

COLUMELLA AURIS AND NERVUS FACIALIS IN THE URODELA.¹

By B. F. KINGSBURY.

The following communication sets forth the results of a study made upon the relations and development of the parts in the otic region of the head in *Necturus maculatus*, and in comparison with that form, *Desmognathus fusca* and *Spelerpes bilineatus*.

The need for a careful study of (1) the relations of the facial nerve to the columella auris in the various Urodela, and (2) the homology of the suspensorio-opercular connections in the different forms of Amphibia has been emphasized by GAUPP.² From a comparison of the statements of WIEDERSHEIM,³ HUXLEY,⁴ PARKER,⁵ and HASSE⁶ he was lead to conclude

¹ This may be considered as a partial preliminary communication upon the development of the skull of *Necturus maculatus*, undertaken at the suggestion of Professors WIEDERSHEIM and GAUPP, in the Anatomisches Institut at Freiburg. I wish to acknowledge my indebtedness to them and to Professor KEIBEL and others, for suggestions and material. Since the completion of this manuscript in May 1902, more than a year has elapsed, and in sending it to the press now, I take the opportunity of noticing papers that have appeared in the meantime—those of KINGSLEY and COGHILL.

² '98, GAUPP, E. Ontogenese und Phylogenese des Schalleitenden Apparates bei den Wirbeltieren. *Merkel u. Bonnet, Ergebnisse d. Anat. u. Entw.*, 1898, Bd. VIII, pp. 989-1149.

³ '77, WIEDERSHEIM, R. Das Kopfskelet der Urodelen. *Morph. Jahrb.*, Bd. III, pp. 352-548.

⁴ '74, HUXLEY, TH. H. On the Structure of the Skull and the Heart of *Menobranchius lateralis*. *Proc. Zool. Soc.*, 1874.

⁵ '77, PARKER, W. K. On the Structure and Development of the Skull in the Urodelaous Amphibia. Pt. I. *Philos. Trans. Roy. Soc.*, Vol. 167, Pt. 2.

'82a, On the Morphology of the Skull in the Amphibia Urodela. *Trans. Linn. Soc.*, Ser. 2, Vol. II.

'82b, On the Structure and Development of the Skull in the Urodeles. *Trans. Zool. Soc.*, London, Vol. XI, pp. 171-214.

⁶ '73, HASSE, C. Ueber den Bau des Gehörorgans von *Siredon pisciformis* und über die vergleichende Anatomie des Kiefersuspensorium. *Anat. Stud.*, Bd. I, No. XV.

that there were apparently two methods of connection of the operculum with the suspensorium (quadratum). Thus, WIEDERSHEIM gives as the universal condition, that the nervus facialis passes *above* the suspensorio-opercular connection; HUXLEY described a suspensorio-stapedial (opercular) ligament *under* the facial nerve; HASSE, in Siredon (*Amblystoma*) described the nerve as under the columella; while the statements of PARKER are not always clear, though it is evident that in the different *Urodela* both relations of columella or suspensorio-opercular ligament and nerve were described.

The study of the relations in the three forms above mentioned, to which *Proteus anguineus*, *Amphiuma* means, and *Amblystoma tigrinum* (larva) may be added, has shown that in all except *Necturus*, the nervus facialis passes below (ventrad to or cephalad of) the suspensorio-opercular connection. In *Necturus*, the ramus jugularis facialis passes above (dorsad to) the ligament, the remainder of the nerve, i. e. ramus mandibularis externus and internus, and ramus palatinus being below (ventrad or cephalad to) this structure. Furthermore, in these three forms, the columella or ligament passes from the operculum to the bone which lies partly upon the ear capsule and partly upon the external surface of the quadratum—and which, as far as I can judge from the evidence at hand, I regard as a squamosum;—and not (primarily) to the cartilage of the quadratum as heretofore stated. This is a fact of considerable morphological importance. A more detailed description of the relations in the forms follows:

Necturus Maculatus. In this form HUXLEY¹ described the “suspensorio-stapedial ligament” as arising from the “middle of the posterior edge of the quadratum—and passing upwards and backwards to the stapes. The Hyomandibular branch of the seventh nerve passes above this ligament to its distribution just as it passes above the columella auris in the Frog.” WIEDERSHEIM made no different statement of relations. This structure described by HUXLEY, which was presumably a sheet of

¹ Op. cit. p. 192.

fascia, is not the true suspensorio-opercular connection, which is correctly described by COPE,¹ as passing from the operculum to

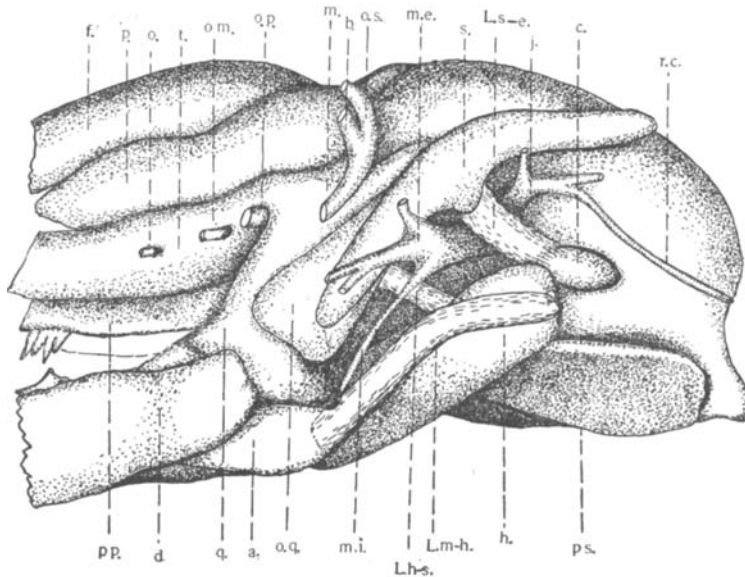


Fig. 1. Diagram from a drawing of the left side of a model of the skull of a *Necturus* 49.5 mm. long.

