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THE RANK OF NECTURUS AMONG THE TAILED AMPHIBIANS AS INDICATED BY THE DISTRIBUTION OF ITS CRANIAL NERVES.

BY H. W. NORRIS.

That "the Proteidae constitute the most primitive of the Urodeles" (Holmes, 1906) is generally accepted as an established fact. But here and there one finds dissenting opinions from this particular view. Kingsbury (1905) has given some very instructive and suggestive comparisons, chiefly of skeletal features, between Necturus and typical Urodela showing that Necturus and the larval stages of Spelerpes have so many characters in common that the similarities must stand for some degree of close relationship. His conclusions are expressed as follows: "I believe that the characters in the cranium of Necturus that are discussed here are those that are also characteristic of the larvae of many tailed Amphibia, especially of certain forms (family Plethodontidae), and that the acceptance of Necturus as a permanent larva best explains at present these features." Moodie (1908a) in his studies on the lateral line system of the extinct Amphibia cites Kingsbury as evidence in these words: "Kingsbury has expressed it as his opinion that Necturus is a primitive form." It is difficult to reconcile this statement with the above quotation from Kingsbury. Moodie draws his own conclusions as to the zoological position of Necturus from the arrangement of the lateral line organs on the tail. According to him Necturus is the only modern amphibian in which the median and dorsal lateral lines of the trunk extend to the extreme tip of the tail, in this respect resembling certain of the Stegocephali. In view of our meager knowledge of the distribution of the lateral line organs on the trunk of modern amphibians the writer does not feel justified in criticising this opinion of Moodie. It may be noted here incidentally that Moodie (1908b) considers the tailed amphibians as the degenerate descendants of the Branchiosauria.

Druner (1904) cites Boas (to whose paper the writer has not had access) to this effect: "dass Siren, Menobranchus (Necturus) und Proteus Larvenformen seien, welche von Caducibranchiaten Urodelen abstammen, die einst eine Umwandlungen besassen and erst spater zum

ausschliesslichen Wasserleben zuruckkehrten." Druner says farther: "Die Perennibranchiaten sind eben Larvenformen ebenso wie die Larvenformen der Salamandriden und Siredon, welche in der Phylogenie des Urodelenstammes niemals realitat besessen haben."

Recently Gaupp (1911) in reference to the reduction of the primordial cranium in Necturus says: "Als 'primitiv' wird man dieses Verhalten wohl nicht bezeichnen konnen."

Miss Emerson (1905) from her studies on Typhlomolge concludes that the latter, which was placed by Stejneger (1895) among the Proteidae with Proteus and Necturus, "should be classed with Spelerpes in the family Salamandridae and the subfamily Plethodontinae." She believes that there are fundamental differences between Typhlomolge and the Proteidae in just those respects in which the former resembles Spelerpes, and that to place Necturus and Proteus in the same family with Spelerpes is untenable. Wilder in a foot-note to the paper by Miss Emerson expresses the opinion that Necturus and Proteus cannot be placed among the Plethodontidae "since all the members of this family are, so far as is known, lungless, a condition which allows Typhlomolge to be included within this family, but seems to exclude the others."

Cope (1889) derived the tailed amphibians from the Stegocephali by way of the Proteidae, considering the Cryptobranchidae as next higher in rank.

The writer, in collaboration with Miss Buckley, in tracing the origin and distribution of the cranial nerves in Necturus was soon convinced that the resemblances to the conditions in Spelerpes bilineatus as described by Miss Bowers (1900) were far from superficial, and that they signified a much closer relationship than has been suspected hitherto. Basing sweeping changes in classification upon a single system of the body is a dangerous procedure, but the nervous system is very conservative and whatever evidence it offers must be taken into consideration. The following comparisons between the cranial nerves of Necturus and Spelerpes are based upon personal investigations in both species, the paper of Miss Bowers being found defective in its omissions and errors.

Lee (1893) has shown that in Spelerpes fuscus the olfactory glomeruli are in two groups, an anterior ventral and a posterior dorsal, not sharply separated from each other. A similar arrangement occurs in S. bilineatus and in Necturus. Horizontal sections through the olfactory lobes of the adult Necturus show that the olfactory nerve arises

by two distinct roots corresponding to the arrangement of the glomeruli, but that the fibers so combine that all indications of their origin are lost in the long nerve trunk. Similarly in Spelerpes it is impossible to distinguish between the anterior and posterior groups of fibers in their destination. The absence of a Jacobson's organ in Necturus makes an important difference between the olfactory nerve of that form and that of Spelerpes, in which there is a special branch to the structure in question. Were the absence of a Jacobson's organ in the Proteidae, although information on this point is lacking for Typhlomolge, to be considered a larval character, there would still remain to be explained the occurence of a well developed Jacobson's organ in the perennibranch Siren.

