V.—*The Lateral Sense Organs of Elasmobranchs. I. The Sensory Canals of Læmargus.* By J. C. EWART, M.D., Regius Professor of Natural History, University of Edinburgh. (Plates I. and II.)

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INTRODUCTORY.

Some years ago, when studying the electrical organs of the torpedo, I was forced to the conclusion that the nerves supplying the batteries had not been accurately described, and that notwithstanding the statements in the most recent works, the first electric nerve is not derived from the trigeminus. Finding some difficulty in making out the arrangement of the cranial nerves in the greatly specialised torpedo, I directed my attention, first to the skate, and later to certain sharks, more especially to the Greenland shark (*Læmargus*). I had not proceeded far before I was convinced that we had still much to learn as to the anatomy of the cranial nerves of both the higher and lower vertebrates.

Up to a certain point I made satisfactory progress, and early in March 1889 was in a position to communicate to the Royal Society a preliminary paper “On the Cranial Nerves of Elasmobranch Fishes” (1); and, in the following year, papers on the cranial nerves of the torpedo (2) and on the development of the ciliary ganglion (3). When, however, I endeavoured to interpret my results, more especially when I endeavoured to compare the cranial nerves in Selachians with those of the higher vertebrates, innumerable difficulties presented themselves. After full consideration, there seemed only two possible lines along which further progress was possible. The one was to study anew the development of the cranial nerves in two or more vertebrate groups; the other to make a special study of the innervation of the more important organs peculiar to fishes.

Many able investigators having already directed their attention to the development of the nervous system, without, it must be confessed, arriving at any very generally accepted conclusions, I ventured to think that, with the help of the embryological facts already established, I would best succeed by trusting mainly to the old methods of the comparative anatomist. I believed that, by a careful study of the conditions in the adult Selachians, certain morphological questions would be settled, and that a new base of operations might be opened up for the embryologist. Hence, instead of publishing the views I entertained as to the relation of, *e.g.*, the complex facial of the Selachian, with its comparatively simple homologue in the higher vertebrates, I decided to first thoroughly work up the lateral sense organs—structures which reach a remarkable development in fishes, but are entirely absent in the higher vertebrates. In this way I hoped to determine which of the many large and well-marked nerves of the fish we should expect to find absent in Sauropsida and Mammalia.

This plan necessitated the delay of any lengthened discussion of the cranial nerves, and the breaking up of the work into a number of more or less independent investigations. Now that the work has advanced towards completion, I am satisfied that the best plan was adopted. When I originally discovered four ganglia in connection with the facial in the fish, I was inclined to believe that I ought to find their counterparts in other vertebrates, and at once set about preparing schemes with a view to establishing their relationships. By a roundabout process, however, I now know that there is no necessity, in many cases, to look in the adult higher vertebrates for even the vestiges of some of the nerves largely developed in fishes.

As the optic and olfactory nerves dwindle or disappear when their related organs are in a vestigial condition or absent, so some of the ancestral ganglia and nerves have disappeared as their organs (only useful for an aquatic life) have degenerated. Prepared for the complete absence of various nerves the work has been simplified, and time saved which might have been wasted in making impossible comparisons. Now that the whole ground has been roughly worked over, I propose, first, to describe the lateral sense organs in several fishes, paying special regard to their innervation. This done, I shall describe fully the cranial nerves in two or more members of the Elasmobranch group; and, finally, complete the work by making a comparative study of the cranial nerves of the more important divisions of the vertebrata.

THE LATERAL SENSE ORGANS.

I. HISTORICAL.

In Elasmobranchs, the lateral sense organs consist of two distinct systems of canals, and, in addition, of minute pit organs or follicles. Hitherto, the two kinds of canals have usually been known as mucous canals; but as they differ in structure and arrangement, and, perhaps, also in function, distinctive names are obviously necessary. The canals of the one system open on the surface of the skin by numerous usually short and simple tubules; and they further, in some cases, give off long branches, also provided with tubules. The canals of the other system radiate from a given number of centres in the head region; and each canal presents an expansion (ampulla) at its proximal end, and opens on the surface of the skin by its distal end. These radiating canals, however, though often running a considerable distance side by side, never communicate with each other; nor do they give off tubules or branches.

The canals with tubules, which include the canal of the lateral line and a number of canals in the head region, I have, for various reasons, decided to speak of as the Sensory Canals. They are not only characterised by their tubules and branches, but also, and very specially, by the presence of numerous sense organs—structures which are present when the tubules are absent, and when grooves or furrows take the place of the canals. The canals without tubules and branches I shall invariably refer to as Ampullary Canals,

chiefly because they are especially characterised by the ampullæ at their proximal ends—the ampullæ of LORENZINI.

In Læmargus, according to the nomenclature I have adopted, there are three main canals in the head region and one in the trunk—the cranial canals having over four hundred sense organs, and a nearly corresponding number of tubules. The ampullary canals, though numbering over one thousand, will be found to radiate from four centres, all situated in the head region. Having indicated the main features of the two canals, and the names by which they will be described, I need only further say, before referring to the history of the subject, that sensory follicles have not yet been found in Læmargus.

The first observations relating to the lateral sense organs of fishes seem to have been made by STENONIS, who, in 1664, described certain openings in the skin of the skate for the discharge of mucus (4); and, in 1669, discovered similar openings in a shark (5). About ten years later (1678), LORENZINI (6) not only found the openings described by STENONIS, but made the important discovery that the openings belonged to two kinds of canals (the sensory and ampullary canals mentioned above), and especially noted the expansion (ampulla) at the proximal end of each of the simple (ampullary) canals.

Since the time of LORENZINI, many anatomists and zoologists have studied the “mucous” canals of fishes; but LORENZINI’s discovery that the canals were of two kinds has been too often overlooked; and it was not until 1813 that it was first suggested these canals played any other part than that of secreting and distributing mucus over the surface of the skin; and not until 1868 that their right, from a morphological point of view, to be considered sensory structures was finally established.

Very little progress was made in working out the structure of the lateral sense organs from the time of LORENZINI to that of MONRO *secundus*, who, in the latter half of the eighteenth century, worked at “The Structure and Physiology of Fishes” (7). MONRO especially directed his attention to the “mucous” canals of the skate, and he made out (what seems to have escaped the notice of LORENZINI) that large nerves proceeded to the gland-like masses (groups of ampullæ) formed by the inner ends of what I have termed the ampullary canals. There is no evidence, however, that MONRO was acquainted with LORENZINI’s work or that he recognised the difference between the branched (sensory) and simple (ampullary) canals, or specially observed the ampullæ of LORENZINI; and though he traced large nerves to the central masses, he apparently considered the canals as mere mucus-producing structures. He describes them as “very elegant structures for the preparation of mucus for keeping moist the surface of the skin.” Nevertheless, MONRO’s noting that large nerves reached the central masses (the groups of ampullæ) may have helped JACOBSON, in 1813, to arrive at the conclusion that the mucous canals of sharks and rays were sensory organs (8).