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| a.—Os articulare (angulare?). | b.—Nervus buccalis. |
| c.—Columella (operculum). | d.—Os dentare. |
| f.—Os frontale. | h.—Ceratohyale. |
| j.—Ramus jugularis VII. | |
| L. h.-s.—Ligamentum hyo-suspensoriale. | |
| L. m.-h.—Ligamentum mandibulo-hyoidale. | |
| L. s.-e.—Ligamentum squamoso-columellare. | |
| m. e. VII.—Ramus mandibularis externus facialis. | |
| m. V.—Nervus maxillo-mandibularis trigemini. | |
| m. i.—Ramus mandibularis internus facialis. | |
| o.—Nervus opticus. | o. m.—Nervus oculomotorius. |
| o. p.—Ramus ophthalmicus profundus trigemini. | |
| o. q.—Os quadratum. | |
| o. s.—R. ophthalmicus superficialis facialis. | p.—Os parietale. |
| p.p.—Os palatopterygoideum. | p.s.—Os parasphenoidale. |
| q.—Quadratum. | r. c.—Ramus communicans glossopharyngei. |
| s.—Os squamosum. | t.—Trabeculum. |

the squamosum, who does not however, give the relation of the nervus facialis. DRÜNER has recently described correctly the relations in both *Necturus* and *Proteus*.

¹ COPE, E. D. The Batrachia of North America. *Bull. U. S. Nat'l. Museum*, No. 34, 18.

The following description of the relations in a *Necturus* of 49.5 mm. length, based in part on a model of this stage (Fig. 1), will serve as a basis of comparison. The operculum at this stage is roughly oval in outline and slightly ridged along its long axis. At its cephalic end it is fused with the otic capsule, projecting backward into the fenestra vestibuli. From the cephalic end a dense ligament passes cephalad and dorsad to the os squamosum at about its middle point. The bone forms a slight curve, the convexity looking upwards, and it lies upon the external semicircular canal of the otic capsule, extending down over the otic process of the quadrate and becoming closely connected with a bone lying upon the external surface of the quadratum, and which it partly covers. This bone¹ I shall describe in another place. The squamoso-opercular ligament is attached to the under side of the squamosum where the bone passes from the ear capsule to cover the outer side of the processus oticus quadrati. At this stage the "stapedial" process of the squamosum present in the adult has just begun to develop. The ligament, in its course from the operculum to the squamosum, passes external (laterad) to the ramus jugularis facialis and the vena jugularis. The ramus jugularis passes outward and slightly backward, between the ligament and the vein to the dorsal edge of the former where it receives the ramus communicans glossopharyngei, which lies close to the ear capsule laterad to the vena jugularis. Beyond the point of the union with the ramus communicans, the jugular branch of the seventh passes outward, under the ventral edge of the squamosum to curve around the dorsal side of the otic division of the *M. depressor mandibuli*. The ramus mandibularis externus facialis from its ganglion which lies immediately outside the foramen for the facial nerve, in a depression just caudad of the

¹ This bone arises in *Necturus* as a separate ossification, whose lower end subsequently is fused with or becomes the ossification of the quadrate. In *Desmognathus* and *Spelerpes* the same bone lies farther back, projecting under the squamosum, and in the adult forms the process of the quadrate named for the purposes of this paper the subsquamosal process.

processus basilaris quadrati, passes forward and outward under the quadratum to the outer surface of the squamosum, passing in front of (ventrad and cephalad to) the ligament.

The ramus palatinus which passes forward through a foramen distinct from that for the rest of the facial nerve, and the ramus mandibularis internus which passes immediately ventrad from the cephalic edge of the accessory lateral line ganglion, do not come into close relation to the columella, but are, of course, morphologically below and in front of it.

In an older *Necturus*, 9.4 c.m. long, the relations are as in the specimen just described, save that the processus "stapedialis" of the squamosum has attained an appreciable length, and the operculum possesses a short ossified stalk to which the liga-

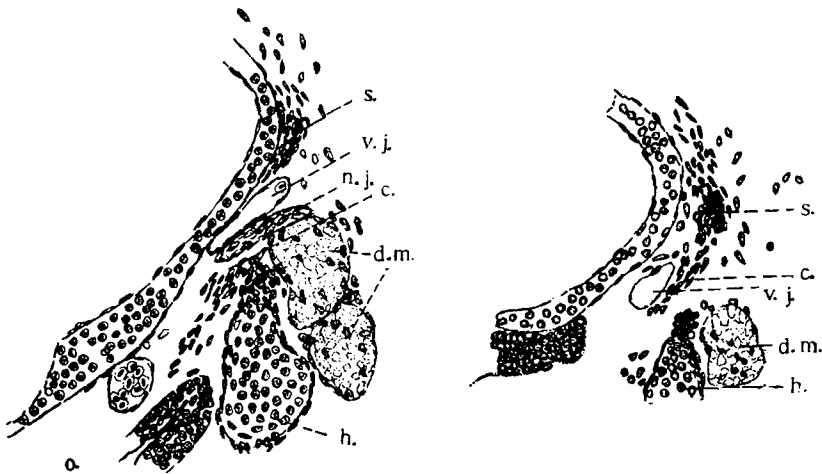


Fig. 2a. Section of the *Necturus* embryo 19 mm. in length. *c.*—anlage of the squamoso-columellar ligament; *h.*—hyoid; *v. j.*—vena jugularis; *n. j.*—nervus jugularis; *d. m.*—*M. depressor mandibuli*; *s.*—squamosum.