In Spelerpes and Necturus the gasserian ganglion is distinct from the auditory and ventral facial ganglia, in marked contrast to the condition in Amphiuma and Siren. Tracing out the three rami mandibularis, ophthalmicus profundus and maxillaris to their branches there will be seen very close resemblances in the two forms. The r. md. gives off first large motor branches to the temporal and masseter muscles, then a large general cutaneous branch to the side of the head. The main nerve continues along the side of the jaw giving off three to five principal branches to the skin. A general cutaneous branch enters a canal in the lower jaw from the dorsal side and in Spelerpes fuses with a branch of the r. alveolaris VII; in Necturus the actual union with the latter nerve was not found but the two come into very close association. A branch of motor and general cutaneous composition passes ventrally through the lower jaw and is distributed to the intermandibular muscle and the overlying skin. In neither Necturus nor Spelerpes does there seem to be any anastomosing between this latter branch and the r. jugularis VII such as occurs in Amblystoma (Coghill, 1902) and Plethodon (Norris, 1909). The r. oph. prof. in both species divides into four main branches. Of these the first given off runs dorsally at the inner posterior border of the eyeball. In Spelerpes it is much larger and arises farther posteriorly. Its more posterior position in the latter form may be explained by the fact of the much larger size of the eyeball. In Spelerpes the trochlear nerve passes to its innervation along a twig of this dorsal branch of the r. oph. prof. An almost exactly similar course seems to occur in Necturus. The three terminal branches of the r. oph. prof. have almost identical modes of origin and distribution in the two species. In neither form was the exact nature of the ophthalmic-palatine anastomosis determined, owing to the nerves at this point being compressed. The ana-

stomosis in both cases seem to be different from that in Amblystoma, Amphiuma and Siren, and much like that described by Coghill (1906) in Triton. The r. max. in both Necturus and Spelerpes leaves the gasserian ganglion as a distinct nerve but almost immediately joins the r. buccalis VII. The two show little if any actual fusion, but run parallel to each other antero-ventrally around the ventro-lateral border of the eyeball, the r. maxillaris on the inner border of the r. buc. At the transverse level of the anterior portion of the eyeball the r. max. is given off in a number of branches, while the r. buc. passes anteriorly to the tip of the snout. This origin and distribution of the infra-orbital trunk is almost identical with that in Amblystoma, and doubtless is characteristic of the Salamandridae. In Necturus a general cutaneous component enters the r. ophthalmicus superficialis VII from the gasserian ganglion. The writer finds no such component in Spelerpes, although it evidently occurs in the closely related genus, Plethodon (Norris, 1909).

Kingsbury (1895) describes the "dorsal VII" as arising from the brain by two rootlets in Necturus. In larvae of Necturus 35 mm. in length the writer finds three rootlets of this nerve, the dorsal of which is very small and almost amyelinic. Similarly in the larvae of Spelerpes there are three rootlets on the dorsal VII, the most dorsal of which is extremely small and barely discernible. In Amphiuma and Siren a similar condition is found, but the dorsal rootlet is much better developed. The general distribution of the lateral line component of the seventh nerve is almost identical in the two species. The ramus palatinus VII is relatively larger in Spelerpes. The ophthalmic-palatine anastomosis has already been mentioned. A definite Jacobson's commissure from the r. pharyngeus IX to the r. palatinus occurs in both species only to the extent mentioned by Druner, that is, twigs from the r. pharyngeus anastomose with twigs from the r. palatinus. This is much like the condition in Amblystoma, only more difuse. In both Necturus and Spelerpes the r. alveolaris VII receives a communis component from the ramus communicans IX-X and VII, in this respect resembling Amblystoma, and differing from Amphiuma and Siren. In Spelerpes the r. alveolaris after reaching the vicinity of the angle of the jaw divides sending a branch into a canal in the jaw (Miss Bowers to the contrary), which branch unites farther anteriorly with a branch of the r. md. V already described. In Necturus the alveolaris does not enter a canal in the jaw, but does come into close relations with a branch of the r. md. V which itself enters a canal in the jaw. In both Necturus and Spelerpes owing to the early separation of the r. jugu-

laris a truncus hyomandibularis can hardly be said to occur. In Necturus the r. jugularis passes out exteriorly dorsal to the squamoso-columellar ligament and the dorso-lateral border of the cephalo-mandibular portion of the depressor mandibular muscle. In Spelerpes the r. jugularis passes out through the cephalo-mandibular portion of the dep. md. muscle and ventral to the above-mentioned ligament. In other respects the ramus has the same course and distribution in the two species

