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The Columella Auris in Amphibia

B. F. KINGSBURY and H. D. REED

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THE COLUMELLA AURIS IN AMPHIBIA.

SECOND CONTRIBUTION.

B. F. KINGSBURY AND H. D. REED.

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In 1908 the authors published a partial report¹ upon the morphological relations of the so-called Sound-transmitting Apparatus in representative Urodeles with a view to establishing the type or types

¹Anatomical Record, Vol. II, No. 3, June, 1908, pp. 81-91.

and their modifications. In this study the following possible general aspects were kept in mind: (1) The primary (primitive) and secondary character of the connections and relations of the structures occupying the *fenestra vestibuli* more generally designated as constituting the Columella auris, (2) comparison with the forms below (fishes) the amphibian group (the hyomandibular homology), (3) homology with the reptilian Columella and mammalian Ossicula auditus, (4) the comparison and homology in Urodela and Anura, (5) the relationships of the different urodele families, (6) the function and functional importance of these structures in the tailed amphibia, (7) the variation in the arrangement of the parts of the apparatus and its significance.

It is not necessary to repeat here the reasons that led us to believe an extensive re-examination of the comparative morphology of the structures fitting into the *fenestra vestibuli* in urodeles to be necessary, as they were briefly set forth in the first paper and previously by others (Gaupp, '98; Drüner, '03). In the examination of the different forms, there have been kept in mind the following morphological relationships:

1. Relation (connection by fusion, articulation or ligament) of the Columella (*stilus columellæ*) to
 - (a) the os. squamosum (*paraquadratum*, Gaupp),
 - (b) os. quadratum or *palatoquadratum*,
 - (c) hyoid (*ceratohyale*);
2. Relation to the carotid artery (*Arteria carotis interna*) and jugular vein (*Vena petroso-lateralis*);
3. Relation to the otic capsule (lips of the *fenestra vestibuli*);
4. Relation to facial nerve (*ramus hyomandibularis VII*);
5. The ligaments coming into relation with the parts involved,—
 - (a) *Ligamentum squamoso-columellare*,
 - (b) *Ligamentum hyo-suspensoriale*,
 - (c) *Ligamentum hyo-mandibulare*,
 - (d) *Ligamentum hyo-columellare*;
6. *Musculus opercularis*.

Since early in the investigation it became apparent that there were two morphologically distinct elements appearing in the different forms, comparable, at least, if not homologous (*vide subseq.*) as we believe with the plectrum (columella) and operculum in the frog. it

became necessary to keep in mind the development of each element in its relation to the ear capsule. In the present paper a *detailed* presentation of the developmental changes, even as far as they have been worked out, is not included.

In addition to the forms briefly described in the first publication made by us, there have been examined by means of serial sections through the head, 14 species representing 1 family and 12 genera. The total number comprises 8 families, 21 genera, and 23 species, in the case of all save 9 of which the structure and morphology in both larvæ and adults were investigated. Bearing in mind that the total number of the families and genera of tailed amphibia is 8 and 45 respectively, it may be seen that a comprehensive and at the same time detailed view has been gained of the relations of the urodele "sound-transmitting" apparatus.

Without entering upon a full discussion of the bearing of our investigation, which is reserved for the last portion of this paper, the more important results may be stated briefly at this point.

1. In the tailed Amphibia, there may be developed two separate fenestral elements fitting into the *fenestra vestibuli*. These have been termed by us *Columella* and *Operculum* respectively.

2. The *Columella* typically possesses a *Stilus* which is connected primarily with the ventral (or ventro-caudal) edge of the squamosum. The *Stilus columellæ* may secondarily become joined to the palatoquadrate.

3. In development its proton appears outside the otic capsule as a group of cells continuous with the cells between the otic process of the palatoquadrate, squamosum and ear capsule.

4. The facial nerve in the forms examined is entirely below (and in front of) the columella save in *Necturus*, *Proteus* and *Typhlomolge*, in which the *Ramus jugularis VII* passes above the squamoso-columellar connection.

5. The *Operculum* is developed out of the otic capsule. Its position relative to the columella is caudal and medial. It possesses no skeletal connections but gives attachment to the *M. opercularis*.

6. In one group of forms, the columella only is present. In the Ambystomidæ the columella is present during the larval period but

becomes fused with the ear capsule at transformation when an operculum is formed. A further reduction and fusion of the columella is encountered in Salamandra, Triton and Diemictylus (Salamandridæ and Pleurodelidæ, Cope). In the Plethodontidæ and Desmognathidæ the fenestral plate of the columella embodies a representative of the operculum which is not separately developed.

7. The hyomandibular homology of the Columella is strengthened.

How widely the results of a detailed examination of a large number of forms depart from the interpretations at present accepted based upon the available information as to the morphology in a more limited number of salamanders, may be seen from a comparison of the above with the statements in two of the standard works: The Comparative Anatomy of Vertebrates, by Dr. Robert Wiedersheim, and the section upon the development of the skull, by Dr. Ernst Gaupp, in Hertwig's Handbuch der Entwicklungsgeschichte der Wirbeltiere.

The former ('06) describes² the *fenestra vestibuli* as filled by a cartilaginous plate, the so-called *Stapedial plate* or *Operculum* which is joined to the Palatoquadrate and Paraquadrate (squamosum) by ligaments, cartilage or bone. This bridge between the stapedial plate and the quadrate (or paraquadrate) is called *Columella* and together with the *Operculum*, in a phylogenetic sense, corresponds with the proximal segment of the hyoid arch (hyomandibulare or possibly symplecticum). Ontogenetically such a relation does not occur, both operculum and columella arising by differentiation in the territory of the otic capsule.

Professor Gaupp ('05) in Hertwig's Handbuch (pp. 696, 697, 605) designates the entire "stapedial" element as *Columella auris*,

²"Sie [Fenestra ovalis] wird von einem durch Bandmassen oder auch durch Knorpel oder Knochen an das Quadratum und Paraquadratum befestigten Knorpeldeckel, der sog. *Stapesplatte* (St) oder dem *Operculum*, verschlossen und soll uns bei der Anatomie des Gehör-Organes wieder beschäftigen. Jene zwischen Stapesplatte und Quadratum resp. Paraquadratum sich erstreckende Brücke heisst *Columella* und entspricht zusamt dem Operculum in phylogenetischer Beziehung dem oberen Abschnitt des *Hyoidbogens*. Ontogenetisch ist von diesen Beziehungen nichts mehr nachzuweisen, sondern es handelt sich sowohl für die *Columella* als für das Operculum hinsichtlich ihrer Entstehung um Differenzierungsprocesse im Bereich der Labyrinthkapsel."

consisting of an *Operculum* which may or may not bear a process, the *Stilus columellæ*. The process when present is usually connected by means of a ligament (*Ligamentum suspensorio-columellare*) with the *Paraquadratum*, *Palatoquadratum* or with both. The facial nerve in most forms passes below the suspensorio-columellar connection. It is stated, however, that there are two such connections, one above and one below the facial nerve. The operculum with a stilus is regarded as the more primitive condition and as such is probably to be homologized with the *Hyomandibulare*. In the *Anura* the *Columella auris* consists of two elements, *Operculum* and *Plectrum*, the latter (*Pars interna plectri*) probably to be interpreted as a stilus which has become secondarily dissociated from the operculum.

Nomenclature. The question of nomenclature is a perplexing one. Gaupp has termed the entire fenestral structure, *Columella auris*, consisting in *Anura* of two elements, *Operculum* and *Plectrum*, in *Urodela* of *Operculum* and (typically) its process, *Stilus Columellæ*. The direct application of the terms used by Gaupp, though desirable, becomes difficult in the light of the existence of a stilus-bearing fenestral plate and a non-stilus-bearing fenestral plate in the same form and at the same time. While there are objections to both the terms *Columella* and *Operculum*, it seemed better to avoid the introduction of new terms and to employ the term *Operculum* for the *stilus-free* structure and to restrict the name *Columella* to the *stilus-bearing* element. This use of terms seems to necessitate less departure from the earlier use of the names. The operculum of *Anura* is directly comparable with that which is termed by us operculum in the *Urodela*. This in *Siredon* was termed *Operculum cartilagineum* by Windischmann in 1831 and subsequently has often been designated *Operculum* in other salamanders. *Columella* was, of course, applied to the anuran structure now named *Plectrum* by Gaupp, and to the stilus in *Urodeles*, or to the entire element (Hasse, '73) called *columella* by us.

As an indifferent name for bony or cartilaginous plate fitting into the *fenestra vestibuli* we employ the term *fenestral plate*. A backward extension of the *Cavum perilymphaticum* beneath the operculum we designate *Recessus perilymphaticus*. For the bulging por-

tion of the ear capsule associated with the outpocketing of the perilymphatic space we employ the name *Prominentia perilymphatica*. Without going into a discussion of homologies, we designate as *Os squamosum* the *Os paraquadratum* of Gaupp, but in the use of other names we adhere to the terms used by him. The term *proton* is used as the equivalent of the German word *Anlage*.

We depart from the usages of the preliminary paper³ in substituting *Vena petroso-lateralis* for *Vena jugularis interna* of which it is a direct continuation, employing the name used by Drüner, likewise using his term, *Musculus cephalo-dorso-mandibularis* for *Muscularis depressor mandibuli*. *Palatoquadratum* is substituted for *Quadratum*.

Acknowledgments. We have received material for study and helpful criticism from many sources and wish especially to express our indebtedness to Professors Wilder and Gage and Dr. W. A. Hilton of Cornell University, Professor Robert Wiedersheim of the University of Freiburg and Mr. B. G. Smith of Syracuse University. Aside from personal obligations we wish to express our appreciation of the works of Wiedersheim and Gaupp in this field of research.

AMBYSTOMIDAE.

*Ambystoma*⁴ *punctatum*. Two reasons determined the choice of this form as one of the species in which to work out quite thoroughly the development of the ear region: (a) the ease with which a large number of stages, larval, transforming and adult, could be procured; (b) its systematic rank as a typical urodele. In all, some forty series were examined and four models prepared. In this way was obtained a complete history of the transformations through which

³*Errata.* At this point we desire to correct errors that were allowed to creep into manuscript and proof in the earlier paper:

- (1) p. 83, line 2, Hemidactylum should read Hemidactylium.
- (2) p. 83, line 11, 4-6 mm. should read 12-14 mm.
- (3) p. 83, line 17, 1888 should read 1879.
- (4) p. 86, line 2, caudal should read dorso-caudal.
- (5) p. 87, line 4, Hemidactylum should read Hemidactylium.
- (6) p. 87, Fig. 4, D.e. should read D.p.—Ductus perilymphaticus.

⁴The same as *Ambystoma* according to older usage.

the structures under consideration pass. The results of the study in this species were given in concise form in our first or preliminary paper. The evidence upon which the conclusions were based was not submitted at that time, however, and may be given now, together with such further details as are important in this connection.

The first definite trace of the columella is to be found in embryos of 11-13 mm. in length, a short time before hatching. At this period while the cupola of the otic capsule is chondrified, the basal plate is still in the pre-cartilage (chondroblastema) stage so that the ventral boundary of the primary fenestra is not yet sharply defined, and the difficulty of delimiting its ventro-medial side is further increased by the fact that the cells of the future floor as well as those occupying the site of the future membrane are equally rich in yolk granules, in which respect they differ from the cells of the surrounding mesenchyma. The squamosum is just appearing as a minute scale of bone above and behind the otic process of the palatoquadrate.

Below and beneath the squamosum, filling in the space between otic capsule, squamosum and otic process of the palatoquadrate, and extending down upon the outer side of the vena petroso-lateralis to the yolk-bearing cells occupying the site of the future membrane, is a dense tissue, with numerous cells and homogeneous matrix, which embodies the proton of the columella, stilus and squamoso-columellar ligament. The derivation of these cells was not definitely determined. Younger embryos lend some support to the view that they migrate down around the vein. The different appearance of the cells of the otic capsule adjoining the lower end of this cell-group argues against their origin from this portion of the otic capsule (membrane or floor).

In a 13-14 mm. specimen the demarcation of the columellar tissue is sharper and the portion against the fenestral membrane denser. The condition at this stage is reproduced in a photograph, Fig. 39, Pl. IV, *col.* At about this time, chondrification begins and in the larva 14-15 mm. in length there is a small cone of cartilage, whose base is against the membrane and whose apex projects out into the dense tissue still connecting with the cell-group between squa-

mosum, otic capsule and otic process of the palatoquadrate. The stilus appears to chondrify out into this tissue, the unchondrified portion of which becomes the Lig. squamoso-columellare.

The development as given above agrees completely with the concise description of Killian ('90) for the development in Siredon. He terms the columella *Operculum* and had no knowledge of the interesting changes occurring at transformation.

During the period of larval growth the portion of the columella fitting into the membrane increases greatly in size, becoming an elongated plate of cartilage which for purposes of convenient reference may be designated *Fenestral Plate*. If at first it is outside the fenestral tissue, it becomes in the process of growth a part of that structure. Whether the enlargement of the plate takes place through marginal growth with the incorporation of fenestral tissue, or through interstitial growth with a simple displacement of the bordering membrane, has not yet been determined. In late larval life the columella apparently becomes joined to the dorso-cephalic margin of the fenestra by delicate cartilage and subsequently more closely connected with the ventro-cephalic edge. Ossification appears late. Two plates of bone are formed, one upon the inner surface of the columella, the other upon its outer surface also extends out upon the stilus. This method of ossification of the columella is quite characteristic for other urodeles as well. Fig. 33 (Pl. III) illustrates the development attained by a 35 mm. larva.

The condition shortly before transformation is shown in Fig. 22 (Plate I), from the model of the ear region in an individual about 45 mm. long. The fenestra vestibuli (*F. v.*) whose complete outline cannot of course be seen from the figure, is an elongated oval whose dorsal border is formed by the crest of cartilage where the lamina horizontalis of the lateral semicircular canal passes into the lateral wall. For purposes of reference we shall refer to this as the Crista semicircularis (*Cr. s.*). At the cephalic end of the fenestra the "lips" join to form an elongated prominence with which the processus basalis palatoquadrati articulates. Its interior is occupied by a cephalic extension of the cavum perilymphaticum. The caudal end of the fenestra attains nearly the end of the caudal

cupola of the otic capsule. It may be noted that the fenestra vestibuli is in the lateral wall of the ear capsule, becoming more ventral in its cephalic portion.

The fenestral plate occupies the larger portion of the window, being most widely separated from the margin of the fenestra at its caudal end. In the model the relations of the arteria carotis interna and vena petroso-lateralis are shown crossing and partially covering the fenestral plate. In Fig. 23 (Plate I), however, in a somewhat later stage, the complete outline of the fenestral plate can be seen. At the cephalic end, on both ventral and dorsal margins, new cartilage, not shown in the model, is just beginning to join the columella to the margin of the fenestra vestibuli. The stilus and ligament connect the fenestral plate with the ventral edge of the squamosum. The palatoquadrate cartilage does not become connected with the ligament. A blunt process of the quadrate underlying the squamosum is not brought into relation with the ligament at this stage.

At transformation the fenestral plate becomes joined to the lips of the opening on all sides save the caudal and the caudal portion of the ventral side. There is, however, a portion of the primary fenestra behind the stilus where even in the fully grown salamander the wall of the otic capsule is very thin,—membranous or filled in with a thin lamina of cartilage (See Fig. 24, Pl. I, "F"). In Fig. 23 the outlines of the old fenestral plate still shows. The delicate new cartilage just forming was not modeled. In Fig. 24, the fusion of the plate with the edge of the fenestra is nearly complete. The outline of the old columella and the newly formed cartilage can be distinguished.

In the process of transformation, due to the shifting of the suspensorium, the attachment of the stilus becomes largely transferred from the squamosum to the palatoquadrate cartilage (Pl. I, Fig. 24).

The operculum present in the transformed salamander (Pl. I, Fig. 24, *Op.*; Pl. II, Fig. 25) occupies the caudal portion of the new fenestra (definitiva) whose dorso-cephalic margin includes the cephalic end of the operculum; the caudal end projects freely and to it is attached the M. opercularis whose tendon fits into and fills a depression upon its external surface (Pl. IV, Fig. 35).

The operculum is formed out of the wall of the ear capsule upon the medial side of the caudal portion of the fenestra. Fig. 23 shows the operculum in process of formation. Along the line marking the medial border of the new fenestra the cartilage breaks down and is absorbed, cutting out in this way a large plate from the ventral wall near the caudal end of the ear capsule. In this histolysis, while the end result is a backward and medial extension of the fenestral opening, it is not accomplished by an actual extension back of the fenestra, but the cartilage is absorbed all along the line of separation, several irregular clefts appearing first which afterwards become confluent with each other and with the fenestra. At its caudal end the separation of the operculum comes later and at this point a new formation of cartilage occurs extending the operculum in that direc-

FIG. 1. Schema illustrating the fusion of the columella with the ear capsule.

tion outside the ear capsule. New cartilage is, however, formed at the edge of the fenestra as well and in the operculum itself which attains massive dimensions in the fully grown *Ambystoma* (Pl. IV, Fig. 35).

The inclusion of the cephalic end of the operculum by the lips of the fenestra (Pl. I, Fig. 24) is accomplished by a deposit of new cartilage which cements in solidly the fenestral plate and extends the fenestral lip backward outside the operculum. The dorso-cephalic portion of the margin is thus formed by the ventral and caudal edges of the larval columella extended by new cartilage formation, while the ventro-cephalic margin is new cartilage formed upon the ventral lip of the primary fenestra which extends to meet that deposited on the fenestral plate. The diagram, Fig. 1, will

illustrate the transformation and the filling in of the primary fenestra and the incorporation of the fenestral plate. The columella, stilus columellæ, and operculum are indicated by *Col.*, *St. C.*, and *Op.* respectively; the new cartilage is line-shaded, while the region of earliest fusion is cross-hatched. The outline of the included portion of the operculum is marked by a broken line.