Fig. 2b. Same, three sections farther forward.

ment attaches. Neither ossification appears to be an ossification of the ligament, but ossifications of the squamosum and operculum at each end of the ligament, accomplishing in that way the increase in length due to growth. In the adult, the operculum possesses an ossified process of some length joined

by ligament to the relatively long stapedial process of the squamosum.

That the relation of ligament to squamosum is a primary condition in this form and not a secondary modification, is seen in tracing the development of these structures. In an embryo 19 mm. in length (Fig. 2), the ossification of the squamosum is just beginning as a formation in a group of cells located upon the external semicircular canal of the ear. It extends down over the otic process of the quadratum covering with its lower (cephalic) end the upper end of a bone which is developed upon the external surface of the quadrate. At this stage, the operculum is just beginning to chondrify as a distinct center, and from it a cord of cells is continued forward, ventral to the vena jugularis and the ramus jugularis, to the cell surrounding the developing squamosum, becoming continuous with them a short distance (50μ) 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 under side 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. It is interesting to note the relatively early development of the ligament—practically at the same time as the squamosum and the operculum—later, however, than the chondrification of the chondrocranium.

Spelerpes bilineatus. In this form, as well as in *Desmognathus*, the suspensorio-opercular connection possesses the same relation to the nervus facialis—that is, the nerve lies entirely cephalad and ventrad to the stilus columellae; in other words, under it. In relation to the jugular vein, the stilus possesses the same relation as the ligament described in *Necturus*—i. e. it passes ventrad to it.

In the adult *Spelerpes* (Figure 3), the stilus is cartilaginous with a perichondral ossification continuous with the ossification of the operculum;—the cartilaginous core of the stilus, however, is distinct from the ring of cartilage within the operculum.

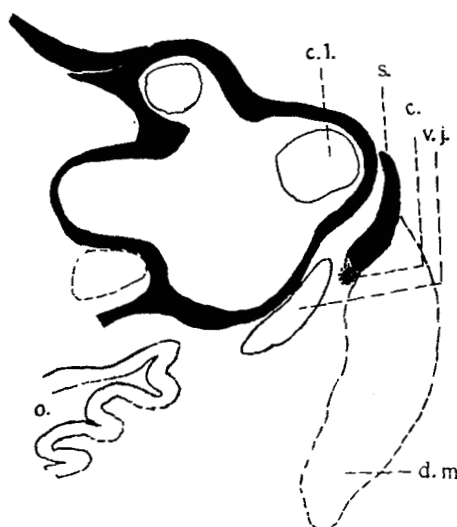


Fig. 3. *Spelerpes bilineatus*, adult 67 mm. long. Section through the right otic capsule. *c.*—Stylus columellae; *o.*—oral cavity; *v. j.*—vena jugularis; *d. m.*—*M. depressor mandibuli*; *S.*—squamosum.

The stilus passes forward, upward and slightly outward to the lower edge of the squamosum with which its cephalic end is joined by connective tissue (Fig. 3), and also with a small cartilage which lies upon the ventral edge of the squamosum. This cartilage extends forward for about 150 microns and is cylindrical. It is free at its caudal end, which articulates with the stilus, and fused with the ventral edge of the squamosum. The stilus and operculum are at about the same level. The former lies at first upon the dorsal side of the external semi-circular canal, gradually moving down to the lateral surface of the otic capsule, as it is traced forward. As it continues to

shift its position ventrally to pass to the outer surface of the quadratum, it becomes farther separated from the ear capsule leaving a space in which the quadratum appears. The ventral (lateral) edge of the squamosum is thin where the bone rests upon the ear capsule, but becomes thicker as the bone leaves that structure, i. e. where the stilus articulates with it, becoming thinner again as the bone applies itself to the quadratum.

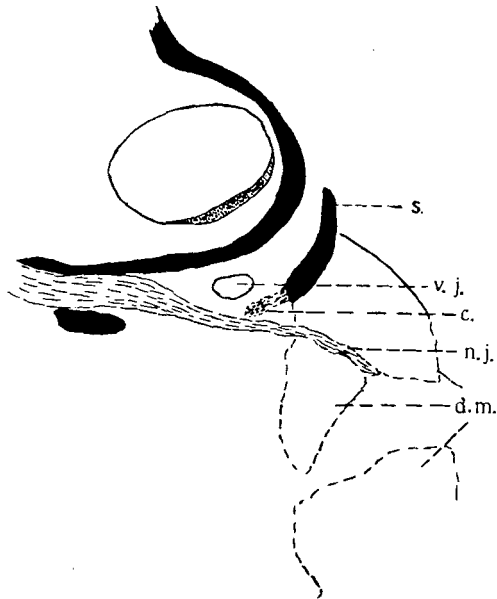


Fig. 4. Larval *Spelerpes bilineatus*, 43 mm. long; *c.*—stilus columellae; *v. j.*—vena jugularis; *n. j.*—nervus jugularis; *d. m.*—*M. depressor mandibuli*; *s.*—Squamosum.

In the interval between the squamosum and the ear capsule, two processes of the quadratum extend backward, (1) a bony process applied immediately to the inner surface of the squamosum, extending back to the level of the cephalic end of the cartilage upon the ventral edge of the squamosum, and (2) a short cartilaginous process lying between the bony process and the ear capsule. The latter seems to be a part of the (morphologically) basilar process of the quadratum and is very short.