During the first half of the present century, the lateral sense organs attracted the attention of several investigators besides JACOBSON, more especially ST HILAIRE, TREVIRANUS, DE BLAINVILLE, DELLA CHIAJE, SAVI, MAYER, and ROBIN. The central

masses (groups of ampullæ) which JACOBSON considered sense organs, ST HILAIRE (1801) described as electric organs (9), and this extraordinary mistake was also made by MAYER (10) (1843), JOBERT DE LAMBALLE (11) (1858), and M'DONNELL (12) (1861). As early as 1822, BLAINVILLE (13) pointed out ST HILAIRE's mistake; and ROBIN (14) and several others have confirmed the observations of BLAINVILLE, as to the correctness of which there can no longer be any doubt, notwithstanding M'DONNELL's statements to the contrary. Unfortunately, Mr DARWIN refers to M'DONNELL's observations, and remarks, in the *Origin of Species* (p. 150, 6th edition):—"In the Ray there is an organ near the head, not known to be electrical, but which appears to be the real homologue of the electric battery of the Torpedo." M'DONNELL's homologue of the torpedo's battery, which exists in sharks, as well as rays, will be afterwards described as the hyoid group of ampullæ.

TREVIRANUS (15), who was one of the first to describe the central masses (ampullary groups) in sharks, considered them as sensory structures. SAVI (16), ROBIN, and others, followed JACOBSON and TREVIRANUS; while DELLA CHIAJE (17), probably unacquainted with JACOBSON's work, like MONRO, considered the mucous canals as simply concerned in the secretion of mucus.

But little real progress was made until LEYDIG and H. MÜLLER directed their attention to the subject. LEYDIG's first paper appeared in 1850 (18); but it was not until 1868 that he published a full account of his observations. LEYDIG's monograph (*Ueber Organe eines sechsten Sinnes*) is by far the most important work that has hitherto been published on the lateral sense organs of fishes (19). The author points out that, from the morphologist's standpoint, not only the mucous canals—the sensory and ampullary canals—but also the peculiar little follicles found in the torpedo by SAVI, are all sensory organs. They were together regarded by LEYDIG as the organs of a sixth sense.

H. MÜLLER, like LEYDIG, considered the follicles of SAVI, as well as the two forms of mucous canals (sensory and ampullary), as concerned in sensation rather than in secretion. His observations (20) were published seventeen years before the important memoir by LEYDIG. KÖLLIKER (21) and MAX SCHULTZE (22), prior to 1868, had pointed out the existence of sensory cells in the follicles of SAVI.

Since 1868, amongst others who have worked at the lateral sense organs of fishes, may be mentioned BOLL, GOETTE, SEMPER, BALFOUR, SAPPEY, BEARD, GARMAN, ALLIS, and FRITSCH. BOLL (23) refers especially to the structure of the ampullæ and their canals. GOETTE (24), SEMPER (25), BALFOUR (26), and BEARD'S (27) work relates chiefly to the development of the canals and their nerves; while SAPPEY'S (28) work is, in a manner, an extension of the investigations of MONRO. GARMAN (29), who studied the canals chiefly with a view to ascertaining their value in classification, shortly describes and figures their arrangement in a large number of sharks and rays; while ALLIS (30) gives an able and exhaustive account of the lateral line system in *Amia*. FRITSCH (31 and 32) deals with the canal system in the *Selachia* as a whole, and also describes shortly the lateral sense organs of the torpedo, and peculiar little follicles (*spalt-papillen*) which he

discovered in the skate. Notwithstanding what has already been done, there does not yet exist a complete and systematic account of the lateral sense organs of a single Elasmobranch. As pointed out by various writers, the general anatomy of the canals has been strangely neglected. When studying the sensory canals of Selachians, we have still to fall back on the very meagre account of these structures given by MONRO, or the more elaborate, but in many respects unsatisfactory, work of SAPPEY.

II. DEVELOPMENT AND GENERAL ANATOMY.

Recent work on the origin and development of the nervous system of vertebrates has necessitated, more than ever, a full account of the structure and general distribution of the sensory canals in both sharks and rays, and especially of an accurate description of their innervation.

Now that the origin and distribution of the cranial nerves—more especially of the trigeminal and facial—are better understood, and that the sensory canals have been shown to be at the outset intimately related to certain cranial ganglia, we are in a position to study their anatomy with the prospect of obtaining more valuable results than was possible even a few years ago.

Although both systems of canals have reached a remarkable development in many fishes, and sensory canals or furrows with well-developed sense organs exist in nearly all fishes, it has not yet been possible to determine the function of either the sensory or ampullary canals. Not only is the use of the lateral sense organs still a mystery, but also very little is known as to their development in Elasmobranchs. From what is known, it appears to me that, in describing the canals, special attention should be given to their innervation. According to BEARD (27), an epiblastic thickening is found in young embryo Selachians over each visceral cleft. Towards this thickening the dorsal root of a cranial nerve grows outwards from the neural crest, reaching and blending with it on a level with the notochord. Where the fusion takes place, the cells proliferate and give rise to the rudiment of a cranial ganglion, and, more superficially, to the rudiment of a lateral (branchial) sense organ. After a time, a separation takes place; and, eventually, the deeper group of cells gives rise to a ganglion, while the superficial gives rise to the sense organ. A connection between the ganglion and the sense organ is maintained by a nerve (the dorsal or supra-branchial nerve), which is split off from the under surface of the epiblastic thickening as development proceeds. Though, by division and growth in different directions, the original simple sense organ may become complex, the dorsal nerve and its branches maintain a connection between the sense organs and their related ganglion.

Taking these and other observations into consideration, together with what has recently been made out as to the innervation of the sensory canals in Læmargus and Raia, it appears that, while the lateral canal of the trunk in Elasmobranchs has been formed in connection with a backward growth of the lateralis division of the vagus, the

principal cranial canals have been formed in connection with three extensions of the facial—two forwards and one outwards. One of these divisions of the facial (the ophthalmicus superficialis) has grown forwards above the eyeball, another (the buccal) has grown forwards under the eyeball, and the third (the hyomandibular) outwards and forwards behind the spiracle. The three canals in relation with these nerves should have a corresponding position; one should run forwards above the eyeball, one curve downwards and forwards below the eyeball, and a third should lie behind the spiracle.

If we turn to *Læmargus* we first of all notice, all over the head, but especially above and below the snout, a large number (over 1500) of small but perfectly distinct pores. The majority of the pores have the margin slightly projecting and deeply pigmented. Without much difficulty it becomes evident that some of the pores serve as openings for ampullary canals; while others lead by short tubules into sensory canals. If the arrangement of the openings of the sensory tubules is studied, or if the canals from which the tubules spring are exposed, it will be found that, as expected, one canal extends above, while a second lies below the eyeball. The first, which is related to the ophthalmicus superficialis nerve, may be known as the supra-orbital canal (S.O., figs. 1 and 2). The second, which is related to the buccal nerve, may be known as the infra-orbital (I.O., figs. 1 and 2). But although the canals of the ophthalmic and buccal divisions of the facial are easily recognised in *Læmargus*, there is some difficulty in distinguishing the canal related to the hyomandibular division. This canal, though not at first evident in *Læmargus* and other Selachians, is easily distinguished in the ganoid *Amia*. By referring to figure 3 (Pl. II.), a canal (H.M.) as complete and distinct as the infra-orbital (I.O.) will be seen beginning on the same level as the infra-orbital, and extending downwards and forwards along the mandible. This canal is supplied throughout its entire length by the hyomandibular division of the facial, and it has the same relation to the hyomandibular as the infra-orbital canal has to the buccal division of the facial.