In the larva approaching transformation (Fig. 22, Pl. I), the operculum is not well outlined, although a slight groove causes a prominence of the wall which later becomes the operculum. As shown in Fig. 31 (Pl. III), in the sections of the ear-capsule of mature larvæ, the region from which the operculum will form, may be recognized. Compare Figs. 31 and 32, in the latter of which the histolysis of the thin cartilage on the medial side of the future operculum is severing its continuity with the remainder of the floor of the otic capsule. The operculum thus arises from a portion of the floor of the ear capsule while the secondary fenestra with the plate of the columella is in the lateral wall. (Cf. Figs. 32 and 33.)

The interior of the ear capsule, opposite the region to become the operculum, is occupied by the cavum perilymphaticum (Figs. 31 and 32, Pl. III). In the transformed animal this portion of the ear capsule becomes somewhat prominent and may be termed the Perilymphatic Prominence (*Prominentia perilymphatica*) (Figs. 30 and 35). The outward and backward extension of the perilymphatic space on the inner side of the operculum, as stated above, is termed *Recessus perilymphaticus*.

The muscle attaching to the operculum to which Gaupp ('93) gave the name of *M. opercularis*⁵ extends caudad and at its caudal end is attached to the outer side of the *Suprascapula*. In the larval *Ambystoma* it is not present. Early in the transformation myoblasts upon the outer edge of the ventral spinal musculature (*M.*

⁵This muscle in the frog was regarded as a portion of the "Occipito-subscapularis" by Dugès ('35), the Levator anguli scapulæ of Ecker. Cope ('88 a and b) has termed it *M. stapedius*, Ivanzoff, *M. protrahens scapulæ*. Gaupp subsequently ('96) designated it the "Pars opercularis of the *M. Levator scapulæ superior*." In Urodela it seems to deserve recognition as a distinct muscle, and its development apparently differs somewhat in the two groups.

intertransversarius capitis inferior of the frog, Gaupp, '96) develop into a fascicle of small fibers which becomes separated off from the above mentioned muscle and gains the attachments to the developing operculum and the suprascapula. Its opercular attachment is shown in the models pictured in Figs. 23 and 24 (Pl. I) and also in Fig. 37 (Pl. IV) in which both attachments are shown.

In accord with the statement of Hasse ('73), the facial nerve is entirely below (in front of) the columellar-squamosal connection, the descriptions of other authors who have given its relations being therefore incorrect. In Fig. 22, the three branches of the hyomandibular division, ramus mandibularis internus, ramus mandibularis externus, and ramus jugularis, are shown. Joining the R. jugularis is the R. communicans IX (not shown) which pursues a course dorsad to the carotid artery to join the R. jugularis where it passes under the ligament.

In *Ambystoma*, therefore, there are two fenestral structures which succeed one another at transformation. The first which appears in the larva, is the columella, whose stilus connects with the squamosum and whose fenestral plate becomes associated with the otic capsule at its cephalic end. At transformation the columella becomes fused with the ear capsule and a second fenestral plate, the Operculum, is cut out. This second structure is caudal and medial to the first, possesses no process (stilus), is not connected with the squamosum or palatoquadrate, but is joined by means of the M. opercularis to the pectoral girdle.

The examination by earlier workers of the otic region in *Ambystoma* or *Siredon*,—which is to be regarded as a permanent larva of an *Ambystoma*,—has not lacked suggestion of the interesting condition found in this form. In *Siredon*, in which the condition has usually been examined, Hasse ('73), Friedenreich and Gegenbaur ('49), as well as Wiedersheim ('77), Parker ('77), and Retzius ('81), described a well ossified "operculum" of conical form, the base of the cone fitting into the fenestra, the apex of the cone prolonged into a bony process attached to the palatoquadrate cartilage by ligament (Gaupp, '99, p. 1040). The plate that fits into the window possesses, according to Retzius, a cartilaginous border and

the tip of the stilus is likewise of cartilage. This description of the condition in Siredon corresponds fairly well with the relations of the columella in Ambystoma before transformation. The names applied to the structure varied: Operculum (Wiedersheim); Columella (Hasse); Stapes (Parker). Windischmann ('31), whose paper we have not been able to examine, described in Siredon a stilus whose (fenestral) plate he termed *Patina*, while behind the *Patina* there was an *Operculum cartilagineum* joined with it only by connective tissue. This description of Windischmann's was discredited by later workers. It is probable, however, in view of the possibility that many, perhaps most, of the so-called Siredons were larval Ambystomas and not super-larvæ (Axolotl) that Windischmann correctly described the condition in a transforming individual. More recently Iwanzoff ('94) describes the condition in Siredon as follows, apparently erring in ascribing the connection of the columella with the squamosum to the operculum:

"Bei Siredon befestigt sich der Musculus protrahens scapulæ mit seinem proximalen Ende am rundlichen Knorpel auf der hinteren Wand des Schädels. Parker und Wiedersheim halten diesen Knorpel einfach für einen Teil des Knorpelschädels, um so mehr, da er schwach von dem letzteren abgegrenzt ist. Aus dem nachgewiesenen Grunde nehme ich ihn für den Stapes, um so mehr, als er demselben auch nach seiner Lage entspricht. Desshalb ist der Teil, welchen die genannten Autoren als Stapes annehmen, nämlich die teils knöcherne, teils knorpelige und bindegewebige Bildung, die vom Stapes zum Quadratknorpel und Squamosum, und dieselbe Lage, wie das Band mit den Columellarknöchelchen bei Pelobates hat, für die Columella zu halten. Auf diese Weise erscheint die gewöhnliche Behauptung, dass bei den Urodelen die Columella gar nicht existirt, für Siredon und einige andere Formen, irrthümlich."

Iwanzoff seems, therefore, to have seen two structures, though their detailed relations were confused. The early description of Windischmann portrays most closely the condition in Ambystoma, though all the descriptions were doubtless approximately correct if the age (larval or adult) is considered. *No one seems to have recognized the fact that the condition changes with age.*

Turning now to the development of the "sound-transmitting" apparatus in Ambystoma, we find that only imperfect glimpses of the true development were obtained, and it is not always easy to determine to which structure they refer. Wiedersheim, Parker, Stöhr, Killian, Witebsky, Winslow, have examined one or more stages in the larval Ambystoma or Siredon (Axolotl). Wiedersheim and Winslow evidently described the development of the columella; Witebsky saw the independent chondrification of the columella but missed the connection of the stilus with the squamosum (or palatoquadrate) and drew from his observations some quite irrelevant conclusions as to the homology of the columella for which he had no sufficient basis in fact, as has been pointed out by Gaupp ('98) from whose paper our information is gained, Witebsky's dissertation being inaccessible to us here. Stöhr made his examination of the development in the Axolotl only incidental to a more detailed study of the development in Triton, so that he simply "confirmed" the results of Parker's more extended investigation, stating that the "operculum" grows out of the cartilaginous border of the fenestra vestibuli. He gives no figures, so that it is difficult to interpret his results. It was apparently the *Columella* (our use) that he had under observation. Parker alone examined an extended series of larval Ambystoma (Axolotl, Siredon) including an adult Ambystoma. For the first seven stages neither his words nor his figures give indubitable proof that he saw the development of the columella or recognized the stilus or its connection. His description (p. 564) of the adult (Ambystoma opacum) indicates that in his stapes he described the operculum.⁶ In two points there was probably mistaken identification; ligament and ossification were doubtless absent. The descriptions of two large Axolotls (8½ and 8¼ inches long) undoubtedly applied to the Columella,⁷ the recognition of the suspensorial connection above the facial nerve being noteworthy.

"The bulging bony floor of the vestibule forms a widely crescentic bulla, and in the notch the fenestra ovalis contains a small lenticular stapes, the center only of which is ossified. The spiracular ligament fastens the stapes to the back of the top of the suspensorium."

⁶Page 559, "the stapes (Figs. 2, 4 and 5, st.) is unusually solid and projecting, its outstanding process looking a little forward. From that process

Winslow ('98), on the other hand, has described and figured models of three stages of the chondrocranium of *Ambystoma*. He describes the columella (Stapes) chondrifying as an independent center in a 12 mm. individual. The condition in a 37 mm. larva he describes as follows: "The fenestra ovalis is now nearly filled by the stapes (s), which has a slight prominence directed outwards and upwards from the antero-dorsal angle of the cartilage towards the otic process of the quadrate. These cartilages, however, do not become united at any time during the development of *Ambystoma* as they do in some other forms." In a young adult, 69 mm. in length, he describes the stapes as in the posterior portion of the fenestra closely applied against the remnant of the cartilaginous wall of the capsule, this time describing the operculum as stapes. His figure bears out the brief description and shows the stilus of the fused columella extending from the ear capsule to the palatoquadrate.

It is hardly necessary to comment on the difficulties of interpretation in such a form as *Ambystoma* if the changes at transformation are ignored. Transformation occurs relatively quickly and at this time the salamanders are less easily procured.

Chondrotus tenebrosus. Three examples of this species were examined; larval, transforming, and adult. It was not surprising to find that the relations in this salamander closely resembled those in *Ambystoma* because of the close relationships of the two genera.

The larva was well advanced (58 mm. long) and the morphological relations diagrammatic in their clearness. The otic capsule as also the remainder of the chondrocranium is unusually heavy, and the columella shares this characteristic. As shown in Fig. 34 (Pl. III) there is a well developed stilus which articulates closely with the lower edge of the squamosum. In no other form examined by us has a single section shown the distal connection as well as the central origin of the stilus from the fenestral plate, as a result of

a ligament arises which spreads into a fan-like fascia, which is inserted along the under and outer edges of the suspensorium from the lobe of the otic process to the lobe of the quadrate . . . it lies some height above the portio dura. . . ." Page 562. "Thus we have here what may be called a *spiracular fascia*, the counterpart of the spiracular cartilage and bone of the *Menopoma* and others."

its more transverse course, since in *Ambystoma* as well as the other forms examined it has a course outward, upward and also forward (See, however, Siren, p. 598). The fenestral plate is at no point connected with the otic capsule, at the edge of the fenestra or elsewhere. A few sections farther forward the distal end of the stilus is joined by connective tissue with the caudal edge of the palatoquadrate, this junction not being as close, however, as that with the squamosum. The relations of artery, vein and facial nerve are as in *Ambystoma* (Pl. III, Fig. 34).

The second specimen was well along in transformation (150 mm. long, gills mere stumps). At this stage the columella is connected by membrane with the lips of the fenestra everywhere save on its cephalo-ventral border where cartilaginous fusion has begun. Its stilus is massive and abuts against the palatoquadrate with which it is joined by connective tissue (Pl. IV, Fig. 36, St. C.). The *Os. pterygoideum* also comes into close relation with it, but the connection with the squamosum existing in the larva is now much less direct (Fig. 36). The characteristic inner and outer ossifications are present, with accompanying changes in the cartilage.

The floor of the ear capsule medial to the caudal portion of the fenestra is nearly completely cut out as the operculum (Pl. IV, Fig. 38, *Op*). In its present development, it may be compared with the stage in *Ambystoma* shown in Fig. 32 (Pl. III). An opercular muscle attaches to the operculum. The recessus perilymphaticus is characteristically present.

The adult individual was 240 mm. long and was examined by dissection. The condition found was much like that in the adult *Ambystoma*. The columella, with its inner and outer bony surfaces, the latter bearing a well ossified stilus, is completely fused with the otic capsule forming the anterior boundary of the nearly circular fenestra into which was fitted a cartilaginous operculum, roughly hemispherical in form, its flattened surface bearing a tendon, doubtless that of the *M. opercularis*, which was not, however, dissected out. Fusion with the otic capsule was apparently by cartilage only, so that, by the use of some force, the stilus and plate could be and were completely broken away. The distal end of the stilus was con-

nected by syndesmosis with the under surface of the squamosal near its caudal edge, and doubtless also with the palatoquadrate cartilage as well, though this relation was not determined.

Examination of the condition in the adult of this salamander by means of dissection was made partly because other adult members of this family had been examined in this way. Of three Asiatic genera, *Hynobius* (*Ellipsoglossa naevius*) *Salamandrella* (*kaiserlingi*), and *Ranidens* (*Randon sibericus*) the "operculum" (columella) is described by Wiedersheim, '77, (503, 519) as a remarkably large cone of bone whose columella [*stilus columellæ*] is closely joined to the lower end of the quadrate. As a result of this intimate connection Wiedersheim called attention to the inevitable shaking of the perilymph that must attend every violent closing of the jaw,—as in the seizing of prey,—an arrangement whose physiological significance it is difficult to comprehend. Granting, however, that as in *Ambystoma* and *Chondrotus*, the columellar plate is fused with the ear capsule, the difficulty found in the close junction of *stilus* and palatoquadrate disappears, a fused element not being subject to violent agitation from movement of the jaw, but on the contrary offering a firmer support for the upper end of the quadrate.

The suggestion is, therefore, made that the columella will be found fused in the other *Ambystomidae*, including these Asiatic forms, and it is not without some direct evidence. Fig. 65 in Wiedersheim's monograph ('77) shows the *stilus* in *Ellipsoglossa* (*Hynobius*) arising, not from the opercular plate, but from the anterior lip of the fenestra, as in *Salamandra*. This is also just as he figures it in *Ambystoma Weismanni* (*tigrinum*) ('79, Fig. 8),—quite different, as might be expected, from the relations in the *Axolotl* ('79, Fig. 12). The operculum had been removed. His ('77) Fig. 67 (*Ranidens*), however, suggests a condition such as is found in *Cryptobranchus*.

Okajima ('08) has recently given a short description of the columella in another member of the family,—*Onychodaetylus japonicus*. An ossified plate, "hollow" in the center with cartilaginous border, he states (p. 353, 354) fits into a lateral fenestra vestibuli. A cartilaginous *stilus* is connected with the cartilaginous portion of the

quadrate. This is evidently the columella; an operculum was not recognized. A text figure of a section through the ear capsule recalls strongly the similar section in just transformed *Chondrotus* (Pl. IV, Fig. 38), already described.

SALAMANDRA.

Salamandra maculosa has proved to be a form of rather unusual interest with regard to its sound-transmitting apparatus both in respect to the elements present and their relations when considered in the light of conditions in other forms.

The skeletal elements of the head of *Salamandra* are quite fully ossified. The os quadratum is composed of a thin outer shell of bone very closely associated with the under surface of the superimposed squamosum. Underneath the os quadratum is the palatoquadrate which is continued into the basal, otic and trabecular (ascending) processes. As has been pointed out by Wiedersheim ('77), the inclination of the supensorium to the long axis of the skull is almost transverse, a condition not met with in many salamanders. The inclination of these elements, whatever its cause, undoubtedly influences the nature of the suspensorio-columellar connection in all forms.

Both columella and operculum are present in the adult. The columella is a plate of partly calcified cartilage fused with the lips of the fenestra vestibuli except in the caudal third of its circumference where it forms the cephalic margin of the definitive fenestra. Fig. 40 (Pl. V) is a photograph of a section through the cephalic portion of the columella and shows how completely it is fused with the ear capsule in this region. In the same figure is shown the short and thick stilus which projects from the dorso-lateral aspect of the columella. It is composed of hyalin cartilage distally continuous with the cartilage of the palatoquadrate; proximally it passes over into the plate of the columella whose cartilage, calcified where it joins the ear capsule, may also be seen in this figure. To the squamosum it is joined by connective tissue representing a short ligament. Describing the "stapes" in *Salamandra*, Parker ('82a) observes:— (pp. 174-5) "There is a well ossified lip, like the mouth of a pitcher,

to the fenestra ovalis: it looks outwards and backwards; the thick, oval closely fitting stapes (operculum) remains cartilaginous and is only attached to the supensorium by ligaments." In a foot-note he adds: "Mr. A. Doran has shown me a stapes, said to belong to this species, which is ossified and has a stalk. I find nothing of the kind in the specimen dissected by me; and I think it probable that that specimen (in the Hunterian museum) belonged to another kind." It is quite likely that Mr. Doran was correct and that the stilus had by some accident been torn from Parker's specimen. The relation of the stilus to the artery, vein and facial nerve is typical.

The operculum occupies the typical position below and behind the columella filling the definitive fenestra vestibuli. It is a relatively large hemispherical mass of cartilage free all round, attached to the lips of the fenestra by membrane only. The cephalic fourth is overlapped by the caudal margin of the columella precisely as in *Ambystoma*. This is made clearer by an examination of Fig. 41 (Pl. V), a photograph showing the operculum internal to an overhanging lip of cartilage, the columella, which conceals the entire cephalic and a portion of the dorsal margin of the operculum. In tracing it forward, it gradually diminishes and finally disappears in the middle region of the perilymphatic prominence. The photograph reproduced in Fig. 42 (Pl. V) is of a section in this region, and shows a small lip of cartilage, a backward continuation of the columella, projecting from the ear capsule upon the dorsal margin of the fenestra. Fig. 65 (Pl. X) is a schematic representation of the position and relations of the columella and operculum as viewed from the side.

The perilymphatic prominence is pronounced. To the caudal surface of the operculum is attached the strong M. opercularis which extends caudad to the suprascapula.

Wiedersheim ('77, p. 504), in commenting upon the columella in *Salamandra*, says: "It is cartilaginous throughout life and rests suspended by the connective tissue in the foramen ovale which is bordered by two thick, crest-like lips. These lips now pass forward and outward in a thin cartilaginous process and this joins the quadrate cartilage,—a remarkable variation of the relations described

above." We are able to confirm these early observations and in the light of the changes which take place in *Ambystoma* at transformation, offer an interpretation of the presence of the fourth process connecting the palatoquadrate with the ear capsule. Undoubtedly as in *Ambystoma* the columella becomes fused with the margin of the fenestra and maintains its connection with the suspensorium through the stilus which is without doubt the cartilaginous process from the fenestral lip to the quadrate cartilage seen by Wiedersheim.

