THE ANATOMICAL RECORD

Vol. II.

SEPTEMBER, 1908

No. 6

A Note on the Presence or Absence of the Glosso-Pharyngeal Nerve in Myxinoids*

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In the course of studies on the morphology of the head in vertebrates I have been much interested in the interpretation of the vagus. The explanation of this as a collection of several true branchial nerves (Johnston, 1905) required some special modification to fit the case of the myxinoids, in which according to earlier writers the IX and X nerves are united. This condition was met by supposing that the process of collecting the branchial nerves, as it proceeded from behind forward, went a step further in myxinoids than it has in gnathostomes, and so carried the whole series of (IX and X) branchial nerves into a single complex.

This view has always seemed to me somewhat strained, but the facts necessary for a more natural explanation were not available until later. The facts referred to concern the disappearance of gills in the cephalic part of the series. This, indeed, was referred to in my paper on the morphology of the head (1905, p. 191), but the meager account by Price (1896) did not lead me to see its bearing on the question of the IX nerve, especially since Price expressed the opinion that as many as twenty-three or twenty-four gills had disappeared.

My remarks on the disappearance of gills in *Bdellostoma* have been seriously criticised by Stockard (1906, p. 487), who says: "Price, working with a limited supply of material, made the mistake of supposing that a great number of gill pouches appear during development, possibly

*Neurological Studies, University of Minnesota, No. 7.

as many as thirty-five. Of these, he thought the posterior ten or fourteen develop into the gills of the adult, while the others entirely disappear. Dean corrected this statement when he found a shifting and not a closing of the gills to take place; and Price, in a subsequent paper on the development of the excretory organs of *Bdellostoma*, based on a more complete series of embryos, has corrected his former statement and accepted Dean's interpretation on this point. Notwithstanding these corrections, Price's original idea has since been utilized by Ayers and Jackson, '00, who try to account for the atrophy of the forward gills as due to the enormous development of the 'club-muscle' in that area. Johnston, '05, also quotes Price's earlier conclusion and states his belief that there is a reduction of the anterior gills on account of the parasitic life of this animal. It has been clearly shown, however, by Howes, '91; Ayers, '93; Jordan and Everman, '96, and Worthington, '05, that these animals are not parasitic but predaceous, attacking disabled fishes. Therefore Johnston's explanation will not suffice. Since, also, there are no forward gills lost, we must accept the position that the gills belonged originally to the head region, and owe their extension into the trunk to the shifting forward of trunk myotomes into the occipital region, the view, by the way, which Johnston rejected in favor of his explanation cited above."

With regard to this criticism it may be said, first, that it is by no means clear that Stockard is warranted in invoking the shifting of myotomes to explain the shifting of gills in myxinoids. Because shifting forward of trunk myotomes into the head has been observed in gnathostomes, and because this affects the relative position of gills and other organs, it does not follow that this will explain the position of gills in myxinoids. In gnathostomes the shifting forward of trunk myotomes is largely due to the abortion of head myotomes, due in turn to the formation of a rigid cranium. In myxinoids this cause for shifting forward of trunk myotomes is not present. Until we have positive evidence on this point, we may assume that in myxinoids, as in *Petromyzon* (Neal, 1897; Koltzoff, 1902), all the cranial myotomes remain throughout life. The postotic myotomes probably reach forward as in *Petromyzon* above and below the orbit into the wall of the buccal funnel, and on this account there may be some shifting forward of trunk myotomes. But that the shifting due to this could possibly account for the adult position of the gills in *Bdellostoma*, no one can be asked to believe. The shifting backward of gills with refer-