I propose to call this canal the hyomandibular canal. ALLIS (30) describes it as the operculo-mandibular; but this name could not well be used for either sharks or rays, in which, though the lower part of the canal is usually more or less complete, the proximal part is never, so far as I know, present.

In the remarkable fish *Chlamydoselachus* (33), the mandibular portion (O.), as shown in figure 4, is complete, and, in addition, there is an extension forwards (*ang.*) to join the infra-orbital and another backwards (*j.*) over the operculum, which bifurcates near its margin, one division running upwards and forwards (*sp.*, fig. 5), the other downwards and forwards (*g.*, fig. 4), to join the mandibular portion.

In *Læmargus*, the lower (mandibular) as well as the upper part of the hyomandibular canal is absent; and the only representative of the long canal of *Amia* is a short horizontal canal (H.M., fig. 1, Pl. I.) which runs backwards from the infra-orbital, external to a well-marked fold of skin at the side of the mouth.

That this short canal belongs to the hyomandibular and not to the infra-orbital,

is clearly indicated by its being innervated by the hyomandibular branch of the facial.

In addition to these three main cranial canals and the lateral canal of the trunk, there are in Læmargus only two other canals:—(1) a canal (*l.c.*, fig. 1, Pl. I.) which lies behind the auditory pores and serves to connect the canal systems of the two sides (as this commissural canal is innervated by the lateralis nerve, it will be considered as part of the lateral canal); (2) a short canal (*o.t.*, fig. 1, Pl. I.) continuous with the lateral canal, which seems to form its most anterior portion, but as it is innervated by the buccal branch of the facial nerve, it will be looked upon as belonging to the infra-orbital canal. It thus appears that in Læmargus all the sensory canals are supplied by two nerves—the vagus and facial, or to be more explicit, by the lateralis division of the vagus and the ophthalmic, buccal, and hyomandibular divisions of the facial; and hence we might speak of the ophthalmic, buccal, hyomandibular, and lateral sensory canals.

Hitherto in Selachians, the sensory (mucous) canals have been studied *per se*, with the result that an extremely complicated nomenclature has arisen. For example, GARMAN (29), who refers shortly to Læmargus under the name of *Somniosus carcharias*, indicates the presence of fourteen cranial canals. In doing this he follows the system of AGASSIZ and most other writers, and practically takes no heed of the relation of the canals to the cranial nerves, as has been recently done to a considerable extent by ALLIS in his description of *Amia*. From the statement of GARMAN, in his introductory chapter, that the canals on “the head are innervated mainly from the fifth pair,” it may be inferred that he has not directed his attention specially to the nerve-supply of the canals; the fifth, as I have already indicated, taking no part in innervating the canals. To admit of the old and complex nomenclature being compared with the simpler one I propose to use, I have reproduced GARMAN’s figures of Læmargus (*Somniosus*—woodcuts A and B), and will indicate, as I proceed, which of his canals correspond to the cranial canals I have already mentioned, viz., the supra- and infra-orbital and hyomandibular canals.

In referring to the development of the lateral sense organs, it was mentioned that while the superficial portion of each epidermic thickening gives rise to the rudiment of a branchial sense organ, the deep portion assists in forming a cranial ganglion. According to BEARD (27), there should be in a typical Selachian seven dorsal (supra-branchial) nerves, and a corresponding number of sense organs—*i.e.*, (1 and 2) an ophthalmicus profundus and an ophthalmicus superficialis of trigeminus in connection with sense organs over the snout; (3 and 4) an ophthalmicus superficialis of facial in connection with the supra-orbital, and a ramus buccalis of facial in connection with the infra-orbital sense organs; (5 and 6) the glossopharyngeus and anterior vagus branches in connection with the supra-temporal sense organs; and (7) the nervus lateralis of vagus with the organs of the lateral line. Whether this supposed typical arrangement obtains in embryo Selachians remains to be seen; but I have not found that BEARD’s scheme holds for either fully developed sharks or rays, and according to ALLIS it does not hold in the case of *Amia*. In *Amia*, ALLIS states that “the trigeminal and ophthalmicus profundus take no part with

any of their branches in the innervation of the canals or pit organs," and that "there is a large and important operculo-mandibular line of organs," in the innervation of which none of the supra-branchial branches given in BEARD's scheme take any part (30).

These statements as to *Amia* apply also to *Læmargus*, and the only essential difference in the innervation of the canals in the two, in many respects, diverse forms, is that in *Læmargus* I have not succeeded in finding a branch from the glossopharyngeal nerve to any of the sense organs.

In view of the statement that the embryonic epidermic thickening assists in forming a cranial ganglion as well as a branchial sense organ, it is worth specially noting that each of the four nerves which sends branches to the sensory canals, *i.e.*, the ophthalmicus superficialis, buccal, and hyomandibular divisions of the facial, and the lateralis division of the vagus, presents some distance from its origin a well-marked ganglionic swelling crowded with large nerve cells. In the skate these ganglia are relatively as large as or larger than the ganglia on the profundus, trigeminal, and glossopharyngeal nerves—nerves which in adult sharks and rays have not yet been found in connection with lateral sense organs. It is further worthy of note that the buccal and superficial ophthalmic ganglia are sometimes in contact with each other by their proximal ends. From this it might be inferred that there has been a splitting of the original epidermic thickening above the spiracular cleft, the splitting resulting not only in the formation of two ganglia, but also of two sensory canals—the supra-orbital above, and the infra-orbital below, the eyeball.

III. THE SENSORY CANALS OF *LÆMARGUS*.

The position of the four main canals already mentioned is indicated by their names. The supra-orbital canal (S.O., fig. 1, Pl. I.) begins some distance in front of the auditory pores and extends forwards towards the tip of the snout, which it perforates, and then runs backwards to unite with the infra-orbital as it bends inwards towards the middle line.

The infra-orbital (less the accessory otic portion; I.O., fig. 1), beginning in connection with the supra-orbital, runs outwards behind the eyeball, and then forwards between the eyeball and the mouth, and after communicating with the supra-orbital it bends inwards and forwards towards the tip of the snout.

The hyomandibular (H.M., fig. 1), communicating in front with the infra-orbital, runs backwards in a nearly horizontal direction.

The laterals (L., fig. 1) continuous in front with the otic portions of the infra-orbitals, after communicating with each other behind the auditory pores, run almost directly backwards, one at each side of the trunk, until on a level with the posterior margin of the lower lobe of the caudal fin, when they bend upwards to terminate on the upper lobe of the fin, one at each side of the terminal portion of the vertebral column.