We feel no hesitation in offering this interpretation of the structures in this form even though developmental stages have not been studied by us. The sound-transmitting apparatus in *Salamandra* is in all essential respects identical with that of *Ambystoma* in which a very large number of developmental stages have been studied carefully, permitting an interpretation of the adult condition which without them would be difficult. Fuchs ('07) has figured and described the chondrification of the otic capsule in *Salamandra*, giving in some detail the formation of the fenestra vestibuli and operculum. Employing the nomenclature of Gaupp, he describes the operculum as formed chiefly by a cutting out of the already chondrified ear capsule and partly by the chondrification of the chondroblastema filling in the fenestra. The latter he recognizes existent from the beginning as an unchondrified portion of the otic capsule. The development of the *Operculum* of *Salamandra* he undoubtedly gives correctly and in the figures of models of three stages shows it forming upon the medial and caudal sides of the fenestra in the manner stated above just as the operculum is formed in *Ambystoma* and in *Triton* presently to be described. He neither discusses nor shows in his figures, however, the process described by Wiedersheim, the detailed development of which in this form would be of particular interest. No hint is given of its origin or relations except in Fig. 3 on page 11 where a slight projection from the dorsal boundary of the fenestra appears to be what we are inclined to interpret as the caudal tip of the columella. A comparison might also be made between his Figs. 3, I, and our Figs. 1 and 23 (Pl. I) of *Ambystoma* and Fig. 27 (Pl. II) of *Triton*.

Fuchs gives no intimation of the ages or sizes of the larvæ or

embryos studied. His theoretical conclusions drawn from the development of the operculum in *Salamandra* will be referred to in the second part of the paper.

TRITON AND DIEMICTYLUS.

In Cope's family of the Pleurodelidæ, the condition of reduction and incorporation,—if we may so state it,—is carried farther than in the form just described,—*Salamandra*. The connection with the squamosum and palatoquadratum is absent, and the fenestral plate forms the portion of the ear capsule bounding the cephalic part of the fenestra vestibuli above and in front. In the adult, the identity is entirely lost and it would be impossible to recognize the true morphological relations were it not for the condition in the larva. In fact, at the time of our first contribution, the existence of the columella in *Diemictylus* was not recognized even though larvæ had been examined. At that time we expressed confidence in its presence at some stage in the development of the larva, but thought that it was absorbed or became incorporated,—possibly with the operculum. It was, indeed, subsequently found to be present and incorporated not with the operculum, but with the edge of the fenestra. It was in the light of the conditions in *Salamandra* that the relations in *Diemictylus* became clear. The existence of the columella was first determined in a 19 mm. larva, the subsequent examination of *Triton* larvæ bringing confirmation. In this last form the significance of the morphological relations is more apparent so that it may best be considered first.

Triton cristatus. Through the kindness of Professor Robert Wiedersheim, we were enabled to examine a series of specimens of this form, serial sections being prepared of larvæ 18, 20, 25, 34, 36, and 37 mm. in length. In the smallest individual at our disposal (18 mm.) both operculum and columella are present, of cartilage, the latter fused more or less completely with the crista semicircularis, hence it has been impossible to determine how early this structure appears; whether at any time its proton is as obviously outside the membrana fenestræ as it is in *Ambystoma*, or whether it undergoes chondrification separate and distinct from the edge of the primary

fenestra, later becoming fused with it. There is some evidence in our series that leads us to believe that it will be found to chondrify as a separate piece of cartilage:—(a) its cartilage differs in its staining from that composing the crista semicircularis, presenting the appearance of “younger” cartilage; (b) it lies outside what might be considered the ideal plane of the fenestra and apparently outside the fenestral membrane; (c) in some of the larvæ a small cleft is left between the crista semicircularis and the columella. This cleft is especially well marked in the 36 mm. larva (Fig. 48, Pl. VII), but present on one side only, being therefore variable in its extent and doubtless simply an indication of imperfect fusion. The columella as in *Ambystoma* fills in the anterior portion of the primitive fenestra in its dorsal part; if the fusion with the ventral lip occurs early, it is conceivable that the dorsal fusion may be delayed.

As to the mode of formation of the operculum, the evidence is indubitable; it is forming in the “floor” of the ear capsule as a chondrification in the “opercular tissue” (*membrana fenestræ*) in its caudal and medial portions. In the 18 and 20 mm. specimens, the operculum is already outlined, but broadly continuous on its medial and caudal sides with the cartilage of the floor, and were it modelled, would doubtless present the appearance shown in the model of a 20 mm. *Triton tæniatus* published by Gaupp ('05, p. 695, Fig. 350). In the older larvæ, save for the larger size of the operculum and its more complete separation from the floor of the otic capsule, conditions have not been essentially changed. A model was made of this region in a 34 mm. larva which is reproduced in Fig. 27 (Plate II). Here the operculum is shown forming in the caudal portion of the fenestra still rather broadly connected with the floor of the otic capsule caudally and medially. The rudimentary fenestral plate is shown fused with the anterior portion of the crista semicircularis. The closure of the anterior portion of the primary fenestra is also being accomplished by a growth of cartilage upon its ventral side. This figure showing the primitive fenestra and its contained cartilages may be directly compared with the stage in *Ambystoma* shown in Fig. 24, Pl. I, and its diagrammatic elucidation in Text Fig. 1.

Three photographs (Pl. VII, Figs. 48, 49 and 50) of sections from the 36 mm. larval Triton are submitted in illustration of what has been said above. Fig. 48 is through the ear capsule cephalad of the (secondary) fenestra at a point where the columella is fused with the ventral lip of the (primary) fenestra (cf. Fig. 27, Pl. II). It shows the cleft between the dorsal margin and the crista semicircularis whose existence has been mentioned above. It might also be compared with Figs. 28 and 29, Plate XV, of Gaupp's ('93) monograph upon the Chondrocranium of the Frog. Fig. 49 is five sections (75 microns) farther caudad through the columella and just ahead of the tip of the operculum, while Fig. 50 is still farther back (210 microns) behind the caudal end of the columella and through the operculum. The position of the artery and vein may be noted, in comparison with Figs. 8, 9 and 10 of Stöhr ('79). It may be remarked that in the oldest of the larval Tritons examined (37 mm.) the M. opercularis has not yet appeared nor has the operculum become completely separated off from the cartilaginous ear capsule.

By comparing these figures (Pl. VII, Figs. 48-50) and the two similar ones of a *Diemictylus* larva (Text Figs. 4-5) with the sections through the ear capsule of the larval and transforming *Ambystoma* (Pl. III, Figs. 31-32-33) the basis of the homologies for Triton becomes evident. In a comparison of Triton and *Ambystoma* the early appearance of the operculum in Triton is noteworthy. Its proton is already partially outlined at 18 mm. in length, and doubtless recognizable at a still earlier stage, while in *Ambystoma* its appearance comes only with the beginning of transformation, and in the larva it is a part of the otic capsule. The columella element, on the contrary, while already evident in the youngest Triton larva, becomes more prominent in the later larval stages; in *Ambystoma* it appears very early. The growth of the columellar plate in Triton during the larval period with an increasing distinctness of demarcation from the crista semicircularis suggests, it must be admitted, the interpretation of a differentiation out of "fenestral tissue" as the fenestra increases in extent. As has been said, the available material does not permit us to determine the early transformations

that take place in the ear capsule in Triton. The presence of a rudimentary columella seems clearly established. The problem of its phylogeny may be better discussed from a comparative view-point.

No trace of a stilus or connection with the squamosum or palatoquadrate was to be found unless, possibly, a scanty group of cells extending from the columella around the outer side of the vena petroso-lateralis was its representative.

In the adult Triton the conditions are much altered. The otic capsule is strongly ossified; the operculum being an oval plate of cartilage filling in the relatively small fenestra vestibuli and projecting back a short distance. On its outer side it gives attachment to a well developed M. opercularis; on its inner side is the cavum perilymphaticum and its backward extension outside the otic capsule is the recessus perilymphaticus. To the otic capsule behind and to the edge of the fenestra the operculum is attached by membrane only. The fenestral margin is osseous behind; dorsal and ventral cartilaginous lips join to form the cephalic border of the fenestra, the cephalic end of the operculum being slightly included. The columella is completely merged with the otic capsule, though doubtless the dorsal and cephalic cartilaginous margin of the fenestra, in part at least, represents it. Figs. 43 (Pl. V) and 44 (Pl. VI) show the relations, shape and cartilaginous consistency of the operculum. The latter figure may be compared with Fig. 42 (Pl. V) of Salamandra in illustration of the more massive character of the operculum in that form. Recurring again to the columella, in these two forms, Triton presents a condition of much greater reduction and incorporation in the absence (in the adult) of a recognizable fenestral plate and stilus columellæ (cf. Figs. 41 and 43, Pl. V).

The development of the otic capsule in Triton has been followed in more or less detail by Reichert '38, Semmer '72, Parker '82b, Wiedersheim '77, and Stöhr '79. From the reduced condition of the columella in this salamander, it was to be expected that its presence, not to mention significance, should be entirely overlooked and that the development of the operculum should be given correctly in all essential points. Hence we find Reichert, Semmer, Wiedersheim, Parker, and finally, Stöhr describing the operculum as formed

out of the otic capsule in this Urodele. Stöhr's classical investigation was undertaken primarily to describe whether or not after all the columella (of reptiles) was not of double origin,—one portion derived from the ear capsule (opercular plate) and a second portion from the hyoid arch, and as a preparatory study it seemed best to him to re-examine conditions in the amphibia (p. 480). Parker, in the meantime, published his first paper, dealing largely with the development of the skull of the Axolotl (to which reference has already been made, p. 562, but including a brief description of the skull of the larval and adult Salamandrina (Seironota) perspicillata. His second paper, dealing with Triton, appeared subsequently to Stöhr's. Wiedersheim ('77) had described (apparently in Triton alpestris) the development of the operculum as cut out of the otic capsule by a circular thinning of the cartilage, which by extension completely separates the operculum from the remainder of the otic capsule as a nearly circular disc.⁸ With this mode of development as with Reichert's view that the operculum appeared as a chondrification in the fenestral membrane, Stöhr disagreed. While he examined, apparently, larvæ of different ages, he described, modelled and figured the condition in a 24 mm. specimen. He says: "Vom vorderen Rande des knorpeligen Fensterrahmens entspringt ein kurzer nach hinten gerichteter Fortsatz (O), der auf der häutigen Fenestra ovalis aufliegt. Zu beiden Seiten des Fortsatzes liegen grosse Blutgefässe (die Rinnen sind auf der Figur sichtbar), die bei der Vergrösserung desselben in so fern eine Rolle spielen mögen, als sie durch Druck die knorpeligen Rinnen, welchen sie anliegen, immer mehr vertiefen und schliesslich den Boden der Rinnen zum völligen Schwund bringen. Die Vergrösserung des Fortsatzes erfolgt aber gewiss auch durch eignes Wachstum. Bei Triton cristatus

⁸('77, p. 501). "Kurz nach Verschmelzung der Parachordal-Elemente mit den Gehörblasen sieht man am äusseren Rand ihrer Unterfläche eine ringförmige Zone auftreten, welche bei genauerem Studium sich als eine circuläre Verdünnung der Knorpelwand herausstellt. Letztere schreitet immer weiter fort und schliesslich hat sich eine rundlich-ovale Knorpelscheibe aus der Labyrinthwand (Fig. 6, Fov, Op) herausgeschnürt, ein deutlicher Beweis, dass das Operculum der Urodelen ontogenetisch nicht vom Kiemen-Apparat, sondern von der Gehörkapsel selbst herzu-leiten ist."

sowohl, wie bei *Triton taeniatus* bleibt der Fortsatz nicht lange mit dem knorpeligen Fenesterrahmen in knorpeliger Verbindung; ehe er noch eine Grösse erreicht, schnürt er sich von seinem Mutterboden ab und stellt nun ein freies, auf der *Fenestra ovalis* aufliegendes Knorpelplättchen dar; das Operculum. * * * *Das Operculum ist demnach ein Theil der knorpeligen Ohrkapsel, hervorgewachsen vom vordern Umfang des ovalen Fensters. Mit dem Hyoidbogen steht es genetisch in keiner Beziehung.*" Interestingly enough, the description and figures indicate that the structure he identified as the Operculum was not the Operculum but the Columella. Its shape, connection with the anterior border of the fenestra, and its position between artery and vein, leave small doubt of this. The development of the *operculum* he seems to have entirely missed, and the mode of development advanced by Wiedersheim appears to be more nearly correct, though doubtless chondrification of opercular tissue in the *fenestra vestibuli* also contributes to its growth. It seems certain that in the growth of the larva both the fenestra and the operculum increase in size, and observation of this enlargement and extension of the rather cleft-like fenestra (*vide* Gaupp '05, Fig. 350) doubtless caused Parker to believe that the oval window arose by "dehiscence," and explains also the mode of origin of the operculum advanced by Semmer and by Wiedersheim. On the other hand, Stöhr's contention that the fenestra exists from the beginning as an unchondrified portion of the ear capsule, is without doubt true for *Triton* as we find it to be for *Diemictylus*, but describes the origin of the primary rather than the secondary fenestra. Stöhr, in a year-old *Triton*, figures the true operculum.

Parker's brief statements ('82b, pp. 198, 199, 203, 206, 209) upon the operculum (Stapes) and fenestra vestibuli (ovalis) in larval and adult *Triton* (*Triton punctatus*) are too indefinite to permit of any conclusions being based on them as to what the conditions were. In the adult he comments upon the cartilaginous nature of the operculum (Stapes) and the lack of a stilus (columella).

Diemictylus viridescens. Little need be said of the conditions in this form since in all essentials it resembles *Triton* closely. In the transformed salamander (red form) as also in the fully adult (Figs.

2-3), the operculum is plate-like, of cartilage, having the same relations to the fenestral margin as in Triton. It is somewhat more massive; the fenestral margin is cartilaginous only in front and above where the cartilage extends back to the caudal end of the fenestra. Below, cartilage extends back only as far as the anterior tip of the operculum. A well developed *M. opercularis* is present.

During the larval stage the morphological relations are essentially those of Triton larvæ, the vestigial plate being somewhat more closely joined to the crista semicircularis (Fig. 4, *Cr. s.*), but its

FIG. 2.

FIG. 2. *Diemictylus viridescens*, land form. *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *D.p.*, ductus perilymphaticus; *H.*, ceratohyale; *Op.*, operculum; *Sq.*, os squamosum.

FIG. 3.

FIG. 3. *Diemictylus viridescens*, land form. *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *D.p.*, ductus perilymphaticus; *H.*, ceratohyale; *Op.*, operculum; *R.p.*, recessus perilymphaticus; *Sq.*, os squamosum.

ventral edge more evidently outside the membrana fenestræ. At 15 mm. in length, neither columella nor operculum have appeared. In a 17 mm. specimen, the columella is developing upon the fenestral membrane in continuity with the fenestral margin above and in front. The operculum is forming on the medial edge of the fenestra in continuity with the cartilage of the capsule. Aside from growth and a more marked differentiation of the operculum, there has been but slight change in a larva 19 mm. long. At 37 mm. the operculum and also the columellar plate are well developed. The relations

of the two structures may be seen from the accompanying figures, 4-5.

These figures may be compared with the similar figures of the 36 mm. Triton larva (Pl. VII, Figs. 49 and 50). Fig. 4 may also be compared with Fig. 41, Plate V, of *Salamandra* and Fig. 32, Plate III, of transforming *Ambystoma*.

Adequate descriptions of the "sound-transmitting apparatus" in *Diemictylus* are lacking. Parker ('82a) describes the condition in both larva and adult (pp. 179, 181), but each statement is brief and without significance; more significant is his comment when

FIG. 4.

FIG. 5.

FIG. 4. *Diemictylus viridescens*, larva 37 mm. long. *C.*, arteria carotis interna; *C.L.*, canalis lateralis; *Col.*, columella; *C.p.*, cavum perilymphaticum; *Cr.s.*, crista semicircularis; *Op.*, operculum; *V.p.l.*, vena petroso-lateralis.

FIG. 5. *Diemictylus viridescens*, larva 37 mm. long. *C.*, arteria carotis interna; *Col.*, columella; *C.p.*, cavum perilymphaticum; *Op.*, operculum; *V.p.l.*, vena petroso-lateralis.

characterizing the skull of *Spelerpes* (See foot-note on p. 578). Cope ('88) is not sufficiently detailed and Wiedersheim ('77) does not particularly emphasize the relations in this portion of the skull of *Diemictylus*.

PLETHODONTIDAE.

Representatives of all the genera of this family have been examined as follows: *Batrachoseps*, *Hemidaetylium*, *Manculus*, and *Autodax*, the adult stage only; *Gyrinophilus*, *Plethodon*, and *Stereochilus*, both larva and adult; *Spelerpes*, adult and a series of twelve developmental stages of larvæ from 15 to 55 mm. in length.

In the fenestra vestibuli of the adult there is a single plate, irregularly oval in outline and free from the ear capsule except on its ventro-cephalic margin where a fusion is found (Pl. X, Fig. 67). From the cephalic and dorsal portion of this plate there projects upwards and forwards a slender stilus (Fig. 67) which in the adult articulates with both quadrate and squamosum. It is slender in all forms except *Batrachoseps* where it is absent or vestigial. In the caudal portion, the fenestral plate extends behind the caudal margin of the fenestra and swells outward, forming a prominence in this region. The cavity of this prominence is an outward and backward extension of the cavum perilymphaticum. In a relatively deep depression on the caudo-lateral aspect of this prominence the *M. opercularis* is attached. The fenestral plate in the *Plethodontidæ* is, as are all the related parts, finer and much less massive than in the families already considered. The stilus is relatively a long and slender rod between the vena petroso-lateralis above and the arteria carotis interna and facial nerve below. The lips of the fenestra vestibuli remain cartilaginous and are connected with the fenestral plate by membrane only, save in the cephalo-ventral portion mentioned above.

The inner and outer bony plates so characteristic of the columella in other forms are here co-ossified, the cartilage persisting only at the circumference. In the central portion of the plate the cartilage which is subsequently replaced by bone, varies markedly in thickness even in the same genus,—for example, in *Spelerpes bislineatus* it is small in amount and early replaced by bone, while in *Spelerpes ruber* quite the reverse is true. A similar comparison could be made between genera. The ossification of the fenestral structures in this family corresponds to the ossification of the skull as a whole, both in time and extent.

