

THE RELATION OF THE CHORDA TYMPANI TO THE VISCERAL ARCHES IN MICROTUS.

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(Contributed from the Biological Laboratory of Pacific University, under the direction of G. E. COGHILL).

The mammalian chorda tympani is a branch of the facial nerve which passes over the tympanic cavity, underneath the auditory ossicles and joins the lingual branch of the trigeminus. It is generally accepted that the tympanic cavity and auditory ossicles are derivatives of the spiracular cleft and visceral arches of fishes. It would seem a natural conclusion, therefore, that the chorda tympani is also homologous with the pre-spiracular branch of the facial nerve of fishes and amphibians. Upon this point, however, authorities are not agreed. On the one hand, a large number of investigators regard the chorda tympani as the homologue of the pre-spiracular (pre-trematic) nerve of fishes, as, for example, BALFOUR, in describing the anterior branch of the seventh nerve of Elasmobranchii, says: "This branch forms the prae-spiracular nerve of the adult and is homologous with the chorda tympani of mammals" (Comparative Embryology, Vol. II, p. 459). STRONG, in his work on the cranial nerves of Amphibia, interprets the r. mandibularis internus of fishes and Anura, and the r. alveolaris of Urodela, as homologous with the mammalian chorda tympani. On the other hand, DRÜNER denies that the r. alveolaris is the homologue of the chorda tympani (*Zool. Jahrb.*, XV, 3); while COGHILL, in his work on the cranial nerves of *Amblystoma*, interprets the r. alveolaris of Urodela as pre-spiracular, and takes the tentative position that the "most complete morphological and physiological representative (of the chorda tympani) in the

Ichthyopsida is probably found in the r. alveolaris of Urodela" (*Jour. Comp. Neurol.*, Vol. XII, p. 269). HERRICK questions whether STRONG's r. mandibularis internus in the homologue of the chorda tympani. He finds no nerve in *Menidia* homologous with the chorda tympani, and does not consider the r. pre-trematicus VII to be so homologous because it does not fuse with the r. mandibularis V and hence it does not distribute to the hyoid and mandibular arches in the way characteristic of mammals" (*Jour. Comp. Neurol.*, Vol. IX, p. 324). And finally, in addition to the r. palatinus, r. pre-trematicus and r. post-trematicus, STANNIUS, as cited by HERRICK (loc. cit.) describes in *Raja* and *Spinax* another branch of the seventh nerve which fulfills every condition for the chorda tympani. This conflict of opinion shows that the homology of the chorda tympani is far from being unquestionably established.

A chief source of this disagreement lies in the fact that the morphological relations of the chorda tympani to the spiracular cleft throughout the ontogeny of mammals is not completely understood. It has been accepted by leading authorities that the chorda tympani is a pre-spiracular nerve in the mammalian embryo. Very recently HERRICK in a literary notice of the work by VERSLUYS on "Die mittlere und aussere Ohrsphäre der Lacertilia und Rhynchocephalia" writes: "The detailed descriptions and figures make it very plain that the chorda tympani of reptiles is pretrematic and therefore morphologically pre-spiracular; and in the absence of very definite proof to the contrary, we must assume the same condition to prevail among the mammals also" (*Jour. Comp. Neurol.*, Vol. XIII, 1). LEWIS in giving "The Anatomy of a Twelve Millimeter Pig," says that the seventh nerve "divides into a pre-trematic and post-trematic branch, but the division is under the spiracle or auditory cleft and not over it as in fishes" (*Am. Jour. Anat.*, Vol. II, 2). In the last quotation it is not clear, however, whether by "division under the spiracle" it is meant that the chorda tympani itself passes over or under the spiracular cleft.

In the adult mammal the nerve in question clearly passes

over and in front of the tympanic cavity, so that, in view of the confusion of ideas as noted above, the question now is whether the pre-tympanic position is primary and maintained throughout the embryonic life, or whether it is a position secondarily acquired in the development of the tympanum. Of course, the further questions of homology cannot be settled till this point in mammalian embryology is determined. It was for the purpose of contributing something to the solution of this question that the following study in the embryology of *Microtus* was undertaken.

The embryos used in this study were killed and preserved in formalin. To insure a correct conception of the relations of the nerves to all parts of the head a model of a 2.3 mm. embryo, magnified 50 diameters, was made by the BORN method. Reproductions of two older embryos, also, were made by KASTCHENKO's method of graphic projection. My observations were made from the same series of serial sections as were employed for the model and projections, and from several other series of slightly different ages and cut in different planes.

First Embryo.

The youngest of the embryos was used for the construction of the model. The model and the sections from which it was made demonstrate clearly all the structures which are of importance for this study: the brain and all its flexures, the roots and ganglia of the fifth, seventh and eighth nerve, the mandibular and hyoid arches, and the posterior visceral arches as they are modified to form the sinus cervicalis. At this period the visceral arches are united only by a membrane composed of the two layers of epithelial cells, and the nerve trunks can be traced only a short distance into the mesenchyme of the arches.

Second Embryo.

From this embryo, more advanced than the first, two graphic projections were made, one of the exterior of the head and the other of the brain, fifth and seventh nerves and pharyngeal cavity. The mandibular and hyoid arches are still conspicuous

as typical visceral arches. The formation of the mandibular and hyoid cartilages has not begun, and these regions are filled with primitive mesenchyme cells.