1. *The Supra-orbital Canal.*—This, the canal of the superficialis ophthalmicus-

division of the facial, represents the cranial (*cr.*), rostral (*r.*), and subrostral (*sr.*) canals of GARMAN (figs. A and B). GARMAN figures and describes the cranial (first portion of the supra-orbital) as beginning in front of, and distinct from, the orbital (*orb.*, fig. A), *i.e.*, the first portion of infra-orbital. This view I was at first prepared to accept; but on cutting into the canals, I found that they not only communicate with each other, but open to the exterior by a common pore.

The course of the supra-orbital canal will be best understood by a reference to figure 1 (Pl. I.). Beginning 3.25 cm.* in front of the auditory pore, and 1 cm. from the middle line, it first bends outwards and forwards, and then forms a wide open curve (S.O.¹), within which lie the openings of numerous ampullary canals.

On approaching the region of the nasal capsule, the canal runs inwards and then forwards to perforate the snout, about $2\frac{1}{2}$ cm. from the middle line, and 1 cm. behind its anterior margin. Turning sharply backwards, it runs outwards, and then returns to the dorsal aspect (S.O.³), arching over the nasal capsule to again reach the ventral surface; where, after curving first inwards and then outwards, it terminates (S.O.⁴) by communicating with the infra-orbital canal (I.O.²).

The supra-orbital canal has, throughout the greater part of its length, a diameter of from 3 to 4 mm.; but the first 3 or 4 cm., and the portion which curves over the nasal capsule, are only from $2\frac{1}{2}$ to 3 mm. in diameter. The walls of the canal are from 1 to $1\frac{1}{2}$ mm. in thickness. The canal not only varies in diameter, but also in its relation to the skin. Some parts lie in contact with the skin; while others lie embedded, some distance from the surface, in the subcutaneous tissue. Usually, the portions in contact with the skin have a smaller calibre than the portions lying deeper. Beginning in contact with the skin, the canal, when about 3 cm. from its origin, sinks to a distance of 4 mm. When on a level with the nasal capsule, it lies 6 mm. from the surface; and the

* The measurements refer throughout the paper to a fish that had a total length of 11 feet.

depth rapidly increases as it runs forwards to perforate the snout. The ventral portion lies at an average depth of 5 mm.; but the part in front of the snout is deeper, while the part over the nasal capsule is immediately under, or actually embedded in, the skin. The supra-orbital canal contains numerous sense organs, and is perforated by two rows of pores or apertures, an inner row for the nerves which reach and end in the sensory hillocks, and an outer row of larger apertures, which lead into the tubules by which the canal communicates with the exterior. The sense organs and tubules are shown on the right side of figure 1.

Eighty-three tubules, and a corresponding number of sense organs, were found in the supra-orbital canal of the specimen examined. Each organ received a delicate branch of the ophthalmicus superficialis nerve, the nerves entering by the minute pores nearly opposite the inner ends of the tubules.

The length of the tubules varies almost constantly with the distance of the canal from the surface. Some of them are under 2 mm. in length, while others are nearly 1 cm. The majority of the tubules run obliquely outwards; but a number proceed from the outer surface of the canal directly through the skin. The openings of the tubules are from 1 to 1.5 mm. in diameter; and the outer 2 or 3 mm. are distinctly pigmented. The openings of the tubules are readily distinguished from the openings of the ampullary canals. They are more regular in their arrangement than the openings of the ampullary canals, and the margins are usually more deeply pigmented.

By comparing the supra-orbital canal of *Læmargus* with that of *Chlamydoselachus* (*cr.*, *r.*, *sr.*, figs. 4 and 5), it will be noticed that it differs in several respects. Not only is it not in a line with the lateral canal as is the case in *Chlamydoselachus*, but it neither directly nor indirectly communicates with this canal; and, further, unlike all the ordinary Selachians, it returns to the dorsal surface of the snout as it proceeds backwards to join the infra-orbital. This return to the dorsal surface seems to be due to the nasal opening occupying a more outlying position than is usually the case. Posteriorly, the two supra-orbitals bend inwards towards each other, and thus approach the arrangement in the *Holocephala*, in which the connection between the canals of the two sides is accomplished by the union of the supra-orbitals instead of the union of the laterals behind the auditory pores.

Innervation of the Supra-orbital Canal.—The nerve (the superficial ophthalmic of facial (*s.o.f.*, fig. 1) of the supra-orbital canal gives off branches as it runs forwards over the eyeball to the first (cranial) part of the canal. On reaching the nasal capsule, it sends a branch downwards and outwards (*s.o.f.*², fig. 1) to supply the sense organs of the ventral part of the canal; and, then, as it passes forwards towards the end of the snout, it gives off twigs for the sense organs in the part of the canal in front of the nasal capsule. A more detailed account of the innervation of this and the other canals will be included in a paper, in course of preparation, on the cranial nerves of *Læmargus*.

2. *The Infra-orbital Canal.*—This canal (I.O.—I.O.⁵, fig. 1), as already mentioned, communicates at its origin with the supra-orbital. From the common opening it runs out-

wards nearly at right angles to the long axis of the head, and passes downwards behind the orbit. Having reached the ventral aspect, it communicates with the hyomandibular canal (H.M., fig. 1), and then bends forwards and inwards to meet and communicate with the supra-orbital canal (S.O.⁴, fig. 1), as it turns sharply inwards towards the middle line.

On the way it forms a characteristic forward projecting loop (I.O.³, fig. 1). On reaching the middle line it blends, for a short distance, with the corresponding canal of the opposite side (I.O.⁴, fig. 1). Leaving its fellow it runs outwards and forwards to sink well into the substance of the snout, and terminate blindly about 6 mm. from its anterior margin, and $1\frac{1}{2}$ cm. from the middle line (I.O.⁵, fig. 1). This canal corresponds to the orbital (*orb.*), suborbital (*so.*), orbito-nasal (*o.n.*), nasal (*n.*), median (half of) (*m.*), and prenasal (*pn.*), canals of GARMAN (figs. A and B).

In diameter the infra-orbital resembles the supra-orbital. Narrow at first, it gradually widens until it reaches the side of the head, where it contracts slightly, to again expand as it reaches the under surface. With the exception of the median and terminal portions, the ventral part of the canal has a diameter of from 3 to 4 mm.

The median portion is from 5 to 6 mm. wide, while the terminal portion varies from 2 to 3 mm. The canal, at first in contact with the skin, soon sinks to a depth of 5 mm., but on reaching the level of the spiracle it again approaches the surface and remains all but in contact with the skin until it joins the hyomandibular. Between this canal and the supra-orbital, it lies at a depth of nearly 5 mm.; but as it bends inwards it becomes more superficial, lying at a depth of 3 mm. until it reaches the under surface of the rostrum, where it sinks to a depth of 5 or 6 mm., and finally, at its termination, to a depth of 1 cm.