Accompanying this marked ossification of the plate there is complete ossification of the base of the stilus; distally it is composed of a shell of bone enclosing a cartilaginous core. In regard to the relation of the peripheral end of the stilus, it should be stated that the articulation with the squamosum, quadrate and palatoquadrate mentioned above applies only to the adult. In the larvæ of the forms

studied (*Gyrinophilus*, *Plethodon*, *Stereochilus*, *Spelerpes*) the connection was with the squamosum only. In the adult there is a very wide variation, from a close articulation with the squamosum only (as in *Maneculus*) to an intimate connection of the stilus with a cartilaginous process of the palatoquadrate, as in *Stereochilus*, *Autodax* and *Plethodon*. The other genera show an intermediate condition; in *Hemidaetylium* and *Spelerpes* the connection with the squamosum is the closest, while in *Gyrinophilus* there is an equally close articulation with the subsquamosal process of the quadrate; in no one of them was the cartilaginous process of the palatoquadrate as well developed as in *Stereochilus*, *Autodax*, and especially *Plethodon*.

The variation in the connections of the distal end of the stilus is undoubtedly associated with the inclination of the suspensorium to the long axis of the skull. During the period of growth, due to the relative displacement of parts, the distal end of the suspensorium is "drawn" forward, bringing its long axis more nearly parallel with that of the skull.

The definitive fenestra vestibuli of the *Plethodontidæ* is large and lateral in position, more nearly representing the primary fenestra of other urodeles,—a condition recognized by Parker.⁹ The columella is correspondingly large, nicely filling the opening, and projecting slightly back of it, as presently to be described. The plan of ossification in the columella is so characteristic that we have come to consider it as the *Plethodontid* type.

The *M. opercularis*, though absent in the larva, is a well developed structure in the adult. It attaches to the caudal portion of the fenestral plate, which there possesses a decided excavation occupied by the tendon of the muscle, giving the "scooped out" appearance noted by Parker.

⁹Parker, '82, p. 199. "The under face of this ear capsule (in *Spelerpes*) is very different from that of most high "Urodelous" skulls.

"In those massive *typical* Caducibranch skulls just described, *e. g.* *Notophthalmus* (Pl. XVII) and *Cynops* (Pl. XVIII), the vestibule is in the form of a smooth *bullæ*, with the stapes set on behind; and that plate is either quite soft or very slightly ossified; it is also relatively small.

"In *Spelerpes* (Pl. XXI, Figs. 2, 3, and Pl. XVIII, Fig. 10) the vestibule is but little protuberant; its fenestra is lateral, and corresponding with the stapes, very large."

Despite the depression for the *M. opercularis* the ear capsule has in this region a bulging appearance due to the growth of the fenestral plate backwards beyond the margin of the fenestra vestibuli. Fig. 47 (Pl. VI) shows not only that the prominence has extended beyond the margin of the fenestra, but also that within the prominence there is a recessus which is continuous with the cavum perilymphaticum.

Earlier in this paper it has been shown that in *Ambystoma* and others there is a perilymphatic prominence in the region of the

FIGS. 6 and 7. *Plethodon cinereus*, embryo. *C.*, arteria carotis interna; *C.l.*, canalis lateralis; *Col.*, columella; *H.*, ceratohyal; *L.h.c.*, ligamentum hyo-columellare; *M.*, musculus cephalo-dorso-mandibularis. *Sq.*, os squamosum; *V.p.l.*, vena petroso-lateralis.

fenestra vestibuli formed by the outward and backward growth of the operculum and that to the lateral aspect of this structure the *M. opercularis* is attached. Within the perilymphatic prominence is the recessus perilymphaticus, a caudal continuation of the perilymphatic cavity. In these respects there is a striking similarity between the caudal portion of the fenestral plate in the *Plethodontidae* and the operculum of other forms. Further than the similarities mentioned in the preceding paragraph there is, in the adult, no evidence as to the constitution of the fenestral plate in the *Plethodontidae*. In the light of development, however, the condition is

somewhat better understood. Eleven larvæ of *Spelerpes bislineatus* ranging in length from 15 to 55 mm. were studied by means of serial sections. Just when the columella makes its appearance we can not say, but in larvæ 15 and 17 mm. long there is present a delicate cord of cells outside the ear capsule extending from the under side of the squamosum towards the fenestral membrane to which it is not closely related at this stage. In a larval *Plethodon cinereus* (Figs. 6 and 7) of a similar stage of development this cord is composed of a greater number of cells and is consequently more com-

FIG. 8. *Spelerpes bislineatus*, larva 23 mm. long. *C.*, arteria carotis interna; *C. l.*, canalis lateralis; *Col.*, columella; *C. p.*, cavum perilymphaticum; *V. p. l.*, vena petroso-lateralis.

pact and larger. Here also, as in *Spelerpes*, this group of cells is not closely connected with the fenestral membrane. It extends forward to the under side of the squamosum and apparently is joined to the ceratohyal by a less marked cord of cells. Figs. 8 and 9 from two sections 25 microns apart may serve to illustrate the extra-otic position of the columella. Comparison with the figures of like stages of *Ambystoma* and *Cryptobranchus* is suggested.

In *Spelerpes* larvæ 23 mm. long the lower end of this cord of cells has become intimately associated with the fenestral membrane at the cephalo-ventral margin of the fenestra. At this point the fenes-

tral plate remains permanently fused with the ear capsule. Chondrification has occurred, forming a stilus and a small fenestral plate (Figs. 8 and 10).

From the place of its attachment the fenestral plate gradually extends backwards, growth being the result of the deposition of cartilage in the free margins of the plate, particularly the caudal. Thus successive rings are added until the plate fills the opening in the ear capsule. In the caudal portion of the fenestra vestibuli the mem-

FIG. 9. *Spelerpes ruber*, larva 71 mm. long. *F.p.*, fenestral plate; *R.p.*, recessus perilymphaticus.

brane forms an outpocketing or prominence (Fig. 12) long before it is invaded by cartilage, but before transformation the extension of the prominence behind the lips of the fenestra is slight if present at all. The prominence forms the outer walls of a recessus which has the same relations as that of the adult. Until transformation there is no indication of the *M. opercularis*, it apparently having no function until adult life is assumed. The conditions in the adult *Plethodontidæ* are well illustrated by the photographs of *Gyrinophilus* in Figs. 45, 46, 47 (Pl. VI).

It appears that the definitive plate of the adult is the result of a direct and continuous growth of cartilage in the membrane which covers the foramen vestibuli. At no time during development are there found separate centers of chondrification in either stilus or fenestral plate.

There appears to be a wide divergence between the sound-transmitting apparatus in the Plethodontidæ and that in *Ambystoma*. This seems particularly true of the development, and as a consequence is also true of the homology of parts. A brief review of the development of the fenestral elements in the forms thus far considered may, therefore, render the situation easier to grasp. In *Ambystoma* the ear capsule chondrifies early and the columella fills the fenestra vestibuli. At transformation (there being no room for growth) the operculum is cut out from the cartilage of the ear capsule itself; an adaptation, it might seem, to mechanical needs. In *Triton* and *Diemictylus* the columella relatively early fuses completely with the

FIG. 10. *Spelerpes bislineatus*, larva 43 mm. long. *C.*, arteria carotis interna; *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *F.p.*, fenestral plate; *L.*, lagena; *M.*, musculus cephalo-dorso-mandibularis.

ear capsule, leaving the foramen free. Here it is found that, while there is a slight cutting out of the operculum from the ear capsule, it results largely from a growth of the cartilage cephalad into the fenestral membrane. The situation in the Plethodontidæ differs from either of these. The columella, when first coming into intimate relation with the ear-capsule, is small as compared with the size of the for-

amen which increases in size with the growth of the skull. The early ossification of the ear capsule renders impossible the formation of an operculum by either the cutting out process or by forward growth into the fenestral membrane. A comparison of Figs. 11 and 12 will help to make clear that the membrane filling the caudal portion of the fenestra corresponds in its position and relation to other parts to that portion of the fenestra in *Ambystoma* which is occupied by the operculum. This, together with the formation of a prominence by the fenestral membrane in this region, which when chondrified affords attachment for the *M. opercularis*, suggests that it is opercular tissue. Taking this view it is perhaps not inappropriate to consider that the caudal portion of the fenestral plate in the *Plethodontidæ* represents the operculum of other forms.

FIG. 11. *Ambystoma punctatum*, transforming larva. *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *D.p.*, ductus perilymphaticus. *M.*, musculus cephalo-dorso-mandibularis; *Op.*, operculum.

FIG. 12. *Spelerpes bislineatus*, larva, 55 mm. long. Lettering as in Fig. 11.

This is from the viewpoint of groups in which the operculum is formed as a separate structure. Looking at it from the reverse point of view the *Plethodontidæ* might be considered as representing the less specialized condition. It is conceivable that in those forms in which an operculum is developed the columellar blastema became fused with the edge of the primitive fenestra both in front and behind, so that when it came to chondrification there were almost of necessity, developed two plates: (1) the fenestral plate of the columella joined to the otic capsule in front, and (2) the operculum joined to the ear capsule on the caudal and medial side. The operculum would thus be a dissociated part of the fenestral plate. In

the Plethodontidæ, due possibly to an early fusion of the columellar blastema in front only, such a division of the plate does not occur. It seems quite possible that a comparative study of the primitive fenestra in urodeles might afford some evidence of this view. What bearing this interpretation might have upon the periotic origin of the operculum is evident.

DESMOGNATHIDÆ.

Desmognathus fusca. In this species, the only member of the small family examined, the "sound-transmitting" apparatus mark-

FIG. 13. *Desmognathus fusca*, larva 26 mm. long. *C.*, arteria carotis interna; *H.*, ceratohyale; *L.h.c.*, ligamentum hyo-columellare; *L.s.c.*, ligamentum squamoso-columellare; *Sq.*, os squamosum; *St.C.*, stilus columellæ; *V.p.l.*, vena petroso-lateralis; *VII.*, nervus facialis.

edly resembles in its general structure and relations that of the Plethodontidæ just described. In fact, they are of the same type. A bony plate with cartilaginous border fits into the fenestra and projects caudad upon the outer wall of the recessus perilymphaticus. The caudal portion is concave externally, and in the depression there is inserted the *M. opercularis*. The cephalo-ventral border is continuous with the cartilaginous border of the fenestra. The stilus is osseous with a cartilaginous core, the distal portion being of cartilage alone. Two figures of an adult, one (Fig. 15) through the caudal portion showing the concave fenestral plate and the recessus; the second (Fig. 14) through the insertion of the stilus, may be

directly compared with the sections through the same regions in the plethodontid, *Gyrinophilus* (Pl. VI, Figs. 46 and 47). Similar comparison may be made with *Spelerpes* (Figs. 6 and 7).

The relations of the stilus to the squamosum, quadrate, facial nerve, artery and vein, have been described in some detail by Kingsbury ('03, pp. 321-325) for larva and adult, two sizes of each, and as our investigations have not added significant details, it will be sufficient to state in confirmation of the description there given that while in the larva the stilus is most closely joined to the ventral edge of the squamosum (Fig. 13); in the adult it becomes shifted so as to articulate closely with the os quadratum, less closely with the cartilaginous process of the palatoquadrate. The relation to artery, vein and nerve is that typical of the majority of urodeles.

FIG. 14. *Desmognathus fusca*, adult. *Col.*, columella; *C.p.*, cavum perilymphaticum; *Sq.*, os squamosum; *St.C.*, stilus columellæ.

An examination of young larvæ and embryos which would determine the origin or origins of the stilus and fenestral plate, has not been undertaken. The mode of insertion of the stilus upon the fenestral plate, as shown in Fig. 14 (compare also Pl. VI, Fig. 46, *Gyrinophilus*), might suggest that the stilus alone developed outside the otic capsule, as the description of Parker would indicate. Since the columella in *Desmognathus* doubtless develops in essentially the same manner as in the *Plethodontidæ* (*Spelerpes*, *Plethodon*) reference may be made to the description of its development in that family, as given on p. 580.

Desmognathus possesses a short but well developed ligamentum hyo-columellare, in this respect also agreeing with many of the *Plethodontidæ*. In Fig. 13 it is indicated in the larva.

TYPHLOMOLGE.

A single adult 95 mm. long was studied by means of serial sections and a model of the entire skull in the otic region. The fenestra vestibuli is filled by a single plate as in the *Plethodontidæ*, connected by a long and slender stilus with the suspensorium. On the cephalo-ventral margin the fenestral plate is fused with the ear capsule.

FIG. 15. *Desmognathus fusca*, adult. *C. p.*, cavum perilymphaticum; *M. op.*, musculus opercularis; *Op.*, operculum; *R. p.*, Recessus perilymphaticus.

The stilus is relatively longer than in any of the other forms examined. This is probably due to the extreme flattening of the skull, which has brought the long axis of the suspensorium more nearly parallel with that of the skull, thus throwing the attachment of the stilus to the suspensorium farther cephalad. It seems likely that this flat condition of the head is the result of an adaptation to sub-

terranean life where a wedge-shaped form is more convenient for making progress in narrow quarters.

Miss Ellen Tucker Emerson, 2d ('05), states in substance that the operculum is not connected with the suspensorium, and her figures show a short stilus, labelled columella, projecting freely from a basal portion in the fenestra vestibuli called operculum. Serial sections and the model of the specimen studied by us show that the columella is morphologically connected with the suspensorium but interrupted. On the right side of our specimen the stilus begins to grow smaller in diameter a little beyond the middle of its extent and finally disappears for a distance of 210 microns. Then it appears again, gradually assuming its normal diameter, and continues uninterruptedly to the suspensorium. Here it is joined to the squamosum, the os quadratum and the palato-quadrata (Pl. II, Fig. 28). Between the free ends of the segments is a well defined ligament within which a few cartilage cells are found at intervals.

On the left side there are three segments (Pl. X, Fig. 68) produced by two interruptions. One of these corresponds in position and extent with the single interruption on the right side. The second occurs just before the stilus joins the suspensorium and is about the same in extent as the first. On this side the distal or third segment extends for a distance along the ventral edge of the squamosal, joining the edge of the os quadratum as well, but without relation to the palato-quadrata. It should be noted in this connection that Kingsbury ('03) described the stilus in adult *Spelerpes* as connected with a rod of cartilage lying along the ventral edge of the squamosum, a condition similar to what is found on the left side of our specimen of *Typhlomolge*.

It may be questioned whether the interrupted condition of the stilus in *Typhlomolge* results from tension and a consequent separation of what otherwise would remain, as developed, a continuous bar of cartilage, or is reminiscent of the condition found in the frog where there are separate centers of chondrification. It should be recalled, however, that in the urodeles where development has been studied, chondrification of the stilus and columella is continuous. Furthermore it is to be noted that in the *Plethodontidæ* there is a

loose connection of the stilus with the suspensorium, probably due to the tilting of the latter in its relation to the long axis of the skull. In *Typhlomolge* this tilting of the suspensorium is extreme and it is, therefore, a fair question as to whether or not the segmentation in the stilus is the result of tension during development. The attachment of the stilus to both suspensorium and columella are at the same horizontal level, there being a slight outward and downward curvature as shown in Plate III, Fig. 28.

The relation of the stilus to the blood vessels and nerves in this region is that found in *Necturus*, namely, the *vena petroso-lateralis* and the *ramus jugularis* of the facial nerve are above, while the main trunk of the facial nerve and the internal carotid artery are below. This condition is illustrated by Fig. 28 (Pl. III) and Text-figure 16.

FIG. 16. *Typhlomolge*, adult. *Q.*, os quadratum; *R.j.VII.*, Ramus jugularis VII.; *St. C.*, stilus columella; *Sq.*, os squamosum.

The fenestra vestibuli is irregularly elliptic in outline as is the fenestral plate. The dorsal and ventral portions are not filled by the plate, there being a relatively wide space both above and below filled only by membrane. In the caudal portion there is a slight outward swelling forming a prominence which projects slightly beyond the caudal lip of the fenestra and which contains a small but well defined recessus within. The *M. opercularis* is absent.

The lips, both of the fenestra vestibuli and the fenestral plate,

remain cartilaginous throughout the greater part of their extent, the bony portion of the plate being much thinner than the margin as in the *Plethodontidæ*. At its base the stilus is composed entirely of bone (Fig. 17) which gradually becomes a sheath surrounding a core of cartilage. In the distal half (Fig. 16) the stilus is composed of cartilage alone.

Between the distal end of the ceratohyal and the otic region of the skull is a wide sheet of fascia, the caudal portion of which is attached to the stilus and in this region becomes a relatively strong ligament between the columella and hyoid (Pl. X, Fig. 68).

Developmental stages have not been studied, but it appears that in *Typhlomolge* the type of sound-transmitting apparatus is essentially that of the *Plethodontidæ*.

FIG. 17. *Typhlomolge*, adult. *C.L.*, canalis lateralis; *Col.*, columella; *St.C.*, stilus columellæ; *Sq.*, os squamosum.

NECTURUS.

Although the relations and development of the otic region of the skull in *Necturus* have been already quite well worked out by several persons, because of its historic interest in this connection and the general acceptance of its low systematic rank, it has been included for brief consideration. In illustration of the conditions in this form four photographs are introduced, Figs. 57, 58, 59 (Pl. VIII), and 60 (Pl. IX).

Miss Platt ('97), p. 430, described the early development in the ear capsule in *Necturus*. In a 19 mm. larva the "operculum" is

pre-cartilage, forming neither from the otic capsule nor the fenestral membrane, but independently lying primarily anterior to the fenestra. She suggested at this time the possible homology of the urodele operculum with the pars interna plectri which is supported in this paper; but evidently without much faith in its correctness, for in a footnote in which she states her objection to the term "operculum" she adds that this cartilage (operculum, *i. e.*, columella) is not the equivalent of the "columella" (plectrum) of the Anura and is of questionable homology with the "stapes" of higher vertebrates.

Kingsbury ('03) examined the early development in *Necturus*. He confirmed Miss Platt's results and in addition described the primary connection with the squamosum and the cells underlying it: "At this stage, the operculum is just beginning to chondrify as a distinct center, and from it a chord of cells is continued forward, ventral to the vena jugularis and the ramus jugularis, to the cells surrounding the developing squamosum, becoming continuous with them a short distance (50 microns) back of the processus oticus quadrati. The cells are of course continuous with those of the squamosum and also with the cells between that bone and the quadratum, so that the squamosum, the quadratum, and the ligament-anlage, may be said to be joined together by a common mass of cells. In the just hatched larva, likewise, the ligament-anlage clearly goes to the underside of the squamosum and inserts itself between that bone and the processus oticus quadrati, so that it might be interpreted as going to both structures. As soon as the connective tissue fibers develop, however, the relation is seen to be with the squamosum and not with the quadratum. In later stages a strong ligamentum squamoso-columellare develops, which connects the stilus columellæ to the columellar process of the squamosum."

