SPECIAL ARTICLES.

A FOOTNOTE TO THE ANCESTRAL HISTORY OF THE VERTEBRATE BRAIN.

THE existence of a pair of newly recognized ganglionated nerves, attached to the fore-brain of that ancient group of fishes—the Selachians—is, perhaps, of sufficient general interest to justify a brief mention in SCIENCE.

In recent numbers of the *Anatomischer Anzeiger* (Vol. XXVI., Nos. 2/3 and 4/5) the writer has described and illustrated the morphology of such nerves in twenty genera, and twenty-seven species, of selachians, and their embryonic history in one. Similar nerves have also been pointed out by Allis, Pinkus and Sewertzoff in two of the Dipnoi (*Protopterus* and *Ceratodus*), and one ganoid (*Amia*). So far as observations go these nerves are absent in all other vertebrates. The facts now made known, although in one sense merely anatomical details, may, nevertheless, be looked on as constituting a footnote to the great chapter in morphological science dealing with the structure and development of the vertebrate brain.

The fore-brain is extremely modified in structure, and so little understood that it is desirable to gain any new facts bearing on its organization. So far, comparative anatomy and embryology combined have supplied only fragmentary views as to its nature, the number of segments that may enter into it (or, indeed, whether it is segmented at all), and as to its line of development. Although the solution of these matters is likely to take many more generations, yet, in the meantime, details of structure hitherto unknown may help, be it ever so little, in the anatomical analysis of that region of the brain.

The new nerves referred to above exist in adult stages of selachians. They are, on the one hand, connected with the fore-brain and, on the other, with the olfactory epithelium. They arise earlier in embryonic history than the olfactory nerves, appearing on the anterior summit of the fore-brain near the neuropore. Peripherally they intermingle with the olfactory fibers, but, at all stages of their existence, they are entirely independent of those fibers, and they never come into relation with glomeruli as the olfactory fibers always do.

As to their surface connections with the brain wall, they exhibit two types: those having a dorsal or semidorsal attachment to the brain-wall, and those having a ventral attachment. It is, however, to be borne in mind that the superficial attachment of a nerve is of small significance in determining its position, as in the case of the fourth nerve, which

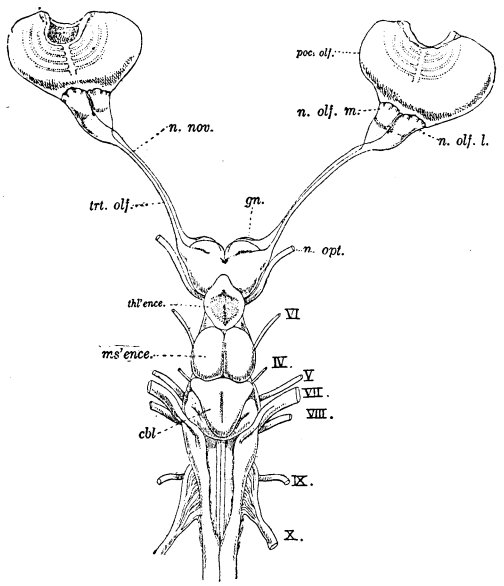

FIG. 1. Brain of *Squatina angelus*, from above, natural size.

emerges from the dorsal surface of the mid-brain, while its neuroblasts lie in the ventral zone.

As an illustration of the first type, reference may be made to Figs. 1 and 2 showing, respectively, the brain of the angel-fish (*Squatina angelus*) and that of the spiny dog-fish (*Squalus acanthias*), one of our commonest selachians.

In Fig. 1 the new nerve (*n. nov.*) is seen attached by two roots to the dorsal surface of the prosencephalon, and, bearing just in front of the brain, a filiform ganglion (*gn.*). From this point it runs like a delicate thread along the olfactory tract, and dips into a fissure separating the two great divisions of

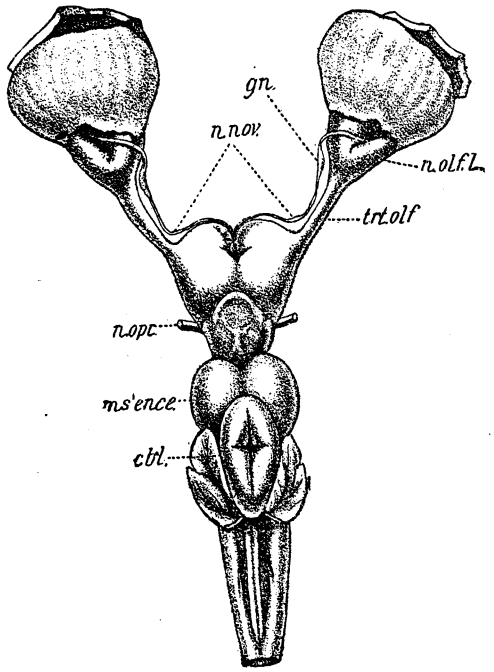

FIG. 2. Brain of adult *Squalus acanthias*, from above, natural size.

the olfactory nerve. Thereafter it branches and passes to portions of the nasal epithelium.