Eighty-seven twigs from the buccal nerve were found penetrating this canal to reach and end in a corresponding number of sense organs. Of these nerves there were 24 in the first part of the canal (orbital and suborbital), 11 in the second (orbito-nasal), 23 in the third (nasal), 3 in the common median part, and 26 in the terminal (prenasal) part. The nerve pores varied considerably in their arrangement; near each other at first, they became less numerous in the descending part of the canal, after which they were fairly regular with the exception of the anterior (prenasal) part, in which they were especially abundant. The distribution of the fibres of the buccal to the nerve hillocks is indicated on the right side of figure 1.

This canal opens through the skin by tubules similar to those of the supra-orbital. Altogether 86 tubules were counted, and, as a rule, they proceeded from the canal opposite the pores for the entrance of the nerves. The majority of the tubules varied in length with the distance of the canal from the surface; the dorsal tubules extended backwards; the majority of the ventral directly outwards; but those from the terminal portion of the canal projected outwards and forwards. The irregular ventral part of the infra-orbital canal comes into intimate relation with numerous ampullary canals; the openings of some of which are with difficulty distinguished from the openings of the tubules.

The infra-orbital canal has a simpler course than in most Selachians, and the absence of the suborbital loop, found, for example, in *Acanthias*, is especially noteworthy.

ALLIS considers the infra-orbital canal of *Amia* as the main canal of the cranial system. He describes it as being "directly continuous with the lateral canal," *i.e.*, as extending in *Amia* to the posterior boundary of the cranium (21, fig. 3, Pl. II.)—some distance beyond the "supra-temporal cross commissure" (*lc.*, fig. 3).

The infra-orbital canal of ALLIS is thus something more than the canal of the buccal nerve, for it receives branches from the glossopharyngeal and vagus nerves; and this being the case, it must presumably have originated from parts of three branchial sense organs. It seems to me most desirable in dealing with the canals, to be guided as far as possible by their innervation. Hitherto the canal of the lateral line has been usually described as terminating at the anterior end of the trunk, *i.e.*, as not extending into the head region; but, seeing that the lateral canal is supplied throughout by a cranial nerve, I fail to see why it may not be considered as extending into the head region. If it is right to consider the supra-orbital canal as co-extensive with branches of the ophthalmicus superficialis nerve, and the hyomandibular with branches of the hyomandibular nerve, in other words, to consider the whole of the canals, or portions of canals, developed in connection with any given nerve as forming one system, it is only logical to look upon the whole of the canal or canals innervated by the lateralis nerve as forming one system, and to consider the infra-orbital canal as coming to an end at the point where it ceases to be supplied by the buccal nerve. Following this plan in the case of *Amia*, I would describe the infra-orbital canal as beginning at the upper end of the hyomandibular canal (HM.¹, fig. 3), and extending forwards and then downwards under the eyeball, after communicating with the supra-orbital. If, as seems probable, the superficial ophthalmic and buccal nerves and their ganglia have resulted from the splitting of a single nerve, it might be more accurate, in the case of *Amia*, to consider the canal between the upper end of the hyomandibular canal and the point at which the supra- and infra-orbital canals separate from each other as a special (say otic) portion (*ot.*, fig. 3)—formed from an unsplit part of an embryonic sense organ—more especially as in *Amia* it is supplied by a nerve (*ot.n.*, fig. 3) which springs, according to ALLIS, directly from the facial ganglion.

The short portion (T., fig. 3) in *Amia*, between the upper end of the hyomandibular (operculo-mandibular of ALLIS) and the supra-temporal cross commissure (*lc.*, fig. 3), I would describe as the temporal canal or canal of the glossopharyngeal nerve; and the whole of the canal behind this, on to the end of the trunk, including the supra-temporal cross commissure, I would describe as the lateral canal—the canal of the lateralis nerve. If in the ancestral forms there was but a single cranial canal, as there is now only a single canal in the trunk, it is possible that the single ancestral cranial canal is now represented by the infra-orbital canal. This is a point, however, that may be made clear when the development of these canals is worked out. Assuming that the infra-orbital is the main canal of the head, as the lateral is the main canal of the trunk, the supra-orbital would require to be looked upon as a dorsal offshoot from the infra-orbital; and

the hyomandibular, either as a ventral offshoot or as an independent canal, developed from a branchial sense organ immediately behind the one in connection with which the infra-orbital canal originated.

The supra-orbital offshoot may have been developed as the eye increased in size; while the hyomandibular offshoot or canal is in all probability correlated to the mandible, and, when present, the operculum. It is, however, extremely probable that from the first the main canal of the head forked on reaching the orbit, and thus formed supra- and infra-orbital canals.

The accessory or proximal portion of the infra-orbital canal in Læmargus may be known as the otic part (*ot.*, fig. 1). Though continuous with the anterior part of the lateral canal, it is not continuous with the infra-orbital. It may be considered as representing that part of the canal system in *Amia* containing the sense organs numbered 15 and 16 (fig. 3), which are supplied by the otic branch of the facial nerve.

The otic canal in the specimen of Læmargus under consideration is 2.5 cm. in length. It begins 1 cm. behind and slightly further from the middle line than the common terminal pore of the supra- and infra-orbital canals. It then bends outwards and backwards, and on the way gradually sinks to a distance of 4 mm. from the surface, and becomes continuous with the cranial portion of the lateral canal.* The canal is penetrated by four branches of the otic nerve, and it opens to the surface by four tubules, the anterior tubule having a length of 3.5 mm., the others increasing in length from before backwards—the fourth measuring 7 mm.—the increase being partly due to the deeper position of the canal, and partly to the posterior tubules running obliquely outwards through the skin.

The part described as the otic canal I expected at first to find supplied by a dorsal branch of the glossopharyngeal nerve—a nerve which, even in *Amia*, takes part in innervating the lateral sense organs. Hitherto, however, I have failed to trace any branches from the glossopharyngeal to either sensory or ampullary canals in Læmargus. It is, however, possible that the most anterior portion of the lateral canal—the part immediately continuous with the otic—is supplied by fibres which spring from the glossopharyngeal nerve before it leaves the cranial cavity.

Innervation of the Infra-orbital Canal.—The otic portion is supplied by fibres which leave the buccal nerve immediately after it separates from the superficial ophthalmic. As the buccal passes outwards and forwards to run under the eyeball it gives off branches for the first portion of the infra-orbital canal proper. It then divides into two main branches, the inner of which supplies the sense organs of that part of the canal which runs inwards and forwards under the rostrum, while the outer division supplies the sense organs of the intermediate part of the canal.

3. *The Hyomandibular Canal.*—This canal (HM., fig. 1) which, as already explained, is only partially represented in Læmargus, consists of a canal about 10 cm. in length, which runs backwards and outwards from the infra-orbital canal. This part of

* This is supposing the glossopharyngeal nerve sends no branches to the sense organs.

the hyomandibular corresponds to the angular and jugular canals (*ang.* and *j.*, fig. A) of GARMAN. It lies immediately under the skin, and gradually diminishes in size from before backwards. It receives eighteen branches from the hyomandibular nerve, and communicates with the surface by eighteen tubules and a small terminal pore. The majority of the tubules run directly outwards, and are consequently extremely short; but a few which run obliquely inwards are slightly longer.