Wilder ('03) in a monograph upon the Skeletal System of *Necturus* takes, however, a different view. He regards the operculum (columella, our term) as a "detached portion of the otic capsule" basing his view upon the condition in a 44 mm. larva which was essentially the same as in a 26 mm. individual examined by him. In the light of the work by Stöhr on Triton and Siredon he regards the statements of Miss Platt as unfounded, admitting, however,

that the proton described by her might represent "a true columella or hyomandibular cartilage which may become fused with the true operculum," although he could find no trace of such a double origin. In comment on the above it may be said that to determine the first development it is necessary to go back of the condition in a 26 mm. larva as was done by Miss Platt. There is certainly no indication of a double origin, although the increase in size in the columella of *Necturus*, as in *Ambystoma* (p. 556), admits of two possibilities of interpretation. The development of the operculum as described by Stöhr in *Triton* and *Siredon* has been discussed on p. 573.

The ramus jugularis VII passes over the ligament (Pl. VIII, Fig. 58), as in *Proteus* and *Typhlomolge* described above.

The relations of the columella, squamosum and facial nerve in *Necturus* are well known through the work of Cope, Drüner, Kingsbury and Wilder, though the significance of the relations has not been adequately considered.

Huxley's classic paper on the skull of *Necturus* was in respect to his description of the relation of the columella, facial nerve, and suspensorium incorrect and misleading, occasioning a wrong idea of the urodele type, persistent even up to the present time. We find no trace of his ligamentum suspensorio-stapiale, over which the facial nerve passes. Operculum (our use) and *M. opercularis* are lacking.

Proteus agrees in all essentials with *Necturus* (Wiedersheim, Drüner, Kingsbury).

CRYPTOBRANCHIDAE.

Cryptobranchus alleganiensis. Through the generosity of Mr. B. G. Smith, of Syracuse University, who kindly sent us a series of embryo, larval and adult specimens, we were enabled to examine the relations in this interesting form with quite satisfactory results.

As the publications of Wiedersheim ('77), Parker ('82b) and Cope ('88) have shown, the Columella in the adult possesses a well developed stilus which articulates with the under (inner) surface of the squamosum. This relation is strikingly shown in the series of sections through the head of an adult 140 mm. long (Pl. VII,

Figs. 54-55; Pl. VIII, Fig. 56) which was at our disposal. The squamosum, furthermore, is the only skeletal element to which the columella is attached, save the os pterygoideum which works its way well up on the inner surface (Pl. VII, Fig. 54) of the palatoquadrate and whose upper edge is somewhat loosely connected with the end of the stilus columellæ. As though determined by the excessive flattening of the head in this form, the mandibular end of the palatoquadrate is well back and lateral, while the cranial attachment by means of the usual three processes is unusually far forward (cephalad). The whole suspensorium is therefore rotated from an "ideal" transverse position, and it would seem as though this displacement might well explain in a mechanical way (a) why the stilus columellæ joins the under surface of the squamosum instead of its caudal edge as in so many of the forms; (b) how it is possible for the os pterygoideum to come into such close relation to the columella; (c) the absence (in the *young* adult at least) of a connection of the stilus with the palatoquadrate or os quadratum.¹⁰

A second interesting feature found in this skull is the presence of what might be interpreted as a Ligamentum hyo-columellare (Pl. VII, Fig. 55, L. h. c.) which is essentially a thickening of the fascia covering the inner (under) surface of the M. cephalo-dorso-mandibularis. It extends from the ceratohyal to the outer surface of the stilus, extending with it to its attachment to the squamosum. As this ligamentous thickening of the fascia is relatively more marked in the larva, it will be mentioned again in connection with that stage.

The columella appears to ossify in the typical way; at the stage of our specimen it consists of a cartilaginous body (Pl. VII, Fig. 55; Pl. VIII, Fig. 56) with an inner and outer plate of perichondral bone, the latter extending out upon the stilus for a distance. The distal portion possesses no bony sheath and it was doubtless this that led Parker to distinguish here two elements, a *Stapes* (bony and

¹⁰From this bone as a center the ossification of the quadrate cartilage apparently proceeds. Kingsbury referred to it as "bone X," Gaupp has suggested tentatively the homology with the os quadrato-maxillare of Anura. Its final interpretation requires additional comparative investigation.

fitting into the fenestra) and articulated with a *Pharyngohyal*,¹¹ consisting of cartilage. This is, of course, incorrect, due to the inadequacy of the method of gross dissection, upon which he based his conclusions.

From the caudal edge of the palatoquadrate a rather delicate process of cartilage extends back to the ceratohyal to which it is applied, curving slightly over its upper surface. The name of Epihyal which Parker gave to this process of the quadrate is likewise certainly incorrect. Cope ('88) has termed this the "Hyo-suspensorial cartilage;" it might more correctly be called *Processus hyoideus palatoquadrati*, since an *articulation* with the quadrate as described by him is not found. In other respects the description of Cope is essentially correct. Wiedersheim, likewise, describes the squamosal connection of the stilus and the position of the facial nerve correctly, though he apparently overlooked the condition here in the general portion of his paper.

Larval Cryptobranchus. Serial sections were made through the head of four *Cryptobranchus* larvæ whose lengths were, respectively, 28 mm., 34 mm., 45 mm., and one just hatched. Since in these series the morphological relations are in all essentials the same, it will be sufficient for the purposes of this paper to describe briefly the relations in the one which is of intermediate size (34 mm.), and supplement this with comments on some interesting features in the youngest,—the newly hatched larva.

The columella in this larva (34 mm.) consists of a roughly oval plate of cartilage resting upon the membrane closing the fenestra vestibuli. From the cartilaginous border of the fenestra the columella is separated by the membrane everywhere except at the cephalic edge where it articulates with the cartilaginous ear capsule at the crista semicircularis. In larvæ 28 mm. and 45 mm. long, the fenestral plate does not come into articular relation with the carti-

¹¹Parker in his earlier paper ('76, pp. 559 and 587) referred to this cartilage as homologous with the elasmobranchian "Spiracular cartilage" and the annulus tympanicus of the Frog, the facial nerve passing below it. In the second paper, however, in which he terms it a pharyngohyal, the facial nerve is described as passing over it.

lage of the ear capsule, so that doubtless this is a variable feature. In the adult there appears to be a very slender cartilaginous connection. The portion of the fenestra vestibuli not occupied by the columella is thus a crescent of somewhat horse-shoe shape.

The stilus of the columella arises gradually from the cephalic half of the fenestral plate, passing at first more laterally and then in a curve cephalad and slightly dorsad to become closely attached to the lower edge of the squamosum. In its course it passes between the vein and artery, as is typical, the vein being above (Pl. VII, Fig. 51). The facial nerve is entirely ventral to it, though the jugular branch and ramus communicans IX come very close, the latter lying at first upon the dorsal side of the columella; it slips over the outer side, however, and joins the R. jugularis in gliding under the stilus just as the latter joins the squamosum.

The sheet of fascia covering the inner surface of the M. cephalo-dorso-mandibularis possesses two thickenings of morphological importance. The more dorsal of these (Ligamentum hyo-columellare) arises over the outer side of the ceratohyal, curves around its upper surface and passes forward to join the stilus columellæ at its bend and, as a sheath upon its outer side, accompanies the latter to its articulation with the squamosum. Fig. 51 (Pl. VII) illustrates the location of this ligament in its course from hyoid to columella and shows the muscle "bellying against" the ligament as a full sail against a rope. A portion of this seems to have been Parker's stapedio-suspensorial ligament. The more ventral and band-like ligamentous thickening passes from the ceratohyal to the caudal edge of the quadrate. It curves around this element and a portion of it joins the tendon of the M. cephalo-dorso-mandibularis at its insertion on the os angulare. This ligament must embody the ligamentum hyo-suspensoriale and as well the ligamentum hyo-mandibulare. In connection with the former, in the adult is developed the cartilaginous process of the palatoquadrate already described. Whether this process develops from an independent center or not, and at what stage it appears, cannot be determined from the material at hand.

In the larva, the suspensorium has not the "rotated" position that

it has in the adult, and the columella has no connection with the palatoquadrate, os pterygoideum or os quadratum. Furthermore, it is to be noted that it articulates with the lower edge of the squamosum and not with its under surface.

The newly hatched *Cryptobranchus* is of interest in this connection for two reasons: (a) the columella is represented by a condensation of cells from which a cord of cells passes cephalad (Pl. VII, Figs. 52-53) and dorsad to the group of cells in whose midst the squamosum is just appearing as a homogeneous scale of bone; (b) the columella at this stage is pre-cartilage and is distinctly forming outside the ear capsule. The chondrocranium is cartilaginous, the fenestra clearly demarcated, and the precartilaginous columella external to the membrana fenestræ (Fig. 52). The development at this stage closely parallels that of *Necturus*, as already described (p. 590). It seems to us safe, therefore, to add *Cryptobranchus* to *Necturus* and *Ambystoma* as a form showing the extra-otic appearance of the columella, and its early connection with the squamosum. It is likewise noteworthy that the columella in all the larvæ examined shows no cartilaginous connection with the otic capsule; and in the adult the fusion is very slender,—if indeed it exists. The source of the cells that form the columella could not be determined from the material at hand, although two embryos were examined. Neither operculum nor opercular muscle are developed.

It is interesting to note in concluding that *Cryptobranchus* is the only form in which there has been general agreement as to the connection of stilus with squamosum; not so, however, the relation to the facial nerve. Both Wiedersheim ('77) and Parker ('82b) described the relation correctly and subsequently altered their statements.

Megalobatrachus. From the description of Parker ('82b), Wiedersheim ('77), Osawa ('99), as from the dissection of a single specimen in connection with this study, suffice it to state that it shows essentially the same relations as *Cryptobranchus*. Osawa (as quoted) describes the stilus as joining the palatoquadrate. Parker states that the hyo-suspensorial cartilage (his epiphyal) *articulates* with the palatoquadrate; in *Cryptobranchus* there is continuity.

AMPHIUMA.

In *Amphiuma* a single plate fills the fenestra vestibuli and is free except on its cephalic end where it is fused with the ear capsule which is cartilaginous. The very large stilus is articulated at its distal end with the squamosum and continuous with a process of the palatoquadrate. Its relation to the facial nerve and blood vessels is typical. On both inner and outer surfaces of the fenestral plate there is a layer of bone (Fig. 18) which is continued for a short

FIG. 18. *Amphiuma means*, adult. *C. l.*, canalis lateralis; *Col.*, columella; *Sq.*, os squamosum; *St. C.*, stilus columellæ; *VII.*, nervus facialis.

distance upon the base of the stilus. A distinct but not strong ligamentum hyo-columellare is present. Its diagrammatic representation is given in Pl. X, Fig. 71.

The fenestral plate becomes narrower in its caudal third and finally tapers to a point. In that portion of the ear capsule forming the caudal margin of the fenestra there is a pronounced prominence within which there is a continuation of the perilymphatic cavity of the ear (Fig. 20).

While complete developmental stages have not been studied, sections through the head of a larva soon after hatching, a transforming individual and an adult furnish some data regarding development. In the youngest larva the fenestral plate is relatively small

and free from the ear capsule all round. Although closely associated with, it appears to be wholly outside of, the fenestral membrane.

At transformation the columella is fused in front with the ear capsule and just fills the opening. Below and behind the columella a portion of the floor of the ear capsule becomes greatly thickened, especially in its lateral half, which is almost completely separated from the capsule (Fig. 19). In this stage there are a few muscle

FIG. 19. *Amphiuma means*, transforming larva. *C.*, arteria carotis interna; *C.p.*, cavum perilymphaticum; *Sq.*, os squamosum; *V.p-l.*, vena petroso-lateralis; *M.i.c.i.*, a portion of the musculus intertransversarius capitis inferior.

fibers partly differentiated off from the *M. intertransversarius capitis inferior* which have a slight attachment to this portion of the ear capsule.

This portion of the floor of the ear capsule which was thickened and partly separated off in the transforming individual is in the adult very much thickened, forming the pronounced prominence which encloses an extension of the perilymphatic cavity as shown in Fig. 20. The *M. intertransversarius capitis inferior* comes into close relation with the prominence of the adult, but there is no differentiation of a distinct opercular muscle.

By comparing Fig. 11 and Fig. 31 (Pl. III) of *Ambystoma* and Fig. 50 (Pl. VII) of *Triton* it is evident that this portion of the otic floor corresponds in position to the operculum. It would seem as though at transformation a beginning of operculum formation was made which does not go through to completion.

FIG. 20. *Amphiuma means*, adult. *C. p.*, cavum perilymphaticum; *Parasphen.*, os parasphenoideum; *Prom. p.*, prominentia perilymphatica. *Sq.*, os squamosum.

SIREN.

The only material examined was an adult specimen 133 mm. long. The fenestra vestibuli is here, as in some other forms, filled by a single plate which is cartilaginous in our specimen although Cope ('88) states that it is bony in this species. It is elliptic in outline, facing outwards and downwards with a short stilus standing almost vertical to the plate and slight inclination being in a backward and downward direction. The connection of the columella with the suspensorium, if it ever existed, has disappeared. The relation of the stilus to the blood vessels and nerves in this region is typical.

The fenestral plate is fused throughout its entire cephalic margin with the ear capsule. This fusion is much greater in extent, relatively, than in either *Typhlomolge* or the *Plethodontidæ*.

The ceratohyal is much produced caudally, its falcate distal portion extending beyond the otic region. A short distance before the caudal extremity is reached there arises from the dorsal edge a broad and strong ligament extending forwards for insertion upon the fenestral plate (Pl. X, Fig. 72). The stilus projects directly into this just cephalad of which there arises another, the hyo-suspensorial ligament, which passes cephalad for insertion upon the palatoquadrate. These ligaments are considered by Cope as one, namely, a hyo-suspensorial ligament extending from the *quadrate* across the ear capsule to the exoccipital. Parker treats them as two separate and distinct ligaments. That portion extending to the quadrate he calls the hyo-suspensorial while to the columellar portion he applies the name suspensorio-stapedial. Functionally they are probably to be considered as distinct, but in serial sections they appear to be thickenings of the same sheet of fascia.

The short and free stilus projecting into the ligamentum hyo-columellare is more comprehensible in the light of the segmented condition of this structure in *Typhlomolge*. Thus in *Siren* all suspensorial communication of the fenestral plate with the exterior, such as is found in other forms, is cut off. But it will be noted that the ligamentum hyo-columellare in this form is strongly developed which together with its firm attachment to the fenestral plate may compensate for the absence of the usual skeletal connections. The relation of the stilus to the facial nerve and blood vessels is that found in the majority of forms.

Three figures (Pl. IX) illustrate the relations of the columella, stilus and hyo-columellar ligament. In Fig. 61 the short stilus is shown projecting out into the dense ligament, the diminutive plate joined to the margin of the fenestra by connective tissue. Fig. 62 is through the caudal end of the columella of the opposite side. In Fig. 63 the section is through the perilymphatic prominence, a caudo-lateral extension of the ear capsule. Slightly farther forwards the cartilage is hollowed out by a small recessus. The fenestra

and the caudal lip of the columella appear in the lateral wall of the prominence. In all essentials, save as noted, the sound-transmitting apparatus of the adult is like that of *Amphiuma*.

GENERAL.

In perusing the preceding portion of this paper, it will have become obvious that considerable confusion in the interpretation of the sound-transmitting apparatus in *Amphibia*,—particularly the *Urodela*,—has been caused by discrepant statements and conflicting descriptions of the conditions existing in the different forms. The differences that apparently existed concern principally (a) the relation to the suspensorium, (b) the relation of the facial nerve to the stilus columellæ, (c) the mode of development of the fenestral structures.

The Suspensorial Connection. Gaupp in his paper on the sound-transmitting apparatus of Vertebrates ('98) was led to the conclusion that there existed two types of connection between the suspensorium and the skeletal element filling the fenestra vestibuli,—one above and one below the facial nerve, and the same view has been taken by Drüner ('03). Gaupp later ('05) says: "Die oft citierte Angabe von Wiedersheim, dass der Nerv bei allen Urodelen ohne Ausnahme über diese Brücke hinweglaufe, ist irrig; vielmehr scheint der Verlauf der Nerven *ventral* von der fraglichen Brücke das häufigere zu sein. Letzteres findet sich bei *Amphiuma* (Hay 1890, auf Grund eines von Prof. Norris hergestellten Modelles kann ich diese Angabe bestätigen), *Siredon* (Hasse 1873, Parker 1877) und zahlreichen anderen Urodelen (*Proteus*, *Desmognathus fusca*, *Spelerpes bilineatus*, nach soeben veröffentlichten Untersuchungen von Kingsbury); der Verlauf des R. jugularis facialis *über* die erwähnte Verbindung findet sich bei *Necturus* (Huxley) und *Proteus* (Drüner, Kingsbury). Es sind somit 2 verschiedene suspensorio-columellare Brücken aus einander zu halten, eine über und eine unter dem Facialis (Gaupp 1899)."

For this divergence of statement, Huxley seems to have been primarily responsible, inasmuch as in *Necturus* he described a "Ligamentum suspensorio-stapediale" and stated that "the hyo-

mandibular branch of the seventh nerve (VII) passes above this ligament to its distribution, just as it passes above the *Columella auris* in the frog."

The real connection of the stilus with the special process of the squamosum¹² (*Processus columellaris*) he seems to have missed entirely. The reference to Huxley of a recognition of such a connection by Gaupp in the passage quoted above is incorrect. It should be remembered, however, that Huxley's observations were based upon minute dissections, in which a strand of fascia could easily be made to assume the appearance of a ligamentous structure, and the obvious passage of the hyomandibular division of the seventh nerve *over* the columella in the frog and the relation in mammals would incline one *a priori* to a similar interpretation in urodeles. Wiedersheim appears to have accepted his statement of relations, and without paying special attention to the point, gave as the universal condition in urodeles that the facial nerve passed above the suspensorial connection. Huxley's description doubtless influenced his friend, W. K. Parker,¹³ who in several forms described the facial nerve as below the columella, yet sometimes located it above, or was vague in his descriptions.

