

ON THE HOMOLOGIES OF THE CHORDA TYMPANI IN SELACHIANS.¹

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With three figures in the text.

Probably few nerves in the human body have given anatomists and morphologists more trouble than the chorda tympani. In the first place the true course of the nerve has long baffled anatomical researchers, and on the other hand any one of the possible paths which these fibers may take presents peculiar difficulties of morphological interpretation.

It will be recalled that the posterior part of the tongue is innervated by the gustatory part of the glossopharyngeus nerve, while the anterior part is supplied by the lingual nerve, which is composed chiefly by the lingual branch of the trigeminus, to which is added the chorda tympani, and an unknown number of sympathetic fibers. Without attempting to summarize at this time the exceedingly diverse views which have been held regarding the courses of the fibers in these nerves, and confining our attention to the gustatory fibers in the lingual nerve, the weight of authority at the present time is clearly in favor of regarding these as derived from the chorda and of denying the gustatory function to any of the trigeminus roots. The lingual branch of the trigeminus is, then, devoted to general sensation of the tongue, while the sense of taste is mediated by glossopharyngeal and facialis fibers. While there is some clinical evidence on the other side, the weight of evidence (particularly anatomical and embryological data) favors this view.

The geniculate ganglion of the facialis being a typical

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cerebro-spinal ganglion, the central processes of its cells enter the portio intermedia of Wrisberg and the fasciculus solitarius to terminate with the gustatory fibers of the glossopharyngeus in the associated grey matter. The peripheral processes of these geniculate ganglion cells in part enter the great superficial petrosal nerve and in much greater number the facialis trunk. Most of the latter fibers leave the trunk within the Fallopian canal and pass back by a separate canal in the temporal bone to cross through the tympanic cavity and join the lingual branch of the trigeminus for taste buds on the tip of the tongue. This is the chorda tympani. A much smaller number of sensory fibers has recently been shown to remain in the facial trunk after the separation of the chorda.

This, I think, may fairly be said to represent the consensus of recent opinion. Its receives strong confirmation from the study of the comparative anatomy of the facial nerve; and not only so, but its morphological interpretation, as well.

It is now pretty generally recognized that the facial nerve of fishes is a very typical branchial nerve, in selachians branching around the spiracular cleft as the IX and X nerves fork around their respective gill clefts and sending forward a palatine branch corresponding to the r. pharyngeus of the other branchial nerves.

The composition of the branchial nerves in the fishes can be stated with precision. The post-trematic branch runs down behind the cleft to supply the half gill on its posterior wall and the muscles of that arch. It is, therefore, of mixed motor and sensory function. The pre-trematic branch supplies the half gill in front of the cleft and the pharyngeal, or palatine, branch the mucosa of the roof of the pharynx adjacent, both of the two latter being wholly sensory. All of the sensory fibers belong to the communis system, fibers associated with the fasciculus communis (f. solitarius) and its terminal nuclei and supplying visceral surfaces and taste buds. The motor fibers belong to the visceromotor system innervating the branchial musculature or its derivatives. The facialis conforms exactly to this scheme, save that in all fishes the post-spiracular half gill

has disappeared and the pre-spiracular or mandibular half gill has in most cases been reduced to a vestigial condition, the pseudobranch.

Even in man these relations are not wholly obscured; for here we can recognize the main facial trunk as homologous with the post-spiracular ramus, the great superficial petrosal as the palatine branch and the chorda tympani as a probable pre-spiracular ramus. These homologies are fairly well established, in the various groups of lower vertebrates; except in the case of the chorda, but on the latter point there has been the greatest diversity of opinion.

Now, first, what are the criteria of the chorda tympani? As to its composition, it is in part, at least, a gustatory nerve and therefore belongs to the communis system of nerves as defined by Strong. As to its course, it forms a part of the sensory facialis root, its fibers are related to cells to the facialis (geniculate) ganglion and they pass out by a circuitous course above and in front (cephalad) of the middle ear and Eustachean tube, then downward along the inner side of the mandible to enter the tongue from the side. Remembering that the Eustachean tube is the phylogenetic derivative of the spiracular canal and that the tongue is built upon the hyoid arch, it is obvious that the chorda is one of the pre-spiracular branches. It has been assumed by some authors who hold this view (e.g., Cole) that it represents the pre-trematic ramus of the fishes in the strict sense, viz., the branch for the gill on the anterior face of the spiracular cleft, or mandibular hemibranch. Stannius, however, has given an account which would seem to put the matter in a slightly different light. In his great monograph on the peripheral nervous system of fishes, published in 1849, he describes for *Raja* and *Spinax* three pre-spiracular twigs, as follows:

“Der N. palatinus ist bei *Raja*, wie bei *Spinax*, complicirter, als bei den Knochenfischen. Er wird durch drei Zweige repräsentirt: einen zarten hinteren und zwei stärkere vordere, welche bei *Raja clavata* und *R. batis* ein zehr zierliches Geflecht bilden.