ence to myotomes and spinal nerves amounts to something like fourteen trunk segments and a long prebranchial pharynx is formed between the mouth and gills. Yet there is no shoving together or telescoping in the postotic region such as occurs in gnathostomes, no fusion of vertebræ with the skull, no abortion of postotic myotomes. Neither is there any shifting or loss of dorsal nerve roots such as occurs in gnathostomes (Worthington, 1905a, for *Bdellostoma*; compare for *Petromyzon*, Johnston, 1905a). There is a translocation backward of the gills in relation to the myotomes, nerves, etc., without any shortening, crowding or telescoping of the latter structures. Indeed, when Stockard comes to describe the shifting of the gills (p. 510) he says nothing of shifting of myotomes, but describes a region of great growth between the second thyroidean gill (third gill behind the mouth) and the following ones. This great growth affects both dorsal musculature and pharynx. The growth of the dorsal part of the neck carries the head forward around the egg and the growth of the pharynx leaves a space between the third and following gills. In this space ventrally the large club muscle develops, and Stockard admits it as a factor in causing the translocation of the gills. The shifting of the gills, then, is due to a great growth and extension of the neck which, in Stockard's phrase, "leaves the gills behind" in the trunk. In brief, what Stockard's account of the development shows is that during the ontogeny there occurs a translocation of parts to bring about an adult condition the two main features of which are the position of the gills far back in the body and the presence of the large club muscle in front of the gills. These features, I assume, are adaptations to the mode of life of the animal. The club muscle serves to move the "tongue" in rasping off the flesh of fishes, the gills being placed far back enables the animal to bury its head in a fish and still breathe while eating. In my paper which Stockard criticises I was covering an enormously wide field and making every possible effort to be brief. On that account I attempted to express the above explanation of the position of the gills by referring to the "parasitic life of the animal." The explanation still seems to me wholly just. The use of the word "parasitic" was a slip of the pen, as I was well aware of the habits of these animals. The morphological considerations are in no way affected by substituting the word "predaceous," since it is quite as necessary for a *Bdellostoma* to breathe while he is eating a "disabled" fish as if he were dining daily at the expense of a permanent host.

Second, Stockard's statement, "since, also, there are no forward gills lost," is inconsistent with his description (p. 498-504) of the growth, reduction and disappearance of the hyomandibular and two post-hyomandibular or thyroidean gills. His concluding paragraph on this point reads: "The three following gills, hyomandibular and the two thyroidean, undergo a distinct retrogressive development; in the young embryo they are the most advanced elements of the entire gill series; they then gradually degenerate and in late stages become entirely lost."

Stockard's excellent work, confirming and supplementing Dean's study of entire embryos, makes clear, therefore, that *Bdellostoma stouti* has sixteen gills behind the mouth, that the cephalic three of these disappear and that the caudal thirteen are carried back into the trunk region. It has been shown by Ayers (1894) and by Worthington (1905) that the number of gills varies in different species of *Bdellostoma* between seven and thirteen or fourteen. Miss Worthington has brought out two further important facts with regard to the Californian species, the same as studied by Stockard. In this species the number of gills varies between individuals, and also the rudimentary or missing gills sometimes occur at the cephalic end of the series. From all of which it would appear that Price was wrong chiefly in the large number of gills which he thought disappeared from the cephalic end of the series. That I followed Price's earlier paper was due to the facts that my 1905 paper was sent to the publisher on October 25, 1904, while Price's second paper was not published until December, 1904. While my paper was awaiting publication I was in Europe, where the American Journal of Anatomy was not to be seen.

Since the hyomandibular and two following gills disappear in *Bdellostoma* it might be expected that their nerves would be greatly reduced or absent. Miss Worthington's (1905a) description of the facial nerve would seem to support this view, since she described the nerve as composed of motor fibers to the muscles of the hyoid arch and of communis components distributed to the skin of the region of the fourth tentacle. We may suppose that these communis fibers supply taste buds. Sensory fibers to the wall of the pharynx are not mentioned.

The main purpose of this note is to point out that the loss of the post-hyomandibular gills has probably resulted in the reduction or disappearance of the IX nerve. If so, the supposition previously made that the process of collecting branchial nerves had gone on forward in the myxinooids until the vagus had joined the glossopharyngeus would be superfluous.

Fürbringer (1897, p. 624) argues that the ramus pharyngeus of the vagus contains the representative of the glossopharyngeus. J. Müller had considered this as the IX nerve and, so far as I know, it is generally so treated.

Miss Worthington (1905a) gives the fullest description of the origin, course and distribution of this nerve that I have seen. In *Bdellostoma Dombeyi* Loc. it arises by several mixed roots which are the most cephalic of the IX-X series. It passes out of the cranium through a foramen in common with X, undergoes interchange of fibers with X outside the cranium, is bound up in the same sheath with X until it reaches a point opposite the second permanent gill arch, then separates and innervates "the side of the pharynx near the end of the backward position of the second branchial arch." Since two post-hyomandibular gills have disappeared (Miss Worthington and Stockard both worked on the Californian species) the above description shows that the nerve innervates the side of the pharynx three branchial segments caudal to the area of distribution of the post-trematic ramus of the IX nerve in gnathostomes or petromyzonts. This, taken in connection with its intimate relation with the X nerve in its origin and course, can lead to only one plausible conclusion, namely, that this nerve in the Californian species is in reality only a pharyngeal ramus of the X nerve.