It is in the branchial nerves that we may look for some of the greatest differences between the larval and adult nervous system of any urodele amphibian. On the other hand we find between the IX-X nerve complex of a Necturus larva of 35 mm. length and of an adult scarcely any appreciable differences. At both periods the resemblances to the larval Spelerpes are as striking as in the other cranial nerves. The ramus communicans according to Miss Bowers contains general cutaneous fibers only. In fact it has a communis component also. As the ramus approaches the r. jugularis VII it divides, the general cutaneous part joining the latter ramus and the communis portion passing into the r. alveolaris VII. In Spelerpes the r. communicans, r. pharyngeus IX and r. posttrematicus IX leave the ganglion as a common trunk; in Necturus the r. posttrematicus arises separately. In both species the r. pharyngeus sends a r. pretrematicus along the hyoid arch. In Necturus the r. supratemporalis X, lateral line, leaves the ganglion along with the motor nerve to the levator muscle of the first branchial arch. In Spelerpes the latter nerve is given off from the r. posttrematicus IX. In both species the r. auricularis X is distinct from the r. supratemporalis X, with no such anastomosing as occurs in Amphiuma and Siren. There are, however, some differences in the composition of the main divisions of the nerve in the two forms, the r. auricularis of Spelerpes having apparently almost identical arrangement with that of Amblystoma. The r. posttrematicus IX in both species sends an anastomosis of general cutaneous and motor fibers to the second branchial nerve. In both Necturus and Spelerpes the second branchial nerve (vagus 1) is well developed with characteristic pharyngeal, pre-and posttrematic rami having the usual innervation. Branches of general cutaneous and motor composition supply the levator and depressor muscles of the first and second gills and the overlying skin. In each the branch supplying the depressor and levator muscles of the first gill receives the anastomosis from the first branchial nerve already mentioned. The third branchial nerve (vagus 2) has undergone much reduction. In Necturus it arises close to and is almost a part of the

second branchial nerve. It forms a small pharyngeal-pretrematic branch, a posttrematic branch of communis fibers only, while the main portion of the nerve after receiving an anastomosis from the second branchial supplies the levator and depressor muscles of the third gill. In Spelerpes the nerve is much more rudimentary. It arises as in Necturus close to the second branchial nerve, but it is so small that its exact distribution was not determined. The levator and depressor muscles of the third gill are supplied by a branch of the second branchial, the one which in Necturus anastomoses with the third branchial. The three branchial nerves in Necturus are seen to have essentially the same arrangement and anastomoses as in Amblystoma. Spelerpes differs only to the extent that the third branchial nerve has undergone a greater reduction. The rami laterales X and the ramus intestino-accessorius X have the characteristic arrangement and branching as seen in urodeles in general.

In respect to the formation of the hypoglossal nerve Necturus and Spelerpes show important differences. In Necturus the two anterior spinal nerves are devoid of ganglia and the hypoglossal nerve is formed by the fusion of ventral branches of these two spinal nerves, with apparently a contributory twig from the third spinal nerve. In Spelerpes the second spinal nerve possesses a ganglion, and the hypoglossal nerve is formed chiefly, if not entirely, from the first spinal nerve.

On considering the cranial nerves of Necturus in their entirety, and comparing them with the corresponding structures in other Urodela that have been studied, we see that their characteristics are not primitive but of a rather highly specialized order. Both as larva and adult Necturus resembles in its nerve arrangement the larval stages of Amblystoma and particularly of Spelerpes, rather than the more generalized and we may say more primitive type found in the perennibranch Siren and the derotreme Amphiuma. In some respects the Plethodont type of the Salamandrids is the least primitive. Only three branchial arches develop in the larval stage. Necturus in possessing but three branchial arches shows a very distinct resemblance to the Plethodont form.

There are some strong objections to considering Necturus as a larval Plethodont. Necturus lacks a Jacobson's organ; its r. alveolaris VII does not enter a canal in the lower jaw; its r. jugularis VII passes out dorsal rather than ventral to the squamoso-columellar ligament; its second spinal nerve possesses no ganglion. Then, too, the presence of lungs is another objection of great weight.

But whatever may be the true relationship of Necturus a study of its cranial nerves does not lead one to consider it a primitive urodele. The characters of its cranial nerves are those that are characteristic, with a

few exceptions, of the cranial nerves of the larvae of plethodont forms. In the words of Kingsbury: "The acceptance of Necturus as a permanent larva best explains at present these features."

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