Neither one comes into relation to the columella as do the corresponding processes in *Desmognathus*.

Larval *Spelerpes* of 25 mm., 35 mm., 43 mm. (Fig. 4) and 60 mm. in length, were examined in this connection and showed that the relation between columella and squamosum in this form (Fig. 4) is a primary one, as in *Necturus*. In the 25 mm. larva, the suspensorio-opercular connection is represented by a cord of cells which passes from the operculum forward and upward to the ventral edge of the squamosum. This cell cord lies ventrad to the vena jugularis around which it curves, closely applied to the vein, compressed between it and the R. jugularis facialis, the relation of nerve and suspensorio-opercular connection being thus the opposite of that in *Necturus*. Compare Figs. 2 and 4. In a 35 mm. larva cartilage has appeared in the cord of cells, otherwise the relations are essentially the same as in the younger larva, while in the 43 mm. specimen ossification of the stilus has begun, continuous with the perichondral ossification of the operculum.

The facial nerve, as has been said, lies entirely cephalad and ventrad to the suspensorio-opercular connection. The only branch which comes into contact with the stilus is the ramus jugularis which in the larva passes close to the ventral border of that structure. The ramus communicans glosso-pharyngei likewise, passes below the stilus, curving around it from its dorsal side in a course forward to join the facial. In the adult neither nerve is in as close relation to the stilus as in the larva.

The origin and significance of the small cartilage applied to the ventral border of the squamosum is obscure because of the absence of transforming and young adult material. In the larva it is not present.

With the exception of the R. jugularis and R. communicans, then, the suspensorio-opercular connection in *Spelerpes* has the same morphological relations as the ligament in *Necturus*.

Desmognathus fusca. (76 mm.) In this form it would seem as if, as compared with *Spelerpes*, the suspensorium were

displaced backward in relation to the operculum, so that the stilus is shorter, passes more directly outward and upward, and is joined more closely with the subsquamosal process of the quadrate (Fig. 5) than with the squamosum itself. It is,

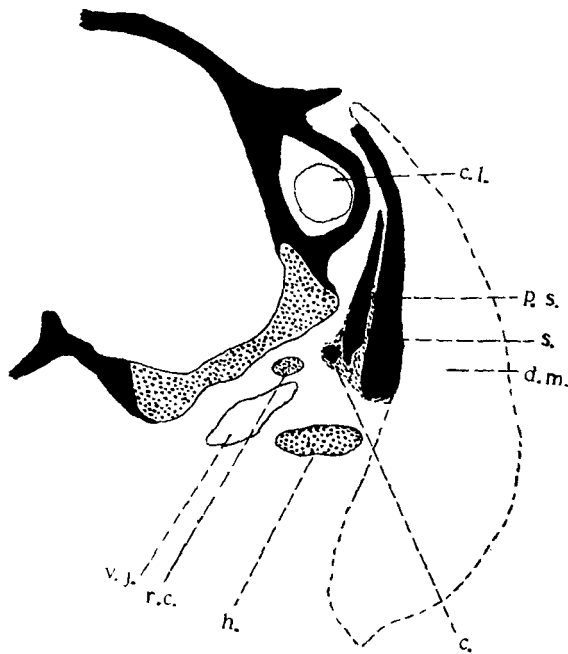


Fig. 5. *Desmognathus fusca*, adult, 76 mm. *c.*—stilus columellae; *c. l.*—canalis lateralis; *h.*—hyoid; *v. j.*—vena jugularis; *r. c.*—ramus communicans; *d. m.*—depressor mandibuli; *p. s.*—subsquamosal process of quadrate; *s.*—squamosum.

however, joined to both bones by connective tissue, and with the cartilaginous process of the quadrate. This process is longer than the corresponding process in *Spelerpes* and is separated from the stilus by an interval of but (ca.) $50\ \mu$ (Fig. 6). The squamosum and the subsquamosal process of the quadrate are essentially the same as in *Spelerpes*. Stilus and operculum are as in *Spelerpes*, though the cartilage in the columella is small.

Turning to the larval form for an interpretation of the condition in the adult, we find in a specimen 21 mm. in length, that the suspensorio-opercular connection is at this stage cellular and extends from the cephalic border of the operculum to the squamosum as a dense cord of cells. It has the same rela-

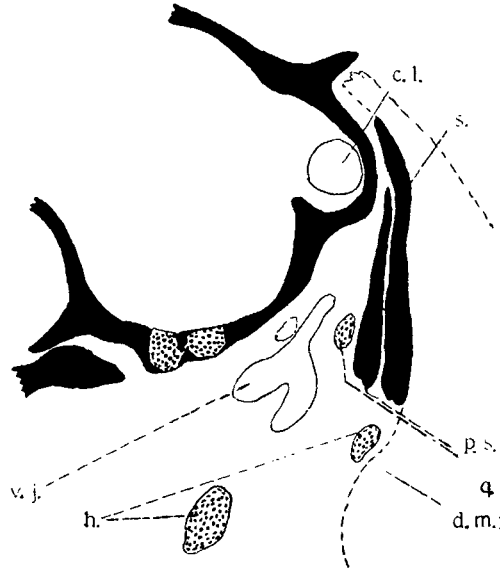


Fig. 6. Same, three sections (75 μ) farther forward; q.—cartilaginous (columellar) process of the quadrate.