One result of this study is to show that a "suspensorial connection" does indeed exist, in all save four of the salamanders examined (*Diemictylus*, *Triton*, *Siren*, *Batrachoseps*) the nervus facialis being below and in front (see, however, p. 610). The connection is not primarily with the palatoquadrate, as has been heretofore believed, but with the bone, partly overlying the palatoquadrate and partly over the lateral semicircular canal of the ear, which we have regarded as *squamosum*. This primary connection of the columella through

¹²The correct relation was described subsequently by Cope ('88, '89), Wilder ('03), Drüner ('11), and Kingsbury ('03); the relation to the facial nerve, by the last two.

¹³Parker, '77 (p. 559), in a footnote says: "Professor Huxley pointed out this anomaly to me, showing me that this ligament cannot correspond to the "suspensorio-stapedial" ligament of *Menobranchus* (*op. cit.*, p. 192)." The reference is to the squamoso-columellar ligament in *Ambystoma*, which is, of course, *above* the facial nerve. See footnote on page 562 for Parker's description.

its stilus with the squamosum is now reported¹⁴ for *Necturus maculatus*, *Proteus*, *Typhlomolge*, *Typhlotriton*, *Spelerpes bilineatus* and *ruber*, *Gyrinophilus prophyrificus*, *Hemidactylium scutatum*, *Plethodon cinereus*, *Stereochilus marginatus*, *Autodax lugubris*, *Manculus quadridigitatus*, *Desmognathus fusca*, *Ambystoma punctatum*, *Chondrotus tenebrosus*, *Cryptobranchus allegheniensis*, *Megalobatrachus maximus*.

In certain of the forms, however, at transformation,—before or after it,—the connection of the stilus tends to shift to the palatoquadrate, presumably in the change of the position and direction of the suspensorium to which Wiedersheim called attention ('77). In this displacement of parts as we interpret it, the squamosum, as in *Ambystoma*, comes to lie more on the dorsal surface of the palatoquadrate. In certain forms a special process of the palatoquadrate develops (e. g., *Plethodon*, *Amphiuma*) which may reach a relatively great length (*Amphiuma*). Hence we see how the more obvious connection has become accepted as the typical one, and the primary connection with the squamosum¹⁵ is overlooked, even though occurring throughout life as the direct articulation in many of the forms. If the anatomical relation of parts is such that the palatoquadrate does not come into the proximity of the distal end of the stilus in the shifting, a connection with it is not established,—as in the case of *Cryptobranchus* (young adult) where the connection of the stilus moves¹⁶ from the caudal edge to the under side of the squamosum. Whether the stilus columellæ maintains the primary relation with the squamosum or becomes more closely joined to the palatoquadrate, any physiological value it may possess as a “suspensorial connection” remains unaffected, so closely is the lower

¹⁴Cope, '89, describes the correct condition in *Necturus* and *Proteus* (p. 22); of the remaining urodeles he says: “The stapes [columella] has no connection with the suspensorium in the adult except in the *Cryptobranchidæ* and *Amphiumidæ*. It is connected with the suspensory cartilage, which is continuous with the quadrate cartilage in the latter families, and in the young of other *Urodela*” (p. 29).

¹⁵The development of the stilus columellæ has not been studied in *Salamandra*, nor in *Amphiuma* has the earliest development been yet worked out (see Kingsbury, '03, p. 325). The squamosal connection will doubtless be found in all salamanders possessing a well developed stilus.

end of the squamosum joined to the quadrate. From a morphological viewpoint, however, it is not a matter of indifferent significance. The connection of the columella with the squamosum and its formative cells is a primary one, while the direct articulation or junction with the palatoquadrate is only secondarily established. The significance of the relation becomes more impressive when the development of the columella is considered. In the forms in which the early development has been traced,—Necturus, Ambystoma, Cryptobranchus, Spelerpes, Plethodon,—before cartilage has appeared in the columella, when the squamosum is but a delicate scale of bone, a cord of cells proceeds from the proton of the columella to the cells underlying the forming bone. The developmental relations will be considered again in connection with the question of hyomandibular homology.

Columella and Operculum. A second complication exists in Amphibia due to the existence of two structures that are found fitting into the fenestra vestibuli, and the failure to recognize this fact has added another source of confusion in the elucidation of the relations in this group. It is the first of these two elements, distinguished by us as *Columella*, which possesses a suspensorial connection. The second, termed by us the *Operculum*, possesses no such relation. In its typical form as it exists in the adult Ambystoma, Diemictylus or Salamandra, the operculum is a spheroid filling in the definitive fenestra with whose lips it is connected by membrane only or possesses a slight cartilaginous connection at its caudal end. It may be massive (spheroidal) as in Salamandra, or more plate-like as in Triton. The cephalic end is included by the lip of the fenestra; the caudal end projects freely, covers the recessus perilymphaticus externally and affords attachment to the M. opercularis. In the families of the Plethodontidæ and Desmognathidæ the condition is characteristic and unique; the oval window has fitted into it a plate whose cephalic portion possesses a well developed stilus and whose caudal portion offers attachment to the M. opercularis and covers externally a recessus perilymphaticus; it seems therefore to *represent* both columella and operculum.

The statement of Gaupp ('05) in reviewing the Amphibian sound-transmitting apparatus (p. 605), that only by a stretch of the

imagination could an extra-otic origin be ascribed to the element filling the fenestra vestibuli in this group, was made in the light of the condition existing in Triton and the fragmentary developmental evidence already at hand, and without knowledge of the existence of two structures in urodeles. It applies, therefore, with full force to the development of the operculum. The columella, however, develops in quite a different manner, and here the evidence of an extra-otic origin is much stronger. Killian ('90) first described this structure as developing outside the ear capsule in *Ambystoma*, and Miss Platt ('97) in *Necturus* advanced the same view. Kingsbury subsequently examined the condition in larval and embryo *Necturi* and came to the same conclusion. In this paper we have shown evidence of an entirely similar mode of origin of the columella, outside the fenestral membrane, in *Cryptobranchus*, *Spelerpes*, and *Plethodon*, and confirmed Killian's observations on *Ambystoma*. Supplementary evidence of an extra-otic origin for the columella is to be found in the fact that from the first, before chondrification has begun, the columella is connected by a dense grouping of cells with the squamosal cells around the outer side of the vena petroso-lateralis.

With the growth of the fenestral plate of the columella it becomes associated or fused with the cephalic edge of the fenestra. This is not, however, a primary connection but a secondary one. Hence the statement that has been made (Winslow, Stöhr) that the columella grows out of the cephalic edge of the window is not correct. In the descriptive portion of this paper, the difficulty in determining just what occurs in the chondrification of the plate of the columella has been pointed out. Even though the columella grew through the incorporation of otic tissue, its origin from without the otic capsule would not be invalidated, which is supported by its relation before chondrification and its early and intimate connection with the sub-squamosal cells.

The tendency of the columella to become fused with the cephalic cartilaginous margin of the fenestra is in some forms carried to an extreme, and results in a more or less complete incorporation of the structure into the ear capsule by extensive fusion with it. In the *Ambystomidae* its boundary is still distinguishable by the charac-

teristic inner and outer bony plates, and by the stilus. *Salamandra* lacks the ossification, the incorporation appears more intimate but the stilus is persistent. In *Triton* and *Diemictylus* stilus and ossification are both lacking and incorporation into the edge of the fenestra is complete.

Attending the fusion of the columella, there is the formation of the operculum to inherit its position and function as a fenestral structure. Concerning its origin and development there is not, as in the case of the columella, opportunity for uncertainty. In *Ambystoma*, in which it appears late,—at the end of transformation,—it is cut out of the floor of the otic capsule medial to the fenestra. In *Diemictylus* and *Triton*, in which it appears early, “cutting out” must play a more secondary part, and marginal growth by chondrification of opercular tissue seems more important. It occupies in either event the same position and seems to be a detached portion of the otic capsule, although extensive cartilage formation in it may give it a thickness several times that of the otic capsule. It undergoes no ossification, remaining cartilaginous throughout life.¹⁶ Its characteristic features, negative and positive, are the lack of connection with the skeleton outside the ear capsule, and the attachment of the *M. opercularis*.

The fusion of the columella causing a more or less extensive filling in of the cephalic portion of the fenestra vestibuli necessitates the recognition of primary, secondary and definitive fenestræ, of somewhat different boundary and location, as in the *Anura* (Gaupp, '93). The question of in how far the cephalo-caudal succession of fenestral elements or the (essentially) cephalo-caudal extension of the fenestra itself is an expression of the play of factors of relative growth of parts,—otic capsule, suspensorium, etc.,—is simply raised. It is hardly necessary to state that the primary character of the fenestra as an unchondrified portion of the otic capsule, as affirmed

¹⁶It is interesting to find Parker ('82a) commenting on this condition; on page 199 he says: “One more point of interest is to be noted here: the lowest *Perennibranchs* have their stapes thoroughly ossified (*i. e.*, the columella); the highest *Caducibranchs*, like the *Batrachia*, have it (*i. e.*, the operculum) soft; here in *Spelerpes* it ossifies early, and becomes a very perfect and elegant shutter to that small oval window.”

by Stöhr and more recently by Fuchs ('07) as contrasted with an appearance secondarily, by dehiscence or absorption, is abundantly established. It must be understood, however, that this applies only to the primary fenestra, while in the formation of the secondary and definitive fenestræ, in some forms, at least, the extension is accomplished essentially as a "dehiscence." The developmental transformations undergone by the primary fenestra require a more detailed study in a number of salamanders before a full interpretation can be made.

In the Plethodontidæ and Desmognathidæ, where the single fenestral plate possesses some of the characters of operculum and columella combined, the development has been followed in *Spelerpes bislineatus*. There is no evidence of a fusion of two structures, the cartilaginous and bony plate which bears the stilus by growth gains the territory which in *Ambystoma* is occupied by the operculum and may therefore be regarded as representing that structure without embodying it.¹⁷

On plate X are set forth in schematic form the morphological relations of the two structures under consideration as they occur in typical forms. Examining the conditions in the Urodela, we find that they may, with the figures of this plate as illustrations, be divided into seven groups, the characters being compared in tabular form on page 607.

Under these seven groups the forms studied distribute themselves as follows: Group I; *Necturus*, *Proteus* (*Typhlomolge*). Group II; Larval *Ambystoma* and urodele larvæ in general, *Cryptobranchus*, *Megalobatrachus*, *Amphiuma*. Group III; Adult *Ambystoma*, Adult *Chondrotus*, probably other members of the *Ambystomidæ*. Group IV; *Salamandra*, and possibly some of the *Ambystomidæ*. Group V; *Diemictylus*, *Triton*, undoubtedly *Salamandrina* and other *Pleurodelidæ*. Group VI; *Siren*. Group VII; the *Plethodontidæ* (as examined),—*Typhlotriton*, *Spelerpes*, *Gyrinophilus*, *Hemidactylum*,

¹⁷The differences between the *Ambystomidæ* and the *Plethodontidæ* in respect to the presence and absence of an operculum, are paralleled in the *Anura* by the similar differences in the Frog (as an example of the type) and *Pipa*. Gaupp's very interesting discussion of the interpretation in the last case ('98, p. 1065) presents the problem for the first case as well.

Plethodon, Stereochilus, Autodax, Manculus (Batracoseps). The Desmognathidæ (Desmognathus fusca.)

Two forms are exceptional; *Batracoseps*, which otherwise falls under group VII, possesses a vestigial stilus and therefore lacks the connection with the suspensorium, usually well developed in the Plethodontidæ. The interesting form *Typhlomolge* is plethodontid in the character of the fenestral plate, but possesses a fragmented stilus. The interesting course of the R. jug. VII over the stilus, and the absence of the M. opercularis, however, places it in Group I.

TABLE TO SHOW THE SEVEN TYPES OF "COLUMELLA AURIS" IN URODELES.

Group		Columella					Operculum	M. operc.
	Fig.	Fenestral plate	Fusion with fenestral margin	Stilus	Connection of stilus with	Relation of R. jug. VII to St.		
I.	68 69	present	none or slight	present	squamosum	above	absent	absent
II.	70 71	present	none or slight	present	squamosum or Sq. and Pal-Quad.	below	absent	absent
III.	64	present	extensive	present	squamosum and palato-quadrates	below	present	present
IV.	65	present, cartilage	complete	present	palato-quadrates	below	present	present
V.	66	present	complete	absent	absent		present	present
VI.	72	present	moderate	present?	ceratohyal		absent	absent
VII.	67	present	slight	present	squamosum, quadrate, or palato-quadrates or all	below	not separately developed	present

Briefly classified from the point of view of the existence of two fenestral structures, *Columella* and *Operculum*, these forms may be divided into the following groups: A, groups I and II; the columella present, free, connected with the suspensorium, no operculum or opercular muscle. B, groups III and IV; the columella present, fused with the otic capsule, connected with the suspensorium, operculum and opercular muscle present. C, group V; columella vestigial, fused with the ear capsule, no connection with the suspensor-

ium. Operculum and opercular muscle present. D, group VII; columella present, joined to otic capsule, connected with the suspensorium; the opercular muscle present, the operculum not developed as such. Up through the groups I to V, evidence of indubitable value is presented of the incorporation and loss of an element (columella) with an attendant loss of its primary connection, a substitute making its appearance (the operculum). The m. opercularis, absent in groups I, II and VI, present in the others, appears to deserve the name given it by Gaupp ('93), since in the Urodela it possesses characteristic attachments and is not a portion of another muscle (Levator anguli scapulæ). When an operculum is developed, an opercular muscle is present, while its insertion in group VII is suggestive, as is also equally, its absence in groups I and II. From the examination of larvæ, it should be stated, however, that it appears to be absent in all urodeles in the larval state. It will be referred to subsequently in connection with the problem of the function of the urodelan "sound-transmitting" apparatus.

Comparison with Anura. In the first contribution a comparison was made of the conditions found in *Ambystoma* to the "columella auris" of the frog, and further investigation has strengthened us in the acceptance of the homologies then advanced,—the columella with the plectrum (pars interna plectri), the operculum being homologized in the two groups. The resemblances and differences between the two forms may perhaps best be presented in tabular form, in parallel columns the resemblance being presented first, enumeration of differences following. The relations in the frog are taken from Gaupp ('93, '05).

The first of the differences (No. 7) is of no marked significance, since in other *Anura* (e. g., *Dactylethra*, Parker, Gaupp '98) the plectrum may overlap the operculum. The next two contrasts partake more of the nature of resemblances than of differences, hence items 10 and 11 are the only points of difference needing comment here, a detailed discussion not being intended, since they are doubtless the ones that will be regarded as the most weighty.

As to the tenth item, it is only necessary to recall the numerous instances of precocious and postponed development of homologous

FROG.

AMBYSTOMA.

1. Two independent elements
(a) Pars interna plectri
(b) Operculum.	Two independent elements
(a) Columella
(b) Operculum.
2. The plectrum develops in the cephalic, the operculum in the caudal portion of the secondary fenestra.	The columella develops in the cephalic, the operculum in the caudal portion of the secondary fenestra.
3. The operculum chondrifies in the opercular tissue and becomes joined to the cartilaginous margin of the fenestra on its dorso-caudal side; becomes completely separated.	The operculum is cut out of the ear capsule, remaining connected longest at its caudal end; becomes completely separated.
4. The plectrum chondrifies as an independent center out into the dense tissue connecting it to the palatoquadrate.	The columella chondrifies as an independent center in dense tissue connecting it with the squamosum (and palatoquadrate).
5. The plectrum becomes connected with the ventral (cephalo-ventral) edge of the fenestra.	The columella becomes fused with the cephalic (cephalo-ventral) edge of the fenestra.
6. The M. opercularis inserts upon the Operculum.	The M. opercularis inserts upon the Operculum.
7. The cephalic end of the operculum <i>overlaps</i> the fenestral plate (pseudoperculum) of the plectrum.	The cephalic end of the operculum <i>underlies</i> the columella.
8. The cephalic portion of the secondary fenestra closes, <i>excluding</i> the pseudoperculum.	The cephalic portion of the secondary fenestra closes, <i>including</i> (incorporating) the columella (fenestral plate).
9. A cephalic extension of the cavum perilymphaticum is beneath the pseudoperculum (Ductus fenestre).	A caudal extension of the cavum perilymphaticum is beneath the operculum (Recessus perilymphaticus).
10. The operculum develops first; the plectrum at transformation.	The columella develops first; the operculum at transformation.
11. The hyomandibular nerve passes <i>above</i> the plectrum.	The hyomandibular nerve (VIIth) is <i>below</i> the stilus columellæ.

structures in different forms (Heterochronia) to appreciate that the relative reversal of sequence in frog and salamander is not intrinsically important. Among the Urodela themselves we have an instance of partial reversal, the operculum appearing early in Triton (about 18 mm.) and late in Ambystoma (at transformation).

The opposite relation of the nervus facialis to the plectrum and stilus columellæ, is perhaps a more serious difference, since it is just this criterion of relative position of sound-transmitting apparatus and nerve that has been considered of decisive moment in the determination of homology. As has been stated above, Huxley introduced confusion into the interpretation in Amphibia by faulty recognition of indifferent connective tissue as the equivalent of the frog's plectrum, hence the course of the facial nerve came to be interpreted as *over* the suspensorial-columellar ligament or stilus, whereas in all forms examined just the opposite relation holds,—the facial nerve is *below* (cephalad or ventrad of) the columella, with three exceptions,—Necturus, Proteus, and Typhlomolge,—and in these cases the *jugular branch alone passes above while the rami mandibulares, internus and externus, are below* and in front of the columella.