“1) Der hintere Zweig ist wesentlich für die Pseudobranchie des Spritzloches bestimmt. Er entsteht bei *Spinax* mit zwei Schenkeln, welche später sich vereinigen, geht schlingenförmige Verbindungen ein mit Fäden des zweiten Astes, begibt sich, neben der von der Pseudobranchie kommenden *Vena arteriosa* gelegen, zum Spritzloche und verläuft längs der Pseudobranchie bogenförmig aufwärts.

“2) Der erste vordere Zweig ist wesentlich für die Schleimhaut der Mundhöhle bestimmt. Nachdem er einen Faden für die membranöse Vorderwand des Spritzloches nach hinten abgegeben, der mit dem Nerven der Pseudobranchie schlingenartig sich verbindet und bald darauf auch mit dem dritten Zweige oder dem eigentlichen *Ramus palatinus* schlingenartige Verbindungen eingegangen ist, strebt er, einen Bogen bildend, an der zwischen Zungenbein und Unterkiefer liegenden Schleimhaut der Mundhöhle abwärts und einwärts, wo denn einzelne Zweige die ventrale Mittellinie erreichen. Die fortsetzung des Stammes gelangt zur Verbindungsstelle von Oberkiefer und Unterkiefer, verläuft dann an der den Unterkiefer inwendig auskleidenden Schleimhaut und erstreckt sich mit seinen Zweigen, welche mit denen des *Ramus mandibularis* vom *N. facialis* Schlingen bilden, bis zur Mittellinie des Unterkiefers.

“3) Der zweite vordere Zweig ist der eigentliche *Ramus palatinus*.”

From this it appears that these selachians possess, in addition to the *R. palatinus* and the true pre-trematic ramus for the mandibular hemibranch, a third pre-spiracular nerve, which runs out between the other two along the anterior lining of the spiracular cleft, then forward and inward under the mucous lining of the mouth between the hyoid and the mandibular arches reaching to the ventral median line. This nerve perfectly fulfils all of the requirements of a *chorda tympani*. Its origin with the palatine and other pre-spiracular nerves indicates that it is of *communis* nature, a supposition which is confirmed by its peripheral course, and its peripheral distribution is just as in the human body, save that the absence of the fleshy tongue

in the fishes precludes its anastomosis with a lingual branch of trigeminus, that nerve not being present in the lower vertebrates.

These homologies were suggested by Herrick in his *Me-nidia* paper in 1899, where he has discussed the literature in some detail.¹ The description of Stannius seemed so fruitful in suggestions that we have examined some other selachians with a view to confirming and extending his observations.

In *Squalus acanthias* we find the conditions corresponding to the description of Stannius, quoted above, almost exactly. The foramen through which the hyomandibular root passes out of the cranium is quite long and the swelling which corresponds to the geniculate ganglion lies far out on the root. Stannius found upon microscopical examination that this swelling in selachians contains ganglion cells. From it a large bundle of fibers is given off into the hyomandibular trunk, the same fibers undoubtedly which peripherally compose the r. mandibularis internus. We also confirm Stannius' description of this nerve. It separates from the trunk near the outer edge of the hyomandibular cartilage and curves inward and forward along the outer face of the hyoid arch under the mucosa of the mouth to the end of that arch then runs forward to the lining of the mouth over the tip of the mandible. It is apparently purely sensory.

¹ Some of the more important articles which have appeared since that paper are as follows.

DIXON, A. F. The Sensory Distribution of the Facial Nerve in Man. *Trans. Roy. Soc. of Medicine in Ireland*, Vol. XVII, Dublin, 1899, pp. 613-641. Also in *Journ. Anat. and Physiol.*, Apr., 1899. With critical examination of the literature.

DIXON, A. F. The course of the Taste Fibers. *Edinburgh Med. Journ.*, Apr. and June, 1897.

GEHUCHTEN, A. VAN. Recherches sur la terminaison centrale des nerfs sensibles périphériques. I. Le nerf intermédiaire de Wrisberg. *Le Neuraxe*, I, 1, 1901.

MAXIMOW, ALEX. Die Veränderungen der Speicheldrüsen nach Durchtrennung der Chorda tympani. Vorläufige Mitt. *Centralblatt f. Physiol.*, XIV, 10, 1900.