As already mentioned, the hyomandibular (operculo-mandibular) is more extensive in *Amia* than in *Læmargus*. Beginning on a level with the infra-orbital canal (HM.¹, fig. 3), it courses downwards and forwards to reach and extend along the entire length of the mandible (HM.², fig. 3). In the case of *Chlamydoselachus*, the lower or mandibular portion (oral of GARMAN) is complete; and there are, in addition, to use GARMAN's terms, angular (*ang.*), jugular (*j.*), spiracular (*sp.*), and gular (*g.*) portions (fig. 4).

In some sharks, the mandibulars are represented by a continuous commissural canal, in others by two short isolated canals; but in the skate, as will be described in a future paper, each hyomandibular gives off a long ventral loop, the outer limb of which reaches the dorsal surface, and runs backwards to terminate in an offshoot from the lateral canal.

Innervation of the Hyomandibular Canal.—The sense organs of the hyomandibular canal in *Læmargus* are supplied by branches of the hyomandibular nerve, which leave the main trunk in the region of the hyoid group of ampullæ.

4. *The Canal of the Lateral Line.*—This canal may be said to consist of three portions:—(1) the trunk portion, which, beginning on a level with the spiracle, extends backwards along the side of the body to end on a level with the terminal portion of the vertebral column; (2) a transverse portion (*lc.*, fig. 1), which runs inwards behind the auditory pore to form with a corresponding portion from the canal of the opposite side the temporal commissure; and (3) a short pre-commissural part (*lp.*, fig. 1) which runs forwards to join the otic portion of the infra-orbital. All the three parts (with the possible exception of the portion immediately behind the otic) are supplied by the *nervus lateralis*. The anterior or pre-commissural portion measured 1.25 cm. in length. It receives branches from the most anterior fibres of the *lateralis* nerve, and opens to the exterior by five tubules which curve outwards and backwards. This portion of the lateral corresponds to a part of the occipital canal of GARMAN (*oc.*, fig. A). Further investigations may show that one or more of its sense organs are, as in *Amia*, supplied by the glossopharyngeal nerve. The commissure (aural canals of GARMAN, *au.*, fig. B) connecting the two main lateral canals was 8 cm. in length. Running across from 3 to 4 mm. beneath the surface and about 6 mm. behind the auditory pores, it opens through the skin by sixteen short, delicate tubules, and its floor is perforated by sixteen pores for branches of the most anterior fasciculus of the *lateralis* nerve. It may be mentioned that in *Chlamydoselachus*, the temporal commissure lies in front of the auditory pores and has no tubules (fig. 5). This difference in the relation of the canal to the auditory pores is more apparent than real; for even in *Chlamydoselachus* the commissure lies behind

the vertical parts of the Fallopian canals; and its apparent altered position is due to these canals being continued some distance backwards under the skin, before opening to the exterior. In *Heptanchus*, the aural portions of the lateral canals do not unite to form a commissure; while in *Acanthias*, the commissure, instead of running right across, bends forwards a short distance between the auditory pores.

The main part of the lateral canal (L., fig. 1) begins on a level with the spiracle (*sp.*, fig. 1), and runs backwards in a nearly straight line until on a level with the posterior margin of the lower lobe of the caudal fin, when it bends downwards to reach the lower edge of the caudal muscles. It then runs obliquely upwards along the edge of the muscles to terminate on a level with the last segment of the vertebral column. Throughout its whole extent, the lateral canal is tubular, and thus differs from the arrangement in *Chlamydoselachus* and *Heptanchus*, in which the lateral canal is represented throughout the whole, or nearly the whole, length by a groove or furrow. Along its entire length, the lateral canal lies immediately beneath the skin, or partly embedded in its substance. The first part of the lateral canal behind the commissure resembles the supra- and infra-orbital canals; it has nearly the same form and diameter as the part of the canal in front of the commissure. But about 8 cm. beyond the commissure, the canal is reduced in size (in the greater part of the trunk to, on an average, 2.5 mm., and in the caudal region to about 2 mm. in breadth); and throughout it presents a somewhat flattened appearance. The tubules are more slender in the trunk than in the head, and the apertures are slightly smaller, and consequently less evident. The anterior tubules, owing to their running obliquely outwards through the skin, are nearly one centimetre in length; the remainder are slightly shorter—the length, in all cases, depending chiefly on the angle at which they traverse the skin. As in the cranial canals, the tubules are all quite simple.

Innervation of the Lateral Canal.—In the embryo Selachian, five sense organs are said to lie above the five branchial clefts; one above the cleft of the glossopharyngeal nerve, and four above the clefts of the four branchial divisions of the vagus. Hence, in a typical condition, we might expect to find, extending from the auditory region backwards, a canal innervated by five dorsal (supra-branchial) branches; one branch from the glossopharyngeal, and four branches from the vagus. If, however, we consider the condition in the adult, we find, *e.g.*, in the case of *Amia*, that while the glossopharyngeal nerve supplies one of the cranial sense organs, all the other (post-auditory) sense organs are innervated by the nervus lateralis of the vagus complex. In *Læmargus*, the glossopharyngeal nerve has the typical branches, and a well-marked ganglion; but I have failed to trace any of its fibres to the sense organs of the lateral canal. The four branchial divisions of the vagus are all well developed; they have in connection with them an extremely large ganglion; nevertheless, they take no part, as far as I can discover, in innervating any portion of the lateral canal.

In all the specimens of *Læmargus* examined, the lateralis division of the vagus has been the only nerve found passing to the lateral canal—the commissural and pre-commissural portions included.

It might be asserted that in the case of *Læmargus*, the sensory fibres of the five dorsal branches of the branchial divisions of the vagus have united together to form the lateralis nerve. A careful examination, however, of the lateralis seems to point to a different conclusion. The fibres which form the lateralis nerve spring from the side of the medulla nearly in a line with the middle roots of the facial nerve; and the anterior fibres lie in front of, and on a higher level than, the roots of the glossopharyngeus.

Further, although the lateralis accompanies the other divisions of the vagus through the long vagus canal behind the auditory capsule, it is only intimately related to the nerve of the first vagus cleft. In connection with the lateralis and the first division of the vagus (vagus I.) there is a ganglionic swelling crowded with large ganglionic cells. Taking these and other facts into consideration, it may be inferred that the lateral canal has been mainly developed from a sense organ on a level with the first vagus cleft, and in relation with a special group of sensory fibres (similar to those of the facial which innervate the three cranial canals already described), which afterwards gave rise to the lateralis nerve. It may be further inferred that by growing in different directions, this embryonic sense organ has given rise to the pre-commissural, commissural, and trunk portions of the lateral canal, with or without involving the branchial sense organs lying above the second, third, and fourth vagus clefts.