If the different relation of the facial nerve to the columella in Urodela and Anura is prohibitive of the plectrum-columella homology, there is necessary the recognition of three morphologically distinct squamoso-columellar connections in tailed amphibia, (1) in the Proteida, (2) in Typhlomolge, (3) the remaining urodeles. This, it is felt, is contrary to the ontogenetic evidence. There is involved in this point the broader question of the value of the relation of nerve to skeletal structure as a criterion of homology. The real value of such a test of homology has already been questioned by one of us (Kingsbury, '03, p. 333) and a few instances given of variation in the relation of nerve, ligament and muscle,—instances which could, of course, be easily multiplied many fold; for example, in the relation of the hyomandibular bone or cartilage to the hyomandibular nerve, in fishes, etc. It was not deemed desirable to introduce here further consideration of such evidence, as it would involve work along broader comparative lines than was desirable at this time. Adherence is given to the view entertained in the first contribution,—

that the columella and its suspensorial connection is homologous throughout the urodele group, and no valid reason is known why the homology should not be extended to include the Anura as well. Inasmuch as a study of the relations and development in that group has not been made, the homology of columella and plectrum is not presented with the emphasis of personal investigation.

Ligaments. The only muscle that is in the region of the head involved in this study is the *Musculus cephalo-dorso-mandibularis* (*M. depressor mandibuli*). It has its origin largely, and in some of the forms entirely, from the squamosum, and inserts by means of a longer or shorter tendon upon the retro-articular process of the os articulare. Beneath the muscle, between it and the ear capsule, palatoquadrate, hyoid and mandible, is the space filled in with connective tissue containing the nerves and blood-vessels. The tissue next the muscle is denser and comes into intimate relation with the squamosum, palatoquadrate, stilus columellæ, ceratohyal, and mandible. (For illustration, see Figs. 43, 51, 55, 61.)

This submuscular fascia appears to be the foundation, out of which, by thickening of different portions three ligamentous structures may be formed:—(a) Ligamentum hyo-suspensoriale (palato-quadrata), (b) Ligamentum hyo-mandibulare, (c) Ligamentum hyo-columellare. These may all be present in the same species, weakly or strongly developed. Of these the last two have long been recognized (Huxley '74) and are in general well described; the hyo-columellar ligament, however, has not been as adequately considered and is of more interest here because of its connection with the columella. It is best developed in Siren (Fig. 61, 62, 63, Pl. IX), but its presence has been mentioned in the first part of this paper in *Amphiuma*, *Cryptobranchus*, *Gyrinophilus*, *Spelerpes*, *Desmognathus*; and seems to be more or less well developed in the *Plethodontidæ* generally. It will be referred to subsequently in connection with the discussion of the function of the urodelan apparatus. It was not recognized in *Ambystoma*, *Triton*, *Diemictylus* or *Salamandra*.

A ligamentum palatoquadrato-columellare corresponding to Huxley's suspensorio-stapedial ligament described by him in *Necturus* it noticeably absent in that form as well as in other urodeles.

Beneath the facial nerve, between columella or operculum and palatoquadrate, is only loose connective tissue, denser in some forms it is true,—especially Siren which possesses well developed hyo-columellar and hyo-suspensorial ligaments giving a less direct suspensorio-columellar bridge of dense connective tissue. It does not seem in any form to possess relations of functional or morphological importance as a “suspensorial” connection of the “sound-transmitting” apparatus.

While the presence or absence and relative development of these ligaments appears to be an expression of the mechanical needs, requirements of support in the nature of a physiological adaptation and therefore secondary phylogenetic importance, their existence may possibly have a deeper significance; the ligamentum hyo-columellare, for example, indicating a primary relationship of columella to the hyoid arch.

The junction of the ceratohyal with the palatoquadrate is quite constant. It is in relation to the hyo-quadrate ligament that the processus hyoideus palatoquadrati is developed in so many forms (see Wiedersheim '77, p. 533).

The diagram reproduced as Fig. 21 illustrates the relations of these three ligaments.

The Hyomandibular-Symplectic Homology. It may be safely stated that from the phylogenetic side the hyomandibular homology of the Amphibian sound-transmitting apparatus is at present generally accepted, as may be seen from the statements in the works of Wiedersheim and Gaupp which were cited (p. 552) as expressing the more recent interpretation. In the earlier form of the theory, however, only a portion was given a hyoid or hyomandibular homology; Reichert, Huxley, Parker, and others regarding the operculum as purely of otic origin.

This hyomandibular homology has been reiterated despite a dearth of evidence from the ontogenetic side. In the Anura, it is true, the embryological evidence has been furnished especially by the monograph of Gaupp, and it has seemed to support the partial homology of the older workers,—if supporting it at all. No direct connection has been found with the ceratohyal in development. In

the Urodela the condition is less satisfactory. Parker, Wiedersheim and Stöhr had emphatically declared the origin of the operculum from the ear capsule and the absence of any association in development with the hyoid arch.

More recently in a paper before the Anatomische Gesellschaft Fuchs ('07) rejected completely the hyomandibular homology¹⁸ of the amphibian structures, basing his conclusions upon the otic origin of the operculum in *Salamandra* (See p. 568). The presence of a stilus was regarded by him as secondary, the operculum without stilus representing the primitive condition. In the discussion, the homology with the hyomandibulare was upheld by several. Gaupp at that time ('07, pp. 31 and 32) stated his conception of the primitive "*Columella auris*" as consisting of an operculum and a stilus, the latter articulated with the palatoquadrate. Since the hyomandibulare in fishes is, in many forms, between the palatoquadrate and the otic capsule, the connection of the stilus with the palatoquadrate strongly suggests the homology. He admitted the lack of ontogenetic evidence, but pointed out the difficulty attending the delimitation of what might be hyal blastema from the periotic blastema. Since the upper end of the hyoid arch closely adjoined the otic capsule, blastema of the hyoid arch, it is easily conceivable, might be early incorporated with the periotic, and the operculum might develop apparently as part of the ear capsule and nevertheless be of hyoid origin. In his rejoinder Fuchs (pp. 33, 34) affirmed his belief that the operculum without stilus was the more primitive; that the fenestra arose as a result of the action of a "biological factor" within the ear itself upon the assumption of terrestrial life; that the "rubbing" of the hyomandibulare could in no wise have caused the appearance of the fenestra vestibuli, since in the numerous fish forms

¹⁸Fuchs ('07, p. 24): "Ich erachte das Operculum bezw. Operculum + Stilus der Urodelen für homolog dem Otostapes der Reptilien und beide für homolog dem Stapes der Säugetiere. Alle drei halte ich ontogenetisch für Abkömmlinge der Gehörkapsel. Auch in phylogenetischer Hinsicht leite ich auf dieselbe zurück und bin ferner der Ansicht, dass sie nicht mit der Hyomandibula der Fische zu vergleichen sind." "Für das Operculum, eventuell Operculum + Stilus, der Urodelen wird dem ja wohl niemand mehr widersprechen. . . ."

in which it does come in contact with the periotic cartilage, no trace of a thinning or fenestration results. Commenting on the position of the hyomandibulare between palatoquadrate and the otic capsule, he expressed the conviction that we must look for the ancestors of terrestrial vertebrates in the low elasmobranchs (Notidanidæ and Pro-Selachia) in which the hyomandibulare has no part in the suspension of the jaw, but affords the hyoid arch an independent articulation with the skull.

Since our results bear directly on the problem and from some points of view, at least, seem to strengthen the homology of the amphibian columella auris with the hyomandibulare, illuminating some of the obscure points of development and relation, it seems desirable to consider it briefly from the following view-points: (a) the extra-otic origin of the columella, (b) the relation to the palatoquadrate, (c) the connection with the squamosum, (d) the relation to the facial nerve, (e) the relation of the columella auris to the ceratohyal.

As Fürbringer pointed out in the discussion of the paper of Fuchs, *Salamandra* is highly specialized and not a form upon which to base conclusions of general applicability. This has been markedly illustrated in this very problem. For the present, the operculum (our use) may be regarded as a part of the otic capsule both in this and the other forms that possess this structure. Fuchs, however, dealt with but half the problem, as has been shown (p. 568). By other workers, in other forms evidence has been given of an extra-otic origin of a part, at least, of the fenestral structures:—In *Necturus* by Miss Platt and by Kingsbury (not published); in *Ambystoma* by Killian and by ourselves in this paper; in *Cryptobranchus*, *Spelerpes* and *Plethodon*, in this paper. In these salamanders, and doubtless in all forms possessing a well developed columella (our use), the first appearance of the sound-transmitting apparatus is as a group of cells outside the otic capsule. Of this the evidence seems quite strong; it is only necessary to refer once more to the figures illustrating the condition (Pl. IV, Fig. 39; Pl. VII, Figs. 52 and 53; Text Figs. 6 and 7). In the growth of this blastema in close association with the otic capsule, the chondrification as stilus and fenestral plate, there is introduced the difficulty mentioned by Gaupp,

namely, that of distinguishing cells of extra-otic origin from the periotic blastema. It has, in fact, been so far impossible in *Ambystoma* and *Spelerpes* to determine whether or not the fenestral plate of the columella embodied a periotic element. It may be said, however, that in its chondrification and growth the stilus is an integral part of the columella as a whole and not an element from outside secondarily fused with the plate,—representing, therefore, a structure which could by itself be homologized with the hyomandibulare, as was done by Parker.

The articulation of the stilus columellæ with the palatoquadrate, which had been mentioned, as quoted above, by Gaupp (cf. Wiedersheim '06, Gaupp '05) as the significant relation for the hyomandibular homology, has been shown to be a connection secondarily established during growth and development apparently due to a shifting of the connection from the squamosum to the palatoquadrate, in many forms a longer or shorter process of that cartilage developing with which it is articulated or fused. If this connection is in the nature of a secondary adaptation,—and this interpretation is the more probable,—its phylogenetic significance becomes doubtful. There is, however, an association of the two structures of a primary ontogenetic character and suggestive of profound significance. It is to be recalled that in those forms in which the early development of the columella has been traced, the cell mass constituting the proton of the columella is directly connected with the cells between squamosum, the otic process of the palatoquadrate and the otic capsule external to the lateral semicircular canal. If a connection with the palatoquadrate is to be considered of value in determining the hyomandibular homology, it would seem to us, therefore, to be expected that in the displacement of the hyomandibulare from the suspensorium, it would be that portion of the upper end of the palatoquadrate which comes to articulate with the otic capsule with which the homolog of the hyomandibulare would be joined rather than a point farther down. If, on the other hand, as maintained by Fuchs, the ancestry of the Amphibia is to be sought far back among the primitive elasmobranchs, it is in this region,—over the lateral semicircular canal caudad of the otic articulation of the palatoquadrate,—that the connection of its vestigium might be sought.

One of the characteristics of the urodele stilus is its early connection with the ventral edge of the squamosum, and from the first it has appealed to us as of profound morphological significance. Its final interpretation, however, is not yet possible, and must await the establishment of many facts of relation and development in the domain of comparative morphology. Although from the development of this bone over the lateral semicircular canal in urodeles (Kingsbury '03; Thyng '06) it is regarded by us as a squamosum, other considerations led Gaupp to bestow upon it the indifferent name of *Paraquadratum*. Granting that it is a squamosum, its development requires further study, and its value in urodeles,—as Dermo-, Auto- or Amphisquamosum has to be considered. As an Autosquamosum deriving its cells (primarily?) from the periotic blastema, it may be pointed out that it has precisely the position and relation to the proton of the columella that would be required of it if the hyomandibular homology of the latter is accepted, since in fishes it seems to afford a portion of the articular surface for that bone. Nor do two considerations that immediately occur appear necessarily antagonistic to this view; the first, that in the event of the acceptance of the elasmobranch origin of the Amphibia, no squamosum (as such) existed in the ancestral forms; the second, that the larval connection of the columella with the squamosum is but a step in the shifting of the suspensorium (palatoquadrate) during growth, which in its second phase again transfers the connection to the palatoquadratum or the os quadratum.

The absence of any connection between the columella and the ceratohyal has possibly been most commonly regarded as the greatest defect in the ontogenetic evidence for the hyomandibular homology. Recognition of the existence of a columellar proton outside the otic capsule, its relations to palatoquadrate, otic capsule, and facial nerve, in comparison with the requirement of a first segment of the hyoid arch, renders less important evidence of a connection of ceratohyal and columella. Yet the evidence of an embryological relation of the two structures seems stronger than is usually recognized. Miss Platt ('97), when describing the extra-otic origin of the columella (her operculum) considered that its lack of connection with the

ceratohyal did not "demonstrate that the cartilage in question may not be a rudimentary element of the hyoid arch, since each element of the cartilaginous arches arises from an independent center of chondrification and secondary fusions of cartilaginous elements do not necessarily show original association."

The cord of cells which extends to the under surface of the squamosum and which must be regarded as a part of the columella blastema, is joined by an extension from the perichondral cells of the ceratohyal, so that, at an early stage (19 mm.) the two structures are in fact connected (Kingsbury '03, p. 318, and Fig. 2a). In *Ambystoma* there is a line of cells from the ceratohyal to the columella in the 13-14 mm. specimen. In *Plethodon* (Text Fig. 6) the juxtaposition is still closer and a cellular continuity exists. In *Cryptobranchus* the ceratohyal is not joined to the columella by cells in the just hatched larva; just what the condition is at an earlier stage we cannot say from lack of material at a suitable stage.

This early connection by cells does not seem a chance association, but rather to indicate that columella and ceratohyal chondrify out of a common blastema. The Ligamentum hyo-columellare previously described as existing in several forms seems to be a secondary development, though it may express a primitive relationship. The diagram introduced to illustrate the ligaments (Fig. 21) may also serve to indicate the skeletal connections and relations of the columella as a probable hyomandibulare.

The position of the columella above and behind the nervus facialis satisfies the requirements of the hyomandibular homology. It is but necessary to recall its position in elasmobranchs and *Polypterus* (Ruge '96, Pollard '92) to recognize this fact. No detailed study has been made of the relation of this nerve in fishes, however; nor has the significance of the rather constant position of the columella between the vena petroso-lateralis and the arteria carotis interna been investigated.

The connections and development of the columella do, we believe, strengthen its homology with the Hyomandibulare of fishes, in support of which so much has been written.

FUNCTION OF THE "SOUND-TRANSMITTING" APPARATUS.

In order to determine the precise function of the so-called sound-transmitting apparatus in Urodeles a series of experiments upon both larvæ and adults is necessary. The skeletal connections of the fenestral elements in the larva, the changes taking place upon the assumption of the terrestrial life and the correlation of structure and habit in certain adults furnishes, however, some basis for judging the function of these structures.

FIG. 21. Schema to illustrate the relation of the ligaments found in this region. *Col.*, columella; *H.*, ceratohyal; *L.h-c.*, ligamentum hyo-columellare; *L.h-m.*, ligamentum hyo-mandibulare; *L.h-s.*, ligamentum hyo-suspensoriale; *L.s-c.*, ligamentum squamoso-columellare; *M.C.*, Meckel's cartilage; *P.asc.*, processus ascendens palatoquadrati; *P.bas.*, processus basalis palatoquadrati; *P.ot.*, processus oticus palatoquadrati; *Pq.*, palatoquadratum; *St.C.*, stylus columellæ; *Sq.*, os squamosum.

It is perhaps not assuming too much to believe that the sound-transmitting apparatus serves as an organ of equilibration and the detection of vibrations of low frequency when such come to the animal through a dense medium such as earth or water. The nature and structure of the apparatus in urodeles seem to preclude the belief that vibrations of any frequency whatsoever can be detected from a medium as rare as the air. There is, however, nothing in the nature of the apparatus to interfere with the view that vibrations

of high frequency are not detected if transmitted to the animal through a dense medium. Experimentation along this line may prove very interesting and valuable.

During the larval period, and in aquatic or partly aquatic forms during adult life, the connection of the fenestral plate is with the suspensorium. Thus it would appear that jars or vibrations are transmitted from the objects, upon which they are resting, to the floor of the mouth, after which the course is through the suspensorium to the columella and thence to the inner ear, as has been

FIG. 21a. Schema to illustrate the possible method of communication between the inner ear and the exterior for larvæ and thoroughly aquatic adult forms. *Col.*, Columella; *F.v.*, fenestra vestibuli; *H.a.*, hyoid arch; *L.s-c.*, ligamentum squamoso-columellare; *M.l.*, skeleton of the lower jaw; *Pq.*, palatoquadratum; *Sp.*, os squamosum; *St.C.*, stilus columellæ.

suggested by Gaupp ('05, '07). The possibility of such a functional mechanism is illustrated in Fig. 21a.

At transformation when terrestrial life is assumed, in certain forms, a different type of communication with the exterior is formed. The columella becomes fused with the ear capsule while a free plate, the operculum, is formed behind and below as in *Ambystoma* or the caudal portion of the fenestral plate remains free as in the *Plethodontidæ* and some others. This plate is placed in communication with the exterior by the *M. opercularis*, connecting it with the shoulder girdle. Thus jars and vibrations may be transmitted through the arm to the *M. opercularis*, thence to the operculum and finally to the inner ear, as shown in Fig. 21 b.

These connections appear to be an adaptation to the habits and environment of the animal. During larval life and in such forms as *Necturus* and *Cryptobranchus* the body is either supported by water, or rests full length upon the bottom or some submerged object, the arms and legs playing a small part, if any, in its support. The primitive connections of the columella here persist and function as the transmission line between the exterior and the inner ear. Some evidence for this view is found in certain Anurans. In *Pelobates* there is no tympanic cavity, and the eustachian tube is much reduced. The fenestral plate in this form is connected by strong ligament

FIG. 21b. Same as Fig. 21a, for terrestrial forms. *Col.*, columella; *H.a.*, hyoid arch; *L.s.c.*, ligamentum squamoso-columellare; *M.op.*, musculus opercularis; *M.l.*, skeleton of lower jaw; *Op.*, operculum; *P.q.*, palatoquadratum; *Sq.*, os squamosum; *S.s.*, suprascapula; *St.C.*, stilus columellae.

with the squamosum. Similar conditions obtain in *Bombinator*, excepting that the fenestral plate is connected with the hyoid. In either case the inner ear is placed in communication with the exterior through the floor of the mouth. It is interesting to note in this connection that *Pelobates* is a thoroughly burrowing form while *Bombinator* is just as thoroughly an aquatic one.