tion to the jugular nerve and vein as in *Spelerpes*, though it does not come into as close contact with either as in that form. Its cephalic end is rather difficult to determine (Fig. 7), since the anlage is continued forward to join the subsquamosal process (of the quadrate) which at this stage is a distinct bone, so that it may be said to be connected with both bones. There is, however, no direct connection with the (cartilaginous) quadrate, and from the conditions in *Necturus* and *Spelerpes*, we are warranted, I think, in emphasizing the connection with the squamosum rather than that with the subsquamosal process of the quadrate which, in fact, is not as direct. In a larva 33

mm. in length (Fig. 7), apparently approaching the period of transformation, the relations are as in the younger specimen save that cartilage has appeared in the suspensorio-opercular connection as a center distinct from the cartilage of the operc-

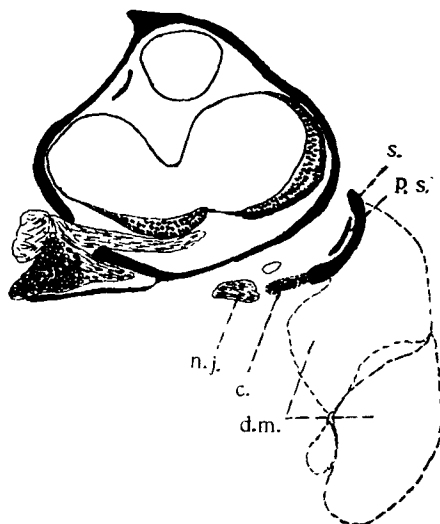


Fig. 7a. Larval *Desmognathus fusca*, 33 mm.; *c.*—stilus columellae; *v. j.*—vena jugularis; *n. j.*—nervus jugularis (*R. communicans*); *d. m.*—*M. depressor mandibuli*; *p. s.*—subsquamosal process of the quadrate; *s.*—squamosum.

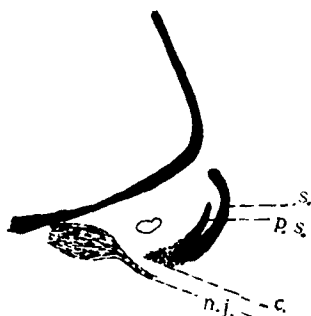


Fig. 7b. Same; three sections farther forward.

ulum. In a small adult (27 mm.), presumably but recently transformed, the cartilaginous stilus is connected more directly with the squamosum, but also by dense connective tissue with

the subsquamosal and the short cartilaginous processes of the quadrate. The shifting of the attachment takes place in the growth of the adult rather than at the transformation of the larva.

Amphiuma means (51 mm). Through the courtesy of my co-worker, Professor H. W. NORRIS, I am enabled to give here the following brief statement of the relations occurring in *Amphiuma* as found by him and verified by myself in his preparations. This form is interesting because it possesses a continuous cartilaginous connection between the quadrate and operculum, as described by WIEDERSHEIM,¹ HAY,² and WINSLOW.³ This has been spoken of as the columella, and as the stapedia process of the quadrate. It evidently, however, represents both the columella (stilus columellae) and the primarily cartilaginous process of the quadrate found in *Desmognathus*. The articulation in the specimen upon which this statement of relations is based is much closer than it is in *Desmognathus*, and in older specimens undoubtedly, as described, there occurs a fusion of the two structures to form one continuous rod between the operculum and the quadratum. In this specimen, the stilus is a cartilaginous process of the operculum which is itself cartilaginous. The stilus columellae goes forward and slightly upward to become applied to the thickened ventral border of the squamosum to which it is joined by connective tissue. It is succeeded by the cartilaginous columellar process of the quadrate to which it is very closely connected. This process lies also against the ventral edge of the squamosum and slightly on its inner side. The connection of the stilus, therefore, is with the squamosum and the cartilaginous process of the quadrate and not at all with the ossification which (from the condition in the adult *Desmognathus* and *Spelerpes*) I have spoken of as the subsquamosal process of the os quadratum.

¹ Op. cit., p. 502.

² '90, HAY, O. P. The Skeletal Anatomy of *Amphiuma* during its earlier Stages. *Journ. Morph.*, Vol. IV.

³ '98, WINSLOW, G. M. The Chondrocranium in the Ichthyopsida. *Tufts College Studies*, No. 5, 1898.

All branches of the facial nerve pass below the stilus columellae (and stapedial process of the quadrate) as has already been stated by HAY, instead of over it.¹

Other Urodela. In *Menopoma* (*Cryptobranchus*) alone is the relation of columella to the squamosum described by WIEDERSHEIM,² and also by PARKER.³

In *Amblystoma* I can only state that there is present in the larva a cord of cells, passing from the operculum to the ventral border of the squamosum, which from the position and relation (dorsal) to the facial nerve is undoubtedly the anlage of the suspensorio-opercular connection. This relation of the "columella" to the facial nerve, has already been affirmed by HASSE and PARKER.

Proteus anguinus. Opportunity for studying the relations in this form was afforded me by the generosity of Professor WIEDERSHEIM. As might be expected from the published figures (WIEDERSHEIM: op. cit., Fig. 19), the relations in *Necturus* and *Proteus* are the same. There is a strong squamoso-opercular ligament passing from the stapedial process of the squamosum to the short stilus columellae, and to this the branches of the facial nerve have the same relation as in *Necturus*; R. jugularis passes above the ligament, R. mandibularis externus below it.

*Nervus facialis.*⁴

Since the homology of the chorda tympani is closely connected with that of the relations and connections of the columella auris, the following brief account of the course of the branches of the facial nerve is offered. The relations of the nerve in the larvae only of *Desmognathus* and *Spelerpes* have

¹ This is also in accord with KINGSLEY'S description. (*Tufts College Studies*, No. 7, p. 305.)