IV. THE DORSAL BRANCHES OF THE CRANIAL NERVES.

Having succeeded in making out the innervation of the cranial canals in an Elasmobranch, in showing that the canals instead of being mostly supplied by the trigeminal, as has been hitherto supposed, are intimately related to certain well-marked divisions or branches of the facial and vagus nerves; and having in previous papers dealt with the cranial nerves of *Læmargus*, *Raia*, and *Torpedo*, it is now possible to construct a plan indicating the arrangement of the dorsal branches in an adult Selachian.

Leaving out of consideration the olfactory and optic nerves, the first nerve with a dorsal branch is the ophthalmicus profundus (*o.n.*, fig. 2). Notwithstanding the fact that this nerve has a distinct root in embryo Elasmobranchs, that it sometimes remains separate from the trigeminal in the adult, and that in *Læmargus*, *Raia*, *Torpedo*, and others, it has a large ganglion lying sometimes a considerable distance in front of the Gasserian ganglion, notwithstanding all these facts, this nerve has sometimes been considered a part of the trigeminal, sometimes as belonging to the oculo-motor, or as "a communicating nerve between the third and fifth" (36, p. 153).

A discussion of the views held as to the oculo-motor and profundus nerves would be out of place in this paper. It is, however, desirable to say a word as to the composition of a dorsal branch. In the case of the dorsal branch of a typical spinal nerve, the fibres seem to be entirely distributed to the skin, and hence may be spoken of as somatic sensory fibres. In the case of a typical cranial nerve, on the other hand, the dorsal branch not only contains ordinary sensory fibres for the skin, but also special (in at least

a physiological sense) sensory fibres for the lateral sense organs. These fibres may be known as special somatic sensory fibres.

In order to distinguish between these two kinds of fibres, those innervating the sense organs might be known as the supra-branchial fibres of the dorsal branch. This would admit of the term dorsal, so long in use, being retained in fishes and also in the higher vertebrates in which the lateral sense organs, with some possible exceptions, and the nerve fibres (supra-branchial) supplying them, have completely disappeared. Seeing that not one of the many hundreds of sense organs in the skin of Selachians has been found in the skin of adult higher vertebrates, we must expect in studying the dorsal branches of the cranial nerves, even in fishes, some of the supra-branchial fibres, either in process of degenerating, or entirely absent.

In the case of the ophthalmicus profundus in Læmargus, there are no lateral sense organs (neither nerve hillocks, ampullæ, nor pit organs) supplied by its dorsal branch, *i.e.*, what I have designated the supra-branchial fibres of the dorsal branch are either absent altogether or have changed their function, and are now playing the part of ordinary sensory somatic fibres. That they have degenerated (supposing they once existed) and not changed their connections, may be inferred from the fact that when the supra-orbital sensory canal disappears, its nerve, the superficial ophthalmic of the facial, also disappears. That there is a supra-branchial sense organ in connection with the ganglion of the profundus in the embryo, seems to have been placed beyond doubt, but it has not yet been shown that the embryonic sense organ in connection with the profundus either develops into canals or pit organs.

What then is the distribution of the dorsal branch of the profundus? The dorsal branch (*o.n.*, fig. 2), on leaving the large profundus ganglion (*o.n.g.*, fig. 2) passes over the eyeball under the rectus superior, rectus internus, and obliquus superior muscles, and eventually reaches the anterior part of the snout, where it terminates in the skin. The profundus, which has a similar distribution in *Raia* and in *Amia*, also gives off several branches which enter the eyeball. Some of these branches (long ciliary) arise from the dorsal branch as it passes through the orbit (*lc.*, fig. 2), others spring from the ganglion, and either pass directly to the eyeball, or unite with a branch of the deep division of the oculo-motor, having a similar destination. The ciliary ganglion (*c.g.*, fig. 2) lies at the junction of the profundus and oculo-motor fibres. Large ganglionic cells sometimes extend a considerable distance along the dorsal branch, and ganglionic cells extend from the profundus ganglion to form the ciliary ganglion at the junction of the deep branch of the profundus (*lr.*, fig. 2) with a branch (*sr.*, fig. 2) from the oculo-motor (3).

The second nerve having a dorsal branch is the trigeminal (*Tr.*, fig. 2); the dorsal branch is the ophthalmicus superficialis trigemini. In sharks and rays this nerve supplies the eyelids, and the skin over the anterior part of the cranium, but it also sends fibres into the snout. More or less distinct in sharks, the superficial ophthalmic of the trigeminal in rays consists of very few fibres which, on leaving the trigeminal, at once more or less completely unite with the superficial ophthalmic of the facial.

The dorsal branch of the trigeminal, like the profundus, neither innervates sensory nor ampullary canals. It may, however, supply some of the taste-buds found in the roof of the mouth of certain fishes. If these taste-buds are modified lateral sense organs, the nerves supplying them are likely to be made up of supra-branchial fibres.

In *Amia* it has a similar distribution, but while not connected with canals or pit organs, it supplies a number of surface sense organs, and anteriorly completely fuses with the ophthalmicus profundus.

While there is no doubt as to the nature of the first two dorsal branches, it is difficult to settle whether the third dorsal branch is represented by one or two nerves—whether the superficial ophthalmic and buccal divisions of the facial together represent a single dorsal branch. This question has been supposed to depend on a still larger question, viz., whether, as suggested by DOHRN (34), there is a hyomandibular segment behind the mouth, and in front of the hyoid. If there are two segments—a hyomandibular and a hyoid—between the mouth and the auditory region, we should expect to find two dorsal nerves. In sharks there are undoubtedly two large nerves, each with a large ganglion, extending forwards one above and one below the eyeball; but these two nerves may have resulted from the splitting of a single dorsal branch. That this is the case, may be inferred from the fact that the sensory thickening, which in the embryo lies above the hyoid arch, bifurcates and grows forwards over the face. The superficial and ophthalmic branches of the facial, and their related canals (supra- and infra-orbital), are developed in connection with the two forward growths from this sense organ above the hyoid.

The superficial ophthalmic of the facial (*s.o.f.*, fig. 2) is the first nerve that innervates lateral sense organs. Unlike the profundus and the ophthalmic branch of the trigeminus, it seems to be entirely made up of supra-branchial fibres, *i.e.*, of special sensory somatic fibres.

Having left the buccal nerve (*bu.*, fig. 2), the facial ophthalmic expands to form a ganglion, and then passes forwards above the contents of the orbit, following more or less closely the supra-orbital canal, all the sense organs of which it supplies. The rest of its fibres reach the superficial ophthalmic group of ampullæ (*S.O.A.*, fig. 2). In *Amia*, this nerve supplies a line of pit organs as well as the supra-orbital canal (*S.O.*, fig. 3).

The buccal nerve (*bu.*, fig. 2) is at first inseparably connected with the superficial ophthalmic of the facial. In some cases (*e.g.*, *Læmargus*) it leaves the ophthalmic on the proximal side of the ganglion; while in others (*e.g.*, *Amia*) the two ganglia are united at their proximal ends. In other words, the fusion is more complete in some cases than in others; or, according to the other and more likely view, the splitting is less extensive in *Amia* than in *Læmargus*. The buccal, which like the ophthalmic of the facial, seems to consist entirely of supra-branchial fibres, having left the ophthalmic, at once passes outwards and downwards under the orbit, and divides into two main branches (*bu.*¹, *bu.*²), which lie in intimate relation with the maxillary and mandibular divisions of the trigeminal. The buccal supplies (1) the sense organs of the infra-orbital canal, and (2) the inner and outer buccal groups of ampullæ.

