.

Fig. 3. Camera drawing of horizontal section of same. Plane of section seen at B.

Fig. 4. Camera drawing of horizontal section of same. Plane of section seen at C.

Fig. 5. Pen sketch of directly lateral view of model of right nasal cavity of medium-sized tadpole of leopard frog, 5 mm. long, *Rana virescens*; constructed from horizontal sections, magnified 1000 diameters. A, B, C, D, and E, indicate the planes of the sections shown in Figs. 1-4, Plate X, and Figs. 1 and 2, Plate VIII.

Fig. 6. Pen sketch of median view of model of right nasal cavity of still older tadpole of leopard frog, *Rana virescens*, built up from perpendicular sections. Magnified 450 diameters.

Fig. 7. Pen sketch of directly dorsal view of same.

PLATE XI, FIGS. 1-8.

Fig. 1. Crayon sketch of dorsal view of model of right nasal cavity of *Salamandra atra* (European salamander); larval, just born, 16 mm. long; magnified 120 diameters.

Fig. 2. Crayon sketch of ventral view of same.

Fig. 3. Crayon sketch of dorsal view of model of right nasal cavity of *Hyla versicolor*. Constructed from transverse sections, magnified 227 diameters. This shows the three cul-de-sacs from before.

Fig. 4. Crayon sketch of ventral view of same.

Fig. 5. Crayon sketch of model of right nasal cavity of very young tadpole, *Rana virescens*; showing, even at this stage, the external and internal nares, and the inner and outer diverticles.

Fig. 6. Crayon sketch of ventral median view of model of right nasal cavity of medium-sized tadpole, *Rana virescens*; showing internal and external nares, glands, and inner larger diverticle. Compare Fig. 5, Plate X.

Fig. 7. Crayon sketch of directly dorsal view of model of left nasal cavity of tadpole of *Rana virescens*, quite old, legs one mm. long. Constructed from transverse sections, magnified 150 diameters.

Fig. 8. Crayon sketch of ventral view of same.

PLATE XII, FIGS. 1-4.

Fig. 1. Crayon sketch of lateral view of model of right nasal cavity of *Bufo lentiginosus*. Constructed from horizontal sections; magnified 80 diameters.

Fig. 2. Crayon sketch of median-ventral view of same.

Fig. 3. Crayon sketch of directly dorsal view of model of right nasal cavity of *Amblystoma punctatum*; constructed from transverse series of sections; magnified 400 diameters; specimen one centimeter long.

Fig. 4. Crayon sketch of ventral view of same showing anterior and posterior nares.