² Op. Cit., p. 502.

³ Op. Cit., Pt. III, p. 184.

⁴ The following names of the branches of the facial nerve are used: R. palatinus; R. jugularis (FISCHER); R. mandibularis internus (R. Alveolaris, FISCHER); R. mandibularis externus (R. mentalis, FISCHER).

been studied, as the changes at transformation introduce complexities unimportant in this connection.

Necturus (9.4 cm.). The ganglion geniculi is intra-cranial, in the beginning of what might be described as a short facial canal, adjoining and cephalad of the cephalic division of the auditory nerve. From this ganglion the ramus palatinus arises as a small nerve which passes cephalad and ventrad through a separate foramen, and goes cephalad at the side of the trabecula, finally passing ventrad between the parasphenoid and the pterygo-palatine to the roof of the oral cavity. The remainder of the nerve passes laterad through its foramen and develops a second ganglion which undoubtedly belongs to the R. mandibularis externus, a part of the lateral line component. At this ganglion the nerve divides into two branches, R. mandibularis facialis, and R. jugularis; the former divides, as soon as it leaves the ganglion into the Rami mandibularis externus and internus. The R. jugularis passes upon the caudal side of the ganglion and has but little if any connection with it. Its course is nearly directly laterad for a short distance, passing dorsad to the ligament between that structure and the jugular vein; beyond the ligament, under the ventral edge of the squamosum it turns ventrad and caudad around the dorsal border of the otic division of the M. depressor mandibuli to pass under the fascia covering the lateral surface of that muscle. At the lateral border of the M. mylohyoideus posterior, it passes to the ventral side of that muscle. It innervates the M. depressor mandibuli, ceratohyoideus, and mylohyoideus posterior. The Ramus communicans glossopharyngei passes forward from the ganglion complex of the IX and X and joins the R. jugularis just beyond the point where it emerges above the columella. The M. depressor mandibuli gains some at least of its innervation from fibers of the R. jugularis which pass back along the R. communicans. R. jugularis seems to be purely a motor nerve, though it is possible that it may have a small lateral line component.

The R. mandibularis externus goes cephalad, laterad and ventrad under the ventral border of the squamosum below (in front of) the point of attachment of the ligament curving

around to the outer surface of the squamosum. After giving a branch to the skin whose destination was undoubtedly the lateral line sense organs, it divides into two branches, one¹ passing farther caudad and mesad, so as to lie on the mesal side of the lower jaw, between the M. submaxillaris and the skin; the other passing to the outer side of the lower jaw. From these two branches, evidently the lines of sense organs called by me² gular, and oral (incl. angular) respectively, receive their innervation. It is possible that the gular division contains communis fibers as well as those destined for the lateral line organs. The M. submaxillaris I find to be innervated by the trigeminus (R. mandibularis internus V), in this supporting Miss PLATT³ as against RUGE.⁴ Both divisions are subcutaneous,—i. e. external to all skeletal and muscular structure.

The rami mandibularis internus, separates from the R. mandibularis externus as it leaves its ganglion, and passes ventrad and cephalad, on the inner (ventral) side of the quadrate soon passing through the suspensorio-hyoid ligament. This is the condition in a specimen 9.4 centimeters in length. In younger specimens the nerve seems to lie on the outer side of the ligament, though very closely applied to it. Beyond the

¹ This is evidently the branch described by VON PLESSÉN and RABINOVICZ (Die Kopfnerven von *Salamandra maculosa* im vorgerückten Embryostadium, 1891) as "Begleiter des R. hyoideo-mandibularis (h. m')"—Hyomandibularis accessorius. By some these branches have been incorrectly called Rami mandibularis internus (alveolaris) and externus. The homology of either of these nerves with the chorda tympani, suggested by HERRICK in his '94 paper (*Amphystoma punctatum*) and accepted by KINGSLEY '02, for *Amphiuma*, can, of course, hardly hold now. COGHILL calls these, Rami mentales externus and internus.

² '95. KINGSBURY, B. F. The Lateral Line System of Sense-organs in some American Salamanders, and Comparison with the Dipnoans. *Proc. Americ. Micr. Soc.*, Vol. XVII, 1895.

³ '98, PLATT, JULIA B. The Development of the Cartilaginous Skull and of the Branchial and Hypoglossal-Musculature in *Necturus*. *Morph. Jahrb.*, Bd. XXV, 1898.

⁴ '96, RUGE, G. Ueber das periphere Gebiet des Nervus facialis bei Wirbelthieren. *Festschrift für Carl Gegenbaur*, 1896, pp. 195-348.

ligament, the nerve is on the inner side of the M. depressor mandibuli, MECKEL's cartilage and the os articulare successively. It is separated by connective tissue from the mucous membrane of the mouth which it gradually approaches, lying on the dorsal (mandibular) side of the depression¹ between the hyoid and mandibular arches. At about the level of the caudal border of the eye, it divides into two branches, one of which continues forward on the inner side of the jaw, the other moves farther ventrad and mesad; both, however, become compressed between the M. submaxillaris and the oral mucous membrane of the floor on the mouth between the hyoid (tongue) and the mandible.

No communication occurs between this nerve and the Ramus mandibularis internus of the fifth.