In the urodele *Siren*, where the usual skeletal connections of the fenestral plate are wanting, they seem to be compensated for by the attachment of the stilus columellae to the hyoid by means of the strong hyo-columellar ligament.

When terrestrial life is assumed the body is more or less supported

by the limbs, thereby raising the floor of the mouth above the ground. Thus communication of the internal ear with the exterior through the suspensorium and floor of the mouth is lost. By the detachment of a portion of the *M. intertransversarius capitis inferior* which becomes the *M. opecularis*, the operculum is connected with the shoulder girdle and communication of the inner ear with the exterior is again established,—through the arm and shoulder girdle.

SUMMARY.

While to a certain extent (hyomandibular homology) comparison has been made with fishes, comparisons between the amphibian auditory apparatus and those of reptiles and mammals have not been attempted. The terms “stapes” and “stapedial” have been purposely avoided since it has seemed to us by no means conclusively shown that the amphibian columella is simply the homolog of the first segment of the mammalian chain of bones. Although we have fully appreciated that this investigation is but a part of the larger problem as was indicated at the beginning of the paper, the main aim has been the determination of *facts* for a large number of tailed amphibians, realizing that weaknesses in broad generalizations are in most instances due to drawing conclusions from insufficient data; for illustration of which it is unnecessary to go outside the limited field of investigation covered by this paper. The amphibian group presents within itself many problems of both local importance and general bearing that require further investigation, and it was this narrower field that particularly engaged our attention. Some of the general aspects of the problem we hope to deal with subsequently.

The main results were given in the first portion of the paper; they are restated below in somewhat extended form.

1. Several (4 to 7) different types of “columella auris” are found in urodeles.

2. There are two morphologically distinct fenestral structures found in the group: Columella and Operculum.

3. The Columella possesses a stilus, tends to fuse with the cephalic portion of the fenestral margin, and in ontogeny seems to come from outside the otic capsule.

4. The Operculum develops out of the otic capsule of which it appears to be primarily a part. It possesses no stilus but gives attachment to a muscle (*M. opercularis*). Its morphological position relative to the Columella is caudal and medial.

5. A Columella only is present in *Necturus*, *Proteus*, *Cryptobranchus*, *Amphiuma*, *Siren*.

6. In *Ambystoma* and *Chondrotus* (*Ambystomidæ*) a Columella is present in the larva but it becomes fused with the otic capsule at transformation, and an Operculum is then developed.

7. A vestigial and fused Columella is found in *Salamandra*, *Triton* and *Diemictylus* (*Salamandridæ*, *Pleurodelidæ*, *Cope*).

8. An Operculum is found (in the adult) in the *Ambystomidæ*, *Salamandridæ*, *Pleurodelidæ*.

9. The *Plethodontidæ* and *Desmognathidæ* possess a single fenestral structure bearing a stilus but also giving attachment of the opercular muscle.

10. *Typhlomolge* possesses a fenestral plate of *plethodontid* character. It has a fragmented stilus and lacks the *M. opercularis*.

11. The *Musculus opercularis* is absent in (a) *Necturus*, *Proteus*, *Cryptobranchus*, *Amphiuma*, *Siren*, *Typhlomolge*; (b) in larvæ generally. It is present in the adult *Ambystomidæ*, *Salamandridæ*, *Pleurodelidæ*, *Plethodontidæ*, and *Desmognathidæ*.

12. The *Stilus columellæ* is distally joined to the *Squamosum*, *Palatoquadratum*, *Quadratum*, singly or in combination. In *Necturus*, *Proteus*, *Cryptobranchus*, *Typhlomolge* and larvæ generally (*Ambystomidæ*, *Plethodontidæ*, *Desmognathidæ*) it is directly connected with the *squamosum*.

13. During growth or at transformation the connection tends to shift, usually to the *Palatoquadratum*.

14. The stilus is fragmented in *Typhlomolge*, vestigial in *Batrachoseps* and *Siren*, absent in *Triton* and *Diemictylus*. In *Salamandra* its distal end is fused with the *Palatoquadratum*.

15. In development the position of the Columella appears to be outside the otic capsule in those forms in which its development has been traced (*Necturus*, *Ambystoma*, *Spelerpes*, *Plethodon*, *Cryptobranchus*).

16. The proton of the Columella is connected by a distinct strand of cells with a group of cells between Squamosum, Processus oticus palatoquadrati and the Prominentia semicircularis lateralis of the otic capsule.

17. The facial nerve is entirely below the Columella (stilus columellæ) in all forms except *Necturus*, *Proteus*, *Typhlomolge*; in these, one ramus (*R. jugularis*) passes above the stilus.

18. The relation of the stilus to the blood vessels of the otic region appears quite characteristic; i. e., below the vein and above the artery.

19. A Ligamentum hyo-columellare is present in *Siren*, *Amphiuma*, *Cryptobranchus*, *Desmognathus* and many *Plethodontidæ*.

20. The hyomandibular homology is favorably discussed.

21. The homology of the Columella of *Urodela* and the Pars interna plectri of *Anura* is accepted.

22. The Operculum is regarded as a secondary development in those forms which possess it.

23. From the standpoint of functional adaptation, there seem to be in the *Urodela* three types of communication of the internal ear with the exterior: (a) through the floor of the mouth, mandible, suspensorium and columella; (b) through the floor of the mouth, the hyoid arch and columella; (c) through the manus, pectoral girdle, *M. opercularis* and operculum.

24. Type (a) is the more usual and is found in typically aquatic forms. Type (b) is best represented in *Siren*. Type (c) occurs in *Salamandra*, *Triton* and *Diemictylus*. A combination of (a), (b), and (c) is found in the *Plethodontidæ* and *Desmognathidæ*.

25. There appears a close correlation of the type present and the habits of the form (aquatic, semi-aquatic, terrestrial, burrowing, etc.).

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ABBREVIATIONS.

A. GENERAL SKELETON.

Col., columella.
 H., ceratohyale.
 H.a., Hyoid arch.
 M.C., Meckel's cartilage.
 M.l., Skeleton of lower jaw.
 Op., Operculum.
 Parasphen., os parasphenoideum.
 P.asc., Processus ascendens palatoquadrati.
 P.bas., processus basalis palatoquadrati.
 P.ot., processus oticus palatoquadrati.
 P.h-p., processus hyoideus palatoquadrati.
 P-q., palatoquadratum.
 Pt., os pterygoideum.
 Q., os quadratum.
 S.s., Suprascapula.
 St.C., stilus columellae.
 Sq., os squamosum.

B. EAR CAPSULE.

C.l., Canalis semicircularis lateralis.
 C.p., cavum perilymphaticum.
 Cr.s., crista semicircularis.
 D.p., ductus perilymphaticus.
 "F", secondary fenestra vestibuli.
 F.p., fenestral plate.
 F.v., fenestra vestibuli.
 L., lagena.
 Prom. l., prominentia semicircularis lateralis.
 Prom.p., prominentia perilymphatica.
 R.p., recessus perilymphaticus.

C. LIGAMENTS.

L.h-c., ligamentum hyo-columellare.
 L.h-m., ligamentum hyo-mandibulare.
 L.h-s., ligamentum hyo-suspensoriale.
 L.s-c., ligamentum squamoso-columellare.

D. NERVES.

VII, nervus facialis (VII).
 R.h.VII, ramus hyomandibularis VII.
 R.c., ramus communicans (IX-VII).
 R.j.VII, ramus jugularis VII.
 R.m.e.VII, ramus mandibularis externus VII.
 R.m.i.VII, ramus mandibularis internus VII.

E. MUSCLES.

M., musculus cephalo-dorso-mandibularis.

M.op., musculus opercularis.

M.i.c.i., musculus intertransversarius capitis inferior.

F. BLOOD VESSELS.

C., arteria carotis interna.

V.p-l., vena petroso-lateralis.

PLATE I.

Models of the ear region of the skull of *Ambystoma punctatum*, drawn from the side and slightly from the caudal and ventral aspects.

Fig. 22. *Ambystoma punctatum*, mature larva about 45 mm. in length, beginning transformation, gills about one-half absorbed.

Fig. 23. *Ambystoma punctatum*, about 42 mm. in length, transformation period, gills mere stumps. In comparison with Fig. 22, there is shown the partially formed operculum with the opercular muscle.

Fig. 24. *Ambystoma punctatum*, young adult, about 52 mm. in length. The columella is now nearly completely fused. Remnants of the secondary fenestra are marked "F." Operculum and opercular muscle.

FIG. 22.

FIG. 23.

FIG. 24.

PLATE II.

Drawings of models of the ear region of the skull.

Fig. 25. *Ambystoma punctatum*, adult. A portion of the ear region of the skull showing the completely fused columella and the fully formed operculum with its attached muscle.

Fig. 26. *Salamandra maculosa*, adult. The region and aspect as in Fig. 25 with which it may be directly compared. The boundary between muscle and operculum is indicated by the broken line.

Fig. 27. *Triton cristatus*, larva 34 mm. long. The ventro-lateral aspect of the cartilaginous ear capsule. The cephalic part of the fenestra is occupied by the small and partially fused columella above, a growth of cartilage below. The operculum is still broadly joined to the ear capsule.

Fig. 28. *Typhlomolge rathbuni*, adult. Lateral aspect of the ear region. Attention is particularly called to the segmented (fragmented) stilus columellæ and its relation to the facial nerve (ramus jugularis).

FIG. 25.

FIG. 26.

FIG. 27.

FIG. 28.

EXPLANATION OF PLATES III-IX.

A series of microphotographs to illustrate particularly the morphological relations of columella and operculum, from sections through the ear region.

PLATE III.

Fig. 29. *Ambystoma punctatum*, adult. Section through the stilus columellae, showing the columellar ligament and its relation to vein and facial nerve.

Fig. 30. The same. Section farther caudad. The fused columella is external to the cephalic end of the operculum.

Fig. 31. *Ambystoma punctatum*, larva, early transformation. There is shown columella and the floor of the ear capsule to become operculum. Compare with Fig. 32.

Fig. 32. *Ambystoma punctatum*, transformation period. The operculum is, at this level, separated from the floor of the ear capsule.

Fig. 33. *Ambystoma punctatum*, larva, 35 mm. in length. It shows the columella, stilus, squamoso-columellar ligament. Note the relation of the vein and artery in this and the two preceding figures.

Fig. 34. *Chondrotus tenebrosus*, larva. Note the massive stilus articulating with the squamosum and its relation to artery, vein and nerve.

FIG. 29.—Adult Ambystoma.

FIG. 30.—Adult Ambystoma.

FIG. 31.—Larval Ambystoma.

FIG. 32.—Larval Ambystoma.

FIG. 33.—Larval Ambystoma.

FIG. 34.—Larval Chondrotus.

FIG. 29.—Adult Ambystoma.

FIG. 30.—Adult Ambystoma.

FIG. 31.—Larval Ambystoma.

FIG. 32.—Larval Ambystoma.

FIG. 33.—Larval Ambystoma.

FIG. 34.—Larval Chondrotus.

PLATE IV.

Fig. 35. *Ambystoma punctatum*, adult. Section farther caudad than Fig. 30. Operculum, opercular muscle and recessus perilymphaticus are shown.

Fig. 36. *Chondrotus tenebrosus*, transformation period. Section through stilus columellæ and the cephalic end of the developing operculum.

Fig. 37. *Ambystoma punctatum*, transforming. Horizontal section showing columella, stilus, squamoso-columellar ligament, the developing operculum and the M. opercularis attached in front to the opercular plate and behind to the suprascapula.

Fig. 38. *Chondrotus tenebrosus*, transformation period. Section farther caudad than Fig. 36. It shows the columella. The operculum is partially cut out from the floor of the ear capsule.

Fig. 39. *Ambystoma punctatum*, embryo 13-14 mm. in length. The columella consists of a mass of cells against the membrane of the fenestra and connected by a strand of dense tissue with the cells upon the prominence of the lateral semicircular canal. Above the columellar proton is the vena petroso-lateralis; below, the carotid artery.

FIG. 35.—Adult Ambystoma.

FIG. 36.—Transforming Chondrotus.

FIG. 37.
Transforming Ambystoma.

FIG. 38.—Transforming Chondrotus.

FIG. 39.
Embryo Ambystoma.

FIG. 35.—Adult Ambystoma.

FIG. 36.—Transforming Chondrotus.

FIG. 37.
Transforming Ambystoma.

FIG. 38.—Transforming Chondrotus.

FIG. 39.
Embryo Ambystoma.

PLATE V.

Fig. 40. *Salamandra maculosa*, adult. Section through the stilus columellæ which is continuous with the palatoquadrate.

Fig. 41. The same. Section farther caudad, through the cephalic end of the operculum.

Fig. 42. The same. Section farther caudad through the operculum and the recessus. The *M. opercularis* would be shown in a section farther caudad.

Fig. 43. *Triton cristatus*, adult. Section through the cephalic portion of the operculum.

FIG. 40.—Adult Salamandra.

FIG. 41.—Adult Salamandra.

FIG. 42.—Adult Salamandra.

FIG. 43.—Adult Triton.

FIG. 40.—Adult Salamandra.

FIG. 41.—Adult Salamandra.

FIG. 42.—Adult Salamandra.

FIG. 43.—Adult Triton.

PLATE VI.

Fig. 44. The same. Section farther caudad, showing the operculum, M. opercularis and recessus perilymphaticus.

Fig. 45. *Gyrinophilus porphyriticus*, adult. Section through the cephalic end of the fenestra vestibuli and the distal end of the stilus columellæ showing its articulation. Note the relation of blood vessels and facial nerve.

Fig. 46. The same. Section through the base of the stilus, a few sections farther caudad.

Fig. 47. The same. Several sections farther caudad, through the caudal portion of the fenestral plate, opercular muscle and recessus.

FIG. 44.—Adult Triton.

FIG. 45.—Adult Gyrinophilus.

FIG. 46.—Adult Gyrinophilus.

FIG. 47.—Adult Gyrinophilus.

FIG. 44.—Adult Triton.

FIG. 45.—Adult Gyrinophilus.

FIG. 46.—Adult Gyrinophilus.

FIG. 47.—Adult Gyrinophilus.

PLATE VII.

Fig. 48. *Triton cristatus*, larva 36 mm. long. The section is through the cephalic end of the columella where it is continuous with the ear capsule on its medial side.

Fig. 49. The same, farther caudad, through the columella and just in front of the cephalic end of the operculum.

Fig. 50. The same. A section still farther caudad, through the operculum and back of the caudal end of the columella. Note the relations of the blood vessels in this and the two preceding figures.

Fig. 51. *Cryptobranchus allegheniensis*, larva 34 mm. long. The ligamentum hyo-columellare is just joining the stilus at its bend.

Fig. 52. *Cryptobranchus allegheniensis*. Just hatched larva. The proton of the columella is seen between the artery and vein.

Fig. 53. The same. A section farther cephalad to show the proton of the squamosal connection of the columella.

Fig. 54. *Cryptobranchus allegheniensis*, adult. A section through the distal end of the stilus to show its articulation.

Fig. 55. The same. A section farther caudad showing the columella and its large stilus illustrating the relation to artery, vein and nerve.

FIG. 48.—Larval Triton.

FIG. 49.—Larval Triton.

FIG. 50.—Larval Triton

FIG. 51.
Larval Cryptobranchus.

FIG. 52.—Just hatched Cryptobranchus.

FIG. 53.
Just hatched Cryptobranchus.

FIG. 54.—Adult Cryptobranchus.

FIG. 55.—Adult Cryptobranchus.

PLATE VIII.

Fig. 56. The same. A few sections farther caudad through the caudal portion of the fenestral plate.

FIG. 57. *Necturus maculosus*, larva. The ligamentum squamoso-columellare is just attaching to the ventral edge of the squamosum.

Fig. 58. The same, a few sections farther caudad. The ramus jugularis VII is shown passing over the ligament.

Fig. 59. The same, still farther caudad through the base of the stilus columellæ. Note the relations of artery, vein and nerve in this and the two preceding figures.

FIG. 56.—Adult Cryptobranchus.

FIG. 57.—Larval Necturus.

FIG. 58.—Larval Necturus.

FIG. 59.—Larval Necturus.

FIG. 56.—Adult *Cryptobranchus*.

FIG. 57.—Larval *Necturus*.

FIG. 58.—Larval *Necturus*.

FIG. 59.—Larval *Necturus*.

PLATE IX.

Fig. 60. The same, still farther caudad, showing the caudal portion of the fenestral plate of the columella with its inner and outer bony plates.

Fig. 61. *Siren lacertina*, adult. Section showing the columella, ceratohyal the hyo-columellar ligament, into which projects the short stilus, and the cartilaginous portion of the ear capsule that forms the perilymphatic prominence.

Fig. 62. The same, a few sections farther caudad. The caudal end of the stilus is in the ligament. The perilymphatic prominence; position of artery and vein.

Fig. 63. The same, farther caudad behind the fenestra and showing the caudal portion of the perilymphatic prominence.

FIG. 60.—Larval Necturus.

FIG. 61.—Adult Siren.

FIG. 62.—Adult Siren.

FIG. 63.—Adult Siren.

FIG. 60.—Larval Necturus.

FIG. 61.—Adult Siren.

FIG. 62.—Adult Siren.

FIG. 63.—Adult Siren.

PLATE X.

(Figures 64-72)

A series of schemas showing the number and relative position of the elements present in the fenestra vestibuli in the various groups of the tailed Amphibia, together with the relation of these elements to the ear capsule, suspensorium, hyoid arch, M. opercularis, and facial nerve. It should be stated that they are to show relations only; the representation of the processes of the palatoquadrate, for example, being purely diagrammatic. In Fig. 67 the relation of the hyoid arch (H.) is intended to represent the condition in certain forms only.

FIG. 64.—*Ambystoma*.

FIG. 65.—*Salamandra*.

FIG. 66.—*Triton* and *Diemictylus*.

FIG. 67.—*Plethodontidae* and *Desmognathidae*.

FIG. 68.—*Typhlomolge*.

FIG. 69.—*Necturus*.

FIG. 70.—*Cryptobranchus*.

FIG. 71.—*Amphiuma*.

FIG. 72.—*Siren*.

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