KIESOW, F. und NADOLECZNY, M. Zur Psychophysiologie der Chorda tympani. *Zeits. f. Psychologie*, XXIII, 1-2, 1900; abstract in *Cent. f. Physiol.*, XIV, 16, p. 430.

The pre-spiracular branches of the facialis are given off together from the geniculate ganglion. All of these fibers appear to arise from this ganglion, i.e., to be of communis nature, though this point cannot be certainly determined in the absence of microscopical examination. The palatine is the largest of

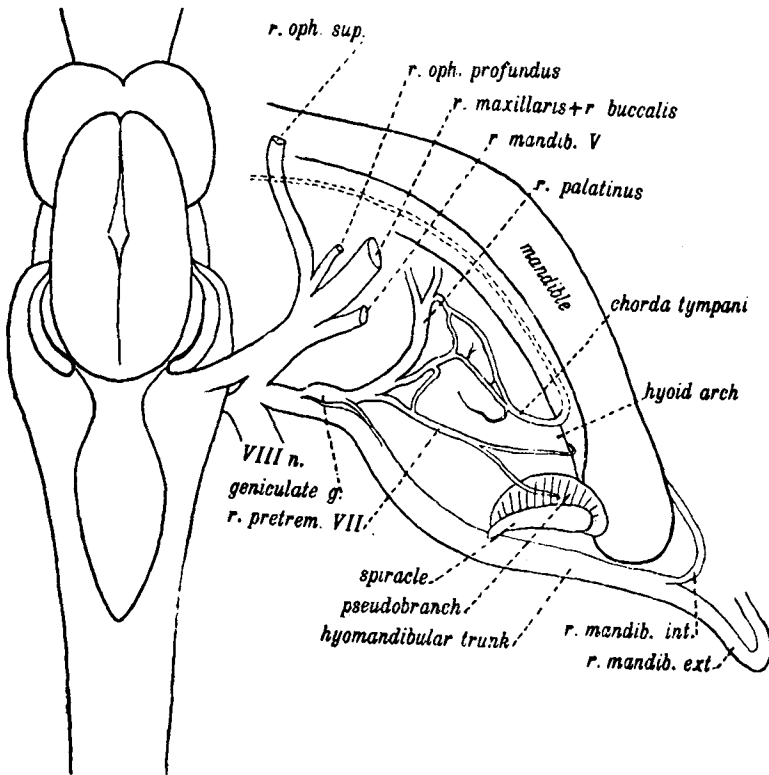


Fig. 1. Dissection of the facial nerve of the spiny dog shark, *Squalus acanthias*, L., as seen from above, the eye and palato-quadrate bar having been removed. $\times 2$. The figure shows the mode of origin of the chorda tympani and its course to the inner edge of the lower jaw. Its further course on the ventral surface is indicated by the dotted line between the mandible and the hyoid arch, only a part of the outer border of the latter being indicated.

them and the r. pre-trematicus in the strict sense is the first branch to be given off, the chorda tympani separating somewhat farther distally. The pre-trematic ramus in this specimen arises by one root and the chorda by two, these all anas-

tomosing with each other. The details of this anastomosis are not exactly the same on the two sides of the specimen so far as the smallest twigs are concerned, though the larger ones on both sides are as figured. The chorda after the union of its two chief roots runs down around the edge of the hyoid arch to the ventral surface in the space between the latter arch and the mandible, then running forward and inward along the inner face of the mandible, keeping all of its course close under the mucous lining of the mouth, until it reaches the ventral median surface under the tip of the mandible. Its principal distribution seems to be to the strong crescentic fold of the mucosa which projects up into the floor of the mouth just behind the teeth of the lower jaw. Near the median line it anastomoses with the terminal twigs of the r. mandibularis internus of the facialis, as Stannius mentions.

In the sand shark, *Carcharis littoralis*, we find the conditions indicated on Fig. 2. The post-spiracular and pre-spiracular nerves go out from the brain together for a short distance, then the post-trematic, or hyomandibular trunk, turns caudad and the palatine nerve cephalad. From the base of the palatine four twigs are given off directed laterally. The first of these is the true pre-trematic branch, which runs backward along the caudal face of the upper jaw embedded in the mucous membrane which forms the anterior (cephalic) wall of the spiracular cleft. Here it divides, one twig passing directly to the pseudo-branch, under which it breaks up, the other twig running a little farther ventrally to supply the mucosa of the outer part of the anterior wall of the spiracle adjacent to the pseudo-branch.