In the larvae of *Spelerpes*² and *Desmognathus* the relations of the four main branches of the seventh nerve are in general essentially as in *Necturus*. The Ramus jugularis, however, instead of curving around the dorsal border of the otic division of the depressor mandibuli as in *Necturus*, in *Spelerpes* passes through that division of the muscle, while in *Desmognathus*, it passes *under* the *entire* muscle. In both *Desmognathus* and *Spelerpes* it contains a cutaneous—undoubtedly lateral line—component which was not found in *Necturus*. As in *Necturus* the M. depressor mandibuli receives its innervation from fibers that accompany the Ramus communicans. The relation of both the R. jugularis and the R. communicans to the stilus columellae has been spoken of in connection with that structure.

¹ "The *R. alveolaris VII*, composed wholly of communis fibers, follows the posterior border of the suspensorium to the angle of the jaw. Along this part of its course, the *R. alveolaris* lies mesially of the hyo-suspensorial ligament, and anteriorly of the deep pharyngeal evagination which represents the embryonic spiracular cleft." '02, COGHILL, G. E. The Cranial Nerves of *Amblystoma tigrinum*. *Journ. Comp. Neurol.*, Vol. XII, p. 228.

² The branches and distribution of the facialis in the larval *Spelerpes* have been correctly given by Miss M. A. BOWERS: The Peripheral Distribution of the Cranial Nerves of *Spelerpes bilineatus*. *Proc. Am. Acad. Arts and Sci.* Vol. XXXVI, 1900.

The *Ramus mandibularis externus* passes cephalad and laterad around the lower edge of the squamosum to its outer surface, where it divides into branches, as in *Necturus*, one of which curves ventrally over the outer surface of the *M. depressor mandibuli* and its tendon to run forward upon the ventral surface of the *M. submaxillaris*. The other division runs cephalad upon the outer side of the lower jaw. Both seem to be purely lateral line nerves.

The *R. mandibularis internus* separates from the *externus* at the cephalic border of the ganglion and goes laterad cephalad and ventrad immediately to the mucous membrane of the oral cavity between the hyoid arch and the quadrate and (farther cephalad) the mandible. In the first part of its course it lies in the connective tissue between the oral mucous membrane, the quadrate and the *M. depressor mandibuli*, the quadrate lying dorsally and the muscle laterally. Farther cephalad it passes on the inner side of the suspensorio-hyoid ligament, MECKEL'S cartilage and the *os articulare* on whose mesal side it divides, one branch passing through a canal in that bone to join the *R. circumflexus V*,¹ which at nearly the same level passes between the *os dentare* and MECKEL'S cartilage. This soon divides on emerging from its canal into the *R. submaxillaris* and *R. mandibularis internus V*. The remainder of the *R. mandibularis internus VII* runs forward between the mucous membrane and the mandible. At the level of the appearance of the *M. submaxillaris*, it is compressed between that muscle and the mucous membrane of the floor of the mouth. The portion of the *R. mandibularis internus VII* which joined the trigeminus I was unable to trace. I was unable to trace the fibers of the *R. mandibularis internus* in any of the forms even into the neighborhood of taste buds. It is clear, that the *R. mandibularis internus (alveolaris)* in *Urodeles* has practically the same course, the only marked differences being that in *Necturus*, and *Proteus*, it does not pass through a canal in the

¹ I use the name applied to the comparable nerve in the frog, believing them homologous. Compare, however, COGHILL, op cit., pp. 265 and 266.

os articulare (angulare?), while in *Amphiuma*,¹ ('02, KINGSLEY), *Desmognathus* and *Spelerpes*, *Amblystoma*, *Salamandra* and *Triton*, (COGHILL, op. cit., p. 269), it occupies such a canal. In *Necturus*, *Proteus*, and *Amphiuma* (KINGSLEY) it does not anastomose with the Vth, while in the other forms it does.

From the above relations it is seen that the only nerve which can be considered as a homologue of the chorda tympani is the *Ramus mandibularis internus VII* which goes to the mucous membrane of the floor of the mouth between the hyoid and mandibular arches.² This, of course, is the homology already advanced by GAUPP,³ STRONG⁴ and others, GAUPP from morphological relations, STRONG from the character of the fibers and their destination. ALLIS,⁵ HERRICK⁶ and GREEN⁷ have since seen reason to doubt the homology on the grounds of the pre-trematic position which the homologue of the chorda tympani must have, the nerve identified by them as *R. mandibularis internus facialis* being a post-spiracular nerve, and a *Ramus facialis pretrematicus* being chosen by them as the homologue of the chorda tympani.

¹ '02, KINGSLEY, J. S. The Cranial Nerves of *Amphiuma*. *Tufts College Studies*, No. 7, pp. 293-321.

² RUGE (op. cit., p. 294) recognizes this nerve as the chorda tympani though he does not identify it as the internal mandibular (alveolaris, FISHER) but seems to find that also present as a cutaneous nerve. COGHILL (op. cit.) regards it as a homologue of the chorda tympani.

³ '93, GAUPP, E. Beiträge zur Morphologie des Schädels. I. Primordial Cranium und Kieferbogen von *Rana fusca*. *Morph. Arbeiten* herausg. von G. SCHWALBE, Bd. II.

⁴ '95, STRONG, O. S. The Cranial Nerves of Amphibia. A Contribution to the Morphology of the Vertebrate Nervous System. *Journ. of Morph.*, Vol. X.

⁵ '97, ALLIS, E. P. The Cranial Muscles and Cranial and first Spinal Nerves in *Amia calva*. *Journ. of Morph.*, Vol. XII, No. 3, 1897.

⁶ '99, HERRICK, C. J. The Cranial and First Spinal Nerves of *Menidia*; a Contribution upon the Nerve Components of the Bony Fishes. *Journ. Comp. Neurol.*, Vol. IX, 3-4.