*The Spiracular Cleft.*¹—In the dorsal part of the external groove between the mandibular and hyoid arches a small pit is found. From the apex of this pit the lumen of the spiracular cleft passes inwards and cephalad, and opens into the pharynx. Beginning in its most external part the lumen is very narrow for a distance of about .07 mm., then it broadens out into a flat cavity with its shortest diameter, as seen in the sagittal section, in a dorso-ventral direction. In the extreme lateral region of the cleft its epithelial walls approach each other in such a manner that the lumen is reduced to a small circular canal, until, finally, for an extremely short distance they come into close contact with each other, so that the lumen seems to be obliterated. *The epithelium of the cleft, however, is perfectly continuous with the epithelium of the skin.*

This relation of the visceral arches and the pharyngeal cavity to this cleft, and the continuity of the inner and outer epithelial plates are essential characteristics which establish its homology with the spiracular cleft of fishes.

The Chorda Tympani and Related Nerves.—The Gasserian, geniculate and auditory ganglia and their roots are clearly defined. The rr. ophthalmicus, maxillaris superior and maxillaris inferior are easily identified in their usual relations. Near its ganglion the r. maxillaris inferior gives off the buccal nerve, and, passing into the mandibular arch, divides to form the inferior dental and the lingual nerves. The latter can be traced into the base of the tongue.

From the geniculate ganglion the facial nerve passes outward and slightly caudad for some distance. Just back of the spiracular cleft it makes a slight turn ventrad. At this angle it gives off the chorda tympani from its anterior border. The

¹ The term *spiracular cleft* is used here as HERTWIG uses the term *sulcus tubo tympanicus*. This usage is justified by the relations as they are described farther on in this paper.

chorda tympani then passes directly forward *beneath* the spiracular cleft and close to its ventral edge. It soon turns inward and passes a considerable distance nearly parallel with the anterior wall of the cleft. Near the rudiment of the tongue it meets and fuses with the lingual brach of the trigeminus.

At this stage of the embryonic development of *Microtus*, therefore, the primitive continuity of the epithelium of the spiracular cleft and the skin still persists, and the chorda tympani passes behind and underneath the cleft and unites in a typical manner with the lingual nerve.

Third Embryo.

In the oldest of the three embryos, from which projections were made as from the second embryo, the pinna has begun to form, the mandibular and hyoid arches no longer appear as visceral arches and have assumed in a general way the adult conditions. The skeletal regions are still for the most part filled with mesenchyme cells, but the fundamentals of MECKEL's cartilage and of the hyoid cartilage are distinguishable.

The Spiracular Cleft and External Auditory Meatus.—The comparatively large orifice of the external auditory meatus is bordered by the ridges or fundamentals of the pinna. The meatus soon narrows into a flattened cavity with its shortest diameter lying in the dorso-ventral plane, as seen in sagittal section. Its course is in a cephalo-ventral direction. It terminates as a blind tube. In a plane about .075 mm. outward from the blind end of the external auditory meatus, and dorsal of the meatus at a distance about equal to the greatest diameter of the meatus at this region, lies the blind end of the cleft which in the second embryo was identified as the spiracular. This cleft is also a flattened cavity with its longest diameter, as seen in sagittal section, lying in nearly the horizontal plane. It passes inward for a short distance, then takes a cephalo-ventral direction and opens into the pharynx. It is an important fact that in this embryo there is no continuity between the epithelium of the spiracular cleft and the skin.

The Chorda Tympani.—The ganglia and the main trunks

of the nerves are essentially the same as described for the second embryo. In addition to the inferior dental and lingual branches of the submaxillary, the mylo-hyoid and masseter branches are clearly defined. The lingual occupies a position along the inner side of MECKEL'S cartilage and can be traced forward into the lateral region of the tongue. Of the facial nerve, also, the supra-maxillary and auriculo-temporal are easily traced in their usual positions. The chorda tympani is easily traced from its point of origin from the facial trunk. It passes behind MECKEL'S cartilage, takes the same general direction that it does in the earlier embryo, and joins the lingual nerve near the point of separation of the latter from the inferior dental. But the relation of the chorda tympani to the spiracular cleft is distinctly different from that found in the earlier embryo. In its course in front of the hyoid cartilage and behind the proximal end of MECKEL'S cartilage, it passes *over* the extreme lateral end of the spiracular cleft and close to its dorsal edge. It remains a question whether this lateral end of the spiracular cleft is the primary end of the cleft or a secondary evagination from it. It might be the latter, since it is generally accepted that the closed end of the cleft by evagination outward towards the external auditory meatus and upward around the chorda tympani and auditory ossicles, forms the tympanic cavity of the adult.

We find, then, at this stage of development that the chorda tympani no longer lies underneath the spiracular cleft but that it passes over the closed end of the cleft, or over the fundamen-
ment of the tympanum. This is the morphological position the nerve holds in the adult.

Conclusions.

The results of this study of the embryological development of the chorda tympani in *Microtus* lead to the following conclusions:

1. In the earlier stages of development the chorda tympani passes behind and underneath the spiracular cleft.
2. In

later stages this nerve occupies a position over and in front of the closed end of the spiracular cleft which is generally accepted to be the fundament of the tympanum. 3. The chorda tympani is, therefore, a post-spiracular nerve, and is to be considered as the homologue of a post-trematic nerve of fishes and amphibians.