It seems at first sight remarkable that the sense organs of the snout in Selachians—the sensory canals and ampullæ—are not supplied as has hitherto been supposed by the trigeminal, but by the facial, a nerve which, without doubt, belongs to a posterior segment. It is, however, no more remarkable than the innervation of the entire length of the lateral canal by the lateralis division of the vagus, and may be accounted for by the two portions of the branchial sense organ, that in the embryo lies above the hyoid cleft, growing forwards over the head (carrying their nerves with them) in very much the same way as the lateral canal grows backwards along the trunk.

Although I have not thought it necessary to discuss the question as to the segmental value of the ophthalmic and buccal divisions of the facial, I may state that, with VAN WIJHE (35), I regard them as together representing a single dorsal branch, *i.e.*, that they have both been developed in connection with a single branchial sense organ.

The next dorsal nerve, the hyomandibular (*hm.*, fig. 2), also belongs to the facial. It is an extremely large nerve in many Selachians, more especially in the skates, and, unlike the dorsal nerves already considered, it runs outwards almost at right angles to the long axis of the head. While the superficial and buccal branches of the facial have in all probability been formed by the splitting of a single dorsal branch, much might be said in favour of considering the large bundle of sensory fibres that proceeds outwards behind the spiracle, as representing an independent dorsal branch. If the sensory fibres of the hyomandibular nerve represent one dorsal branch, and the ophthalmic and buccal branches of the facial together represent a second dorsal branch, there is no escape from the conclusion that there are two nerves between the trigeminal and auditory—a conclusion which supports strongly DOHRN's contention that there is a hyomandibular as well as a hyoid segment. On the other hand, it is possible that all the three dorsal nerves, *viz.*, ophthalmic, buccal, and hyomandibular, and their respective canals and ganglia, have been formed in connection with a single branchial sense organ which grew outwards behind the spiracle, as well as forwards above and below the orbit.

The large nerve which supplies the hyoid and mandibular* groups of ampullæ, and the hyomandibular sensory canal, has until recently been looked upon as a branch of the trigeminal, and strangely enough has not found a place in the various schemes prepared with a view to illustrating the branchial sense organs, and the segmental arrangement of the cranial nerves. The hyomandibular nerve, made up entirely of supra-branchial fibres, extends outwards behind the spiracle towards the great hyoid group of ampullæ (*H.A.*, fig. 2). A large number of the fibres abruptly end in the ampullæ, others pass in front of or through the ampullary capsule and end in the sense organs of the hyomandibular canal (*H.M.*, fig. 2), and the mandibular group of ampullæ (*M.A.*, fig. 2). A nerve (*f.a.*, fig. 2) corresponding to the facial of the higher vertebrates lies in contact with the hyomandibular. It contains no supra-branchial fibres, but a branch which runs backwards to the first branchial cleft may include some fibres for the skin.

* The mandibular group of ampullæ, which is easily found in the skate, has not hitherto been referred to by any writers on the lateral sense organs.

Leaving out of consideration the auditory nerve (*Au.*, fig. 2), the next dorsal branch springs from the glossopharyngeus. This nerve I have traced to the skin over the auditory region, but though I have not yet succeeded in tracing it to any of the sense organs of sharks, I am inclined to believe that, as shown in the scheme (*gl.*, fig. 2), it innervates one or more of the sense organs immediately in front of the most anterior organs supplied by the lateralis nerve, and also the auditory group of follicles (pit organs) found in the skate. ALLIS has shown that it supplies one sense organ, and a long transverse row of pit organs in *Amia* (*gl.*, fig. 3). Hence its direct relation to sense organs has been sufficiently established in at least one group of fishes. Pit, or at least pit-like, organs are sometimes found in the mouth and pharynx of fishes, almost identical with those in the skin. Sometimes they lie in the sides of the branchial clefts, and they are even said to extend into the œsophagus. The pit-like organs in the mouth are usually described as taste-buds. In the mammal they are said to be innervated by the glossopharyngeal nerve, and it has been suggested by BEARD and others that they are modified lateral sense organs that have reached the back of the tongue, palate, &c. through one or more branchial clefts. If the taste-buds are altered lateral sense organs innervated by the glossopharyngeus, the fibres reaching them will belong to the dorsal branch. It does not, however, follow that because the taste-buds are innervated by the glossopharyngeal they are altered lateral sense organs, for the nerves reaching them may spring from the pharyngeal branch, and consist of special sensory splanchnic fibres.

The next dorsal branch (*ln.*, fig. 2) arises from the great vagus complex. It is not yet possible to speak definitely as to the dorsal branches of the vagus for the reason that it has not yet been determined how many of the branchial sense organs lying above the branchial clefts of the vagus take part in the formation of the lateral canal. According to BEARD (27), "the 'lateral line' has arisen solely by the extension and multiplication of the primitive branchial sense organs of the vagus." He observes they are "connected in development, being formed from one continuous sensory rudiment, and as they form one physiological whole, we could expect a connection in the adult." BEARD describes first what he terms vagus I., *i.e.*, the nerve of the first vagus cleft. It appears that from the long sensory thickening above the vagus clefts, to which the broad band representing all the vagus nerves grows out, there is soon slightly separated the anterior portion which gives rise to the ganglion of vagus I., and later, to part of the supra-temporal branchial sense organs. The rest of the sensory thickening is described as growing backwards along the lateral surface of the trunk, *i.e.*, the sensory cells, "which anteriorly give rise to the compound vagus ganglion (*v.g.* 2, 3, and 4), repeatedly and rapidly divide," and thus give rise to the "lateral line." Again, it is stated, "each of the elementary nerves making up the vagus compound, *viz.*, *v.g.* 2 and 3, and the intestinal branch, *v.g.* 4 and 5; takes part in the formation of the so-called 'lateral line.'" In other words, "the lateral line is made up of supra-branchial nerves of at least four segmental nerves, probably of more than four, *viz.*, vagus 2, 3, 4, and 5." It is further stated, that there is only one supra-branchial branch—the lateral nerve—for all the elements of the vagus except the first (27).

From these statements I infer that while the supra-branchial branch of vagus I. (the nerve of the first vagus cleft) supplies the supra-temporal sense organs, the united supra-branchial branches of vagus II., III., IV., and V. form the lateralis nerve and innervate the sense organs of the lateral canal of the trunk, or, more accurately, the sense organs of the lateral canal not supplied by vagus I.

In the case of the facial the majority of the sensory fibres for the sensory canals, *i.e.*, the fibres of which the superficial ophthalmic, buccal, and the greater part of the hyomandibular nerves are largely composed, escape at a comparatively high level from the side of the medulla. From the side of the medulla in front of and on a higher level than the root of the glossopharyngeal and the rootlets which