⁷ '00, GREEN, H. A. On the Homologies of the Chorda Tympani in Selachians. *Journ. Comp. Neurol.*, Vol. X, 4.

The question seems to me to involve the correctness of the interpretation of the chorda tympani as pretrematic, and the homology of the mandibularis internus VII, in Menidia, Amia and Selachia, which appears to have a course somewhat different from that of the branch in Urodeles. For a comparison of the relations in fishes and Amphibia, the effect of the morphological differences in the suspension of the jaw and the value of the relation of nerves to skeletal structures in determining their homology, are involved; and for the larger question of the chorda tympani, the homology of the sound-transmitting apparatus in the different classes, as well; so that it seems to me a close consideration of homologies is yet premature.

The pre- or post-trematic origin of the R. mandibularis internus in Urodeles cannot, of course, be determined, since the first gill cleft does not come to development. From its point of origin and course, it certainly could be pretrematic, as COLE¹ has pointed out, and it seems to me the possibility that this nerve represents a pre-trematic nerve such as GREEN, (e. g.) described in Selachia,² is worth considering. In this connection the different relations of the facial nerve and columella auris in Anura and Urodela must also be considered. There is here presented in allied forms, a difference of relation

¹ '96, COLE, F. J. On the Cranial Nerves of *Chimaera monstrosa* (Linn) with a Discussion of the Lateral Line System and of the Morphology of the Chorda Tympani. *Trans. Roy Soc.*, Edinburgh, Vol. XXXVIII, Pt. III, (No. 19).

² I have already referred to the statement by COGHILL (p. 228) that this nerve could be considered pre-trematic. In the forms studied by me, however, the conditions, I believe, hardly warrant a definite conclusion. COGHILL, even, would regard the R. mandibularis internus in Urodela and Anura, as not homologous (p. 265), and this, too, seems to me rather extreme. The entire hyomandibular nerve in the frog crosses over and behind the columella auris and in Urodela under and in front of it. As stated in a previous paper ('95, The Structure and Morphology of the Oblongata in Fishes; *Journ. Comp. Neurol.*, Vol. VII, p. 30) where I quote also the opinion of Miss PLATT to that effect, I feel that the origin and distribution of a nerve are of more importance than its course, which may vary, and consequently should not be too closely made the basis of homologies. We also see that the relation of a nerve to a muscle cannot be relied upon as a test.

of nerve to skeletal structure of extreme type. As is well known,¹ in the frog the hyomandibular nerve crosses above the columella and passes down behind it to its destination, whereas in *Urodeles* it passes in front of or below the same structure. Other cases of similar differences of relation in this region, mentioned in this paper, are (a), the relation of the jugular nerve in *Necturus* on the one hand and in the other salamanders investigated on the other hand; in the first case it passes above the columella (*stilus columellae*), in the second, below. (b), *Necturus* also offers a difference in the relation of the internal mandibular branch to the quadrato-hyoid ligament. In *Desmognathus* and *Spelerpes* the nerve passes on the inner side of the ligament; in *Necturus*, through the ligament, or on its outer side in younger individuals. Further (c), the R. jugularis in *Necturus* passes over the depressor mandibuli; in *Spelerpes* larvae, through it; in *Desmognathus* larvae, under it.

The differences, in the last two cases at least, it seems to me, might possibly be explained on a more or less mechanical basis. The nerves (and muscles) are already developed and their course and positions established before the anlage of the columella or that of the quadrato-hyoid ligament has appeared, and the relations the latter structures assume when they do develop, has been determined for them by the position of the structures earlier developed. This explanation would not, of course, be an ultimate one.

The nomenclature employed in the above descriptions is that suggested by Professor GAUPP. *Columella*, including operculum and its process, *stilus columellae*, which may be joined to the suspensorium by an appreciable ligament—*ligamentum suspensorio-columellare (operculare)*. I regard the suspensorio-columellar (opercular) connection in the forms studied as homologous. The term *stilus columellae* is used in describ-

¹ '93, GAUPP, E. Beiträge zur Morphologie des Schädels. I. Primordial Cranium und Kieferbogen von *Rana fusca*. *Morph. Arbeiten*, herausgegeben von G. Schwalbe, Bd. II.

'99. ECKER'S u. R. WIEDERSHEIM'S Anatomie des Frosches, auf Grund eigener Untersuchungen durchaus neu bearbeitet. II Abth. 1899.

ing the relations in *Desmognathus* and *Spelerpes*, in view of the structure in the adult, despite the fact that the "stilus" probably begins as a chondrification in the cord of cells extending from the operculum to the squamosum. This point of a separate chondrification, however, has not been firmly established. In that case the ligamentum squamoso-columellare (operculare) and the stilus columellae of *Spelerpes* I should regard as homologous—despite the different relations to the facial nerve.

In conclusion, I may say that the points which I wish to emphasize are:

- (1) The primary connection of the columella with the bone which I regard as the squamosum.
- (2) The different relations of the facial nerve to the ("squamoso-opercular" connection) stilus columellaris in the frog, *Necturus* (and *Proteus*) and other Urodela.
- (3) The secondary nature of the connection of the columella with the quadrate cartilage, where such connection occurs.
- (4) The different relations of the ramus jugularis VII, to the musculus depressor mandibuli in *Necturus*, *Spelerpes*, and *Desmognathus*.
- (5) The course and relations of the R. mandibularis internus VII, in view of the possible homology with the chorda tympani.
- (6) The question of the value of the relation of a nerve to skeletal parts and muscles, as a criterion of homology.

Anatomisches Institute, Freiburg i. B., May 1, 1902.

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