In *Squalus acanthias*, Fig. 2, the central ends of the nerve are located within the median furrow of the fore-brain, and its ganglion (*gn.*) is near the base of the olfactory bulb.

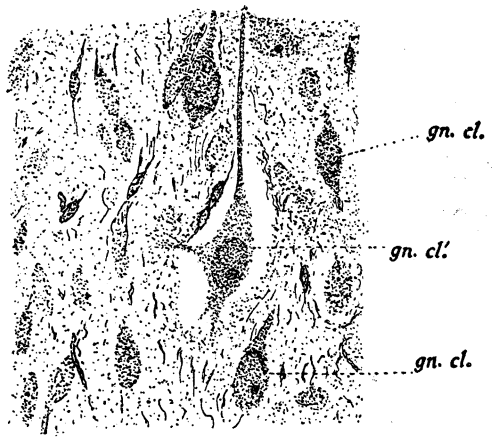

FIG. 3. Section of the ganglion of the new nerve of *Squalus acanthias*, × oc. 2, obj. 2/3 in.

The microscopic structure of the ganglion, shown in Fig. 3, resembles that of a spinal ganglion. It is surrounded by a covering of connective tissue from which supporting strands pass into the interior of the ganglion. The ganglion-cells are arranged in clusters and layers between the nerve fibers and connective tissue elements. The nerve-cells are for the most part bipolar (*gn. cl.*), but a limited number of other ganglion cells (*gn. cl.'*), with angular outlines and several processes leading from them, may also be seen, which suggest the presence of multipolar cells.

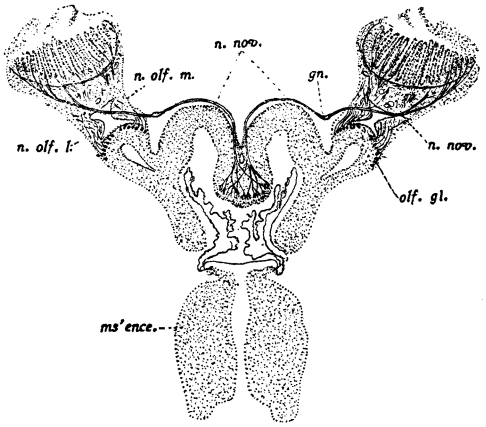

FIG. 4. Partly diagrammatic figure of a horizontal section of the brain of *Squalus acanthias* six inches long. Showing portion of the central and peripheral endings of the new nerve.

The central terminations and peripheral distribution of the new nerve are shown in Fig. 4. This is partly diagrammatic, being based on a section in the horizontal plane of the brain of a *Squalus acanthias* about six inches long. Centrally, the nerve fibers enter the brain substance, and after much branching are distributed mainly within an eminence upon a median infolding of the pallium. This eminence is supposed to correspond to that designated '*eminentia septalis*' by von Kupffer in the amphibian brain.

The study of serial sections shows that the fibers of the chief branches of the nerve are distributed, peripherally, to the olfactory membrane, in the antero-lateral portion of the olfactory cup. There are also some smaller

branches passing to the median portion of the cup. While the terminal twigs mingle intimately with the olfactory fibers, they retain

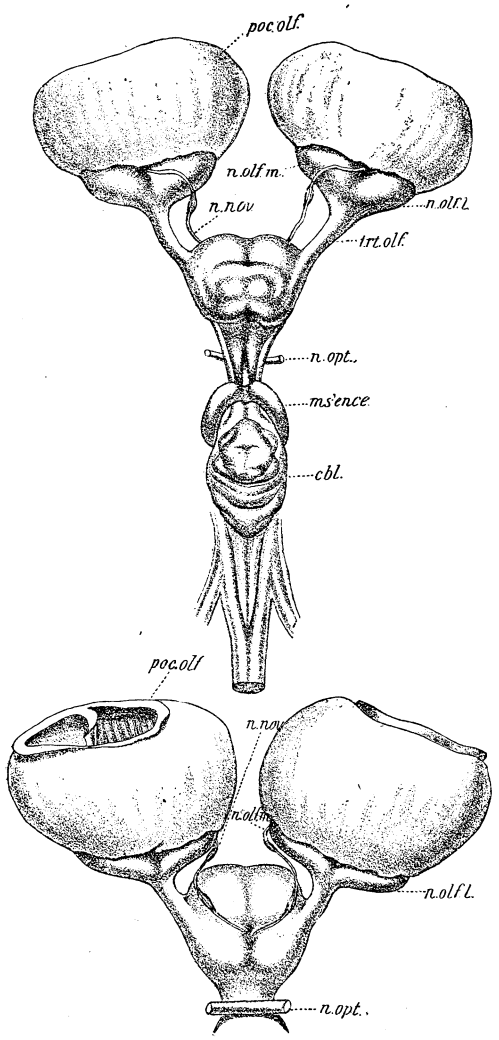

Fig. 5. Brain of adult *Mustelus canis*, from above, and portion of the same from below, both natural size.

their independence and do not anastomose with them.

The dorsal attachment of the nerve to the brain has been determined in eleven genera, and sets aside the idea that it is usually, or normally, connected with the ventral surface, as has been suggested on account of its ventral position in *Amia, Ceratodus* and *Protopterus*.