The descriptions by Fürbringer seem to show a different condition in some other species. The nerve in question may separate from the X nerve at or soon after its exit from the foramen. In *Bdellostoma bischoffi* this ramus innervates the greater part of the pre-branchial pharynx and reaches nearly to the first gill sac. In *Bdellostoma stouti* this ramus extends over only the first half or two-thirds of the pre-branchial pharynx. Since Fürbringer's *B. stouti* is in all probability the same species as Miss Worthington used, Fürbringer seems to have described a ramus not seen by Miss Worthington. Fürbringer concludes: ". . . , bin ich geneigt, den Ram. pharyngeus Vagi als einen Nerven anzusehen, dessen Grundstock dem N. glossopharyngeus der höheren Wirbelthiere entspricht, dem sich aber auch eine mässige Anzahl von Vaguszweigen einstmals branchialer Natur angeschlossen hat."

After the disappearance of the two post-hyomandibular gills the only visceral structures requiring innervation in the territory of the glossopharyngeus and first division of the vagus are the muscles and mucosa of the slender pre-branchial pharynx. An objection to Fürbringer's

conclusion is that one can scarcely see any reason for the union of the rudimentary IX nerve with the X, when at an early stage of development the persistent gills are carried so far apart from the gill of the glossopharyngeal segment, which aborts *in situ*. We should rather expect the IX and X nerves to diverge widely and to maintain their distinct foramina.

Since two gill sacs following the hyomandibular have aborted, the first branchial division of the vagus must be reduced as well as the glossopharyngeus. Therefore, of the "IX-X complex" in myxinoids, the first two segmental units are necessarily very small if not absent. It is very evident from its course and innervation territory that the nerve described by Miss Worthington has no resemblance to a true N. glossopharyngeus. Unless she has overlooked a separate nerve, I am of the opinion that the glossopharyngeus is absent in the animals studied. In the forms described by Fürbringer from dissections we cannot come to a definite conclusion until we have histological and embryological studies, including the tracing of nerve components. In particular it is very desirable to know the facts regarding cutaneous components which are present in both the facialis and glossopharyngeus in petromyzonts (Johnston, 1905a). The most probable view at present is that the pharyngeal ramus in question represents part of the first or second division of the vagus. The visceral sensory component may represent the r. pharyngeus of X1 and possibly X2. The motor component may be the remnant of the post-trematic ramus of X1. The reasons for this may be summarized as follows:

1. The reduction of both IX and X1.
2. The improbability of union of IX and X owing to shifting of the gills.
3. The close union of the pharyngeal ramus in question with the X nerve.
4. The numerous instances in which one nerve has taken over the innervation territory of another; trigeminus, r. palatinus VII, etc.

The bearing of this on the supposition that a gill arch has been lost in the gnathostomes must not be overlooked. I have shown elsewhere (1905) that the arguments formerly made in favor of a lost gill fall to the ground when the question is considered from the standpoint of the nerve relations. Now that it has been clearly shown that gill slits are lost in myxinoids between the mouth and the persistent gills, this fact may be taken by some to support the hypothesis that a gill has been lost

in gnathostomes. But the fact that two gills abort in myxinoids is not in itself good evidence that any do so in gnathostomes. The abortion of the forward gills and shifting back of others in myxinoids finds a natural explanation in the habits of the animals. As pointed out above, the most simple and direct conclusion to be drawn from this is that the loss of the gills has been followed by the loss of the IX nerve as well. In all gnathostomes, however, the IX nerve is present. The conditions in myxinoids are, therefore, peculiar and do not lend support to the view that a gill has been lost in the middle of the series in gnathostomes.

It should, of course, be understood that by placing the terms myxinoids and gnathostomes in contrast I do not mean to express any opinion regarding the relations of these groups. I have always regarded the cyclostomes as primitive forms and am in thorough sympathy with the modern view, which compares the so-called tongue with the lower jaw of gnathostomes. On the other hand, although primitive, the cyclostomes do not stand in the direct line of evolution of gnathostomes, and the loss of gills at the cephalic end of the series and of part or all of the IX and first division of the X nerve may prove to be among their most striking peculiarities.

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