The second branch runs out laterally to the edge of the roof of the mouth, where it turns down to supply the adjacent mucosa. It is to be regarded as a detached filament of the r. palatinus.

The third and fourth branches run out laterally to the inner surface of the palato-quadrato and then unite, afterwards pursuing a course approximately parallel with that of the pre-trematic ramus, but farther ventrally. Running back along the

inner face of the palato-quadrate and in front of the spiracular cleft, just in front of the point of articulation of the mandible it turns inward in the mucosa of the pharynx to the point where the hyoid and mandibular arches separate. Here the nerve breaks up. Most of the fibers appear to run forward

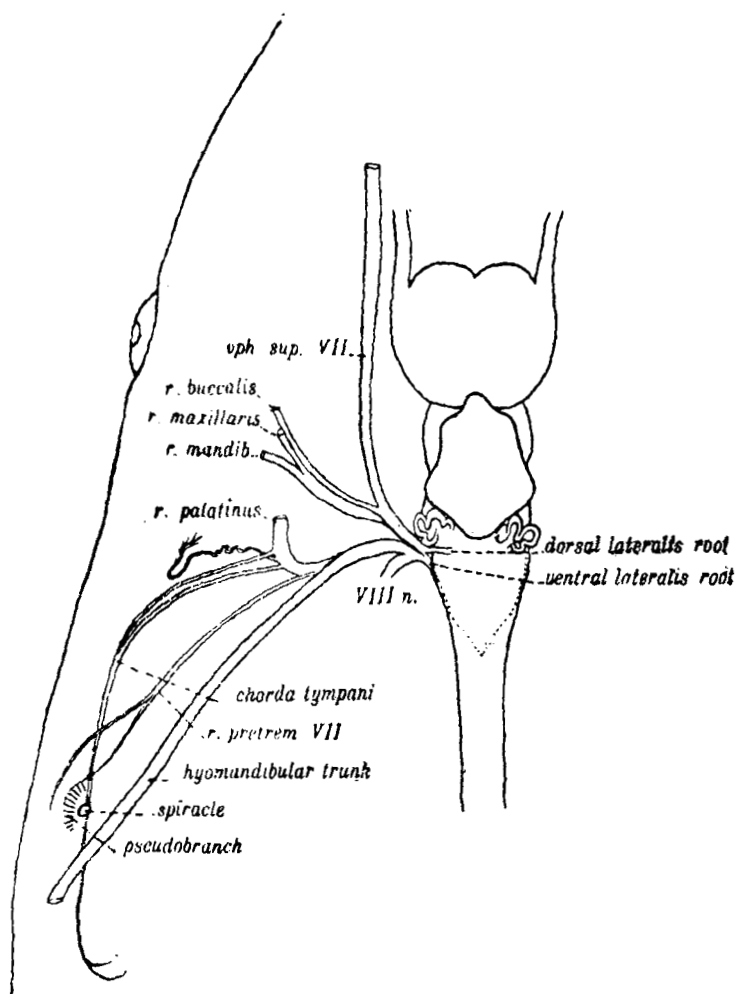


Fig. 2. Dissection of the facial nerve of the sand shark, *Carcharias littoralis*, Mitchill, from above. Natural size.

on the inner face of the mandible, though some may also go out on the hyoid.