As an illustration of the other type, having a ventral attachment with the brain, we may take the brain of the common smooth hound (*Mustelus canis*) of the Atlantic coast, which is shown in Fig. 5. Here, the nerve emerges from (or enters) the brain substance on the ventral surface, about midway between the anterior border of the prosencephalon and the optic chiasma. It is interesting to note that, in embryonic development, it first arises upon the dorsal part of the primary fore-brain and is carried to its ventral position through the unequal growth of the brain-wall. The nerve penetrates the brain substance, and, after branching, terminates in the same region as in the brain of *Squalus acanthias*.

As shown in the figure, the nerve has two ganglia—a distal and a proximal one—as is the case with the ninth nerve. The peripheral distribution of the fibers is similar to that in *Squalus acanthias*.

A few comments in reference to this nerve may not be out of place. The only similar nerve known outside the group of selachians is in *Amia, Protopterus* and *Ceratodus*. In the two former genera no ganglion was observed by either Allis or Pinkus, but Sewertzoff, in 1902, noted a ganglion on this nerve in embryonic stages of *Ceratodus*. The ventral position of the nerve, close to the *recessus præopticus* in the three forms mentioned, led Sewertzoff to propose for it the name of '*Nervus præopticus*,' but its dorsal position in so many selachians would make that name inappropriate. Earlier (1899) I had suggested in a tentative way the name '*accessory olfactory*,' which is also objectional, as it prejudices the question of its function. Since this nerve arises on the morphological tip of the primary fore-brain, and during some stage of its existence is closely connected with the *lamina terminalis*, I think the designation '*Nervus terminalis*' will fit all cases and will be a suitable name for it.

Both its anatomy and embryology, as given in my paper in the *Anatomischer Anzeiger*, bring out its marked individuality and separateness from other cranial nerves. This would justify calling it a 'new nerve' and, therefore, giving it a new name.

In the selachians, its close association with the main olfactory and its distribution within the olfactory cup, might give ground for the suggestion that it is a radix mesialis of the olfactory nerve. This, however, appears to me not well founded, since the nerve has no connection, at any time of its growth, with olfactory glomeruli. Even if it be one of the olfactory bundles in an unusual position, its method of origin, and difference from all other olfactory radices would still justify the use of the designation 'new nerve.'

It is a relatively simple ganglionated nerve that has apparently undergone little modification. This, in itself, is a very notable circumstance, on account of its position on the brain in a region of extreme modification. Since it has remained in a relatively archaic condition, we may conclude that its function has not been greatly elaborated. It may have been largely supplanted by the development of the olfactory, or some of the branches of the trigeminus.

When all circumstances of its structure and development are taken into account, it seems to me not unlikely that we have here the remnant of a very ancient nerve, whose original function is unknown, which in the process of development has been reduced to secondary rank, through the prodigious development of adjacent nerves and brain territories.

It has been shown that this nerve precedes the olfactory in embryonic origin, but the assumption would not be justified on this account, that it is, therefore, older in phylogenetic history, though such may be the case.

Its development in so many adult selachians would indicate that it is still functional, though reduced to a subsidiary rank.

Its ganglion will throw it among sensory nerves.

But, while it has a sensory moiety, some considerations indicate that possibly it has also a motor moiety. It has two roots, and in the skate, both medullated and non-medullated fibers have been observed in it.

It will be extremely difficult to determine its physiological properties by experimentation. Its minuteness will render any manipulation or experimental study difficult without giving injury to the olfactory.

It is doubtful if any trace of it be preserved in higher vertebrates. Whatever its original function may have been, it was in some way superseded in the evolution of animal life, and having first lost its importance, it thereafter disappeared. I have looked with especial care for it in a number of amphibians and teleosts, and in the chick. Both embryonic and adult stages have been examined in *Necturus, Amblystoma,* the frog, the toad, the trout, the catfish and the chick, but in none of them has the nerve been found.

From any point of view, it is extremely interesting that we have preserved so fully in selachians and Dipnoi a ganglionated nerve in front of the optic, bearing in its anatomy testimony as to its ancient features, but of which all traces have disappeared in higher animals.

NOTE.—Since the above was sent to the printer the 'Nervus terminalis' has been observed in two rare selachians of ancient type —*Chlamydoselachus* and *Mitsukurina.* Professor Burt G. Wilder noted its occurrence in the former, photographed it, and, subsequently, sent me a portion of the brain embracing the nerve. In *Chlamydoselachus* it is similar in position and anatomical features to the nerve in *Hexanchus.* It is connected with the forebrain, within the median furrow, and upon the terma about midway between the dorsal and ventral surfaces. It runs directly to the olfactory cup. Near the base of the cup it has an enlargement which, upon microscopic examination, proved to contain ganglion-cells. As in *Hexanchus,* the main branch of the nerve joins the median instead of the lateral division of the olfactory fibers.

Professor Wilder also generously sent for my examination the anterior portion of the brain of *Mitsukurina.* In that rare and costly form the nerve is connected with the ventral surface of the brain by two roots. It has a very distinct ganglion lying on the olfactory crus near the base of the bulbus.

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