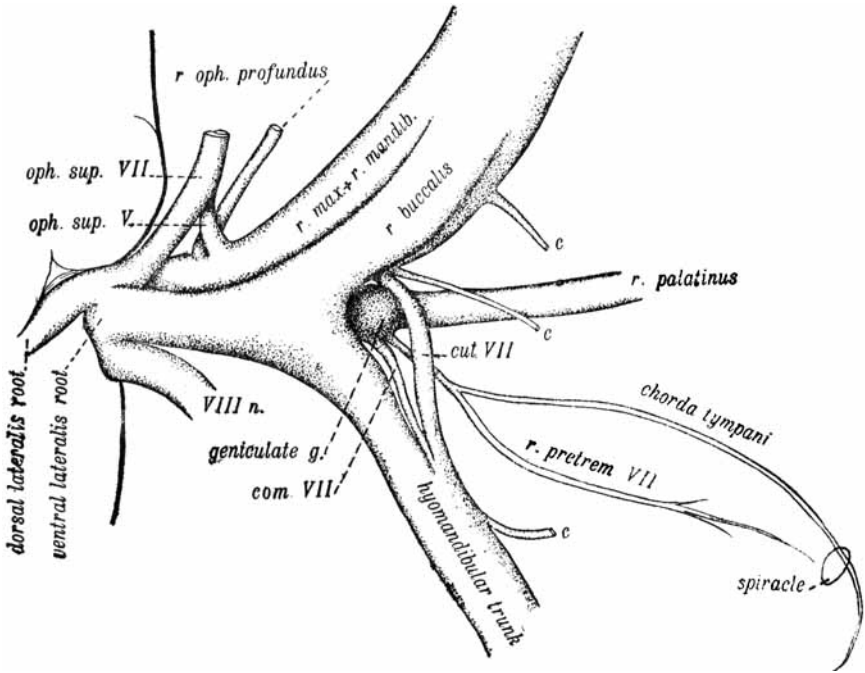


Fig. 3. Dissection of the trigemino-facial roots of the right side of the smooth dog shark, *Galeus canis*, seen from above. $\times 2$. *c, c, c*, general cutaneous twigs for the skin of the caudal border of the orbit. *com. VII*, communis fibers from the geniculate ganglion to the hyomandibular trunk. *cut. VII*, general cutaneous fibers from the trigeminus to enter the hyomandibular trunk, displaced outward during the dissection so as to expose the geniculate ganglion.

These relations correspond to those of *Squalus acanthias* save that we have not succeeded in following the nerve regarded as the chorda so far downward as to reach the ventral median line. Its proximal connections could not be made out, as the several ganglia of the $V + VII$ complex cannot be clearly separated by gross methods in *Carcharias*. Their origin from the base of the palatine, which is known to be a communis nerve, would, however, strongly indicate that they too are communis nerves.

In the smooth dog fish, *Mustelus canis*, the proximal relations are much clearer (Fig. 3). Here the acustico-lateral, general cutaneous and communis ganglia of the trigemino-facial complex can be quite sharply analyzed by simple dissection. The acustico-lateral system lies dorsally to the others so as to obscure the relations somewhat, but the figure shows the roots and ganglia in their normal relations save that the general cutaneous branch, *cut. VII*, for the hyomandibular trunk has been displaced laterally to expose the geniculate, or communis ganglion of the facialis. The pre-trematic ramus and chorda tympani are seen to arise together from this ganglion independently of the palatine ramus. *Mustelus*, it will be recalled, lacks a spiracular pseudobranch, but the pre-trematic ramus, after giving off several twigs for the mucosa of the anterior wall of the spiracle, terminates in the exact region where it would be if it were present. The chorda curves around the anterior wall of the spiracle to the point of divarication of hyoid and mandibular arches just as in *Carcharis*.

It will also be noted in this dissection that the geniculate ganglion clearly sends a branch backward into the hyomandibular trunk, showing that here, as in *Squalus acanthias*, this nerve contains visceral sensory fibers in addition to the lateralis and motor components, while the branch, *cut. VII*, referred to above, seems to carry general cutaneous fibers from the Gasserian ganglion into it also. Whether the geniculate ganglion contributes to the maxillary or mandibular rami of the trigeminus could not be determined.

The spiracular nerves of the common skate, *Raja erinacea*, and of *Torpedo ocellata*, were also examined, but in these cases the nerves corresponding to what we have termed the chorda were less perfectly developed than in the other species and they could not be traced far down toward the ventral surface.

It is obvious that the facialis of fishes departs from the typical arrangement of branchial nerves by reason of the loss or reduction of the hemibranchs primitively innervated by its post- and pre-trematic branches. The post-trematic, or hyo-

mandibular ramus receives the typical motor and communis roots and in addition secondary accessions from the acustico-lateralis and general cutaneous systems. Its gill has disappeared completely, but the arch has been enlarged and accordingly the nerve runs far out onto the hyoidean apparatus, some of its branches also extending still farther to the tip of the mandible. This last applies also to its cenogenetic additions, notably the lateralis component. The anterior hemibranch of the facialis segment is either absent or greatly reduced. In either case its nerve persists in a vestigial condition. The pharyngeal branch is present and of typical composition, but enlarged, so as to extend far cephalad of its segment into the anterior part of the mouth cavity as the r. palatinus. Between the pre-trematic and palatine nerves another has been interpolated in the facial segment, which runs forward between the hyoid and mandibular arches. It may be extended out upon the mandible in the lower vertebrates, but in the higher it is extended out upon the hyoid and in forms which possess a fleshy tongue it joins the lingual branch of the trigeminus to innervate this organ, thus forming the chorda tympani. The motive for the forward extension of all of these facial branches is the same; viz. the forward growth of the facial skeleton in gnathostomes and the necessity for the innervation of the sense organs about the mouth from the post-oral segments. The evolution of a chorda tympani is only one incident in this progressive specialization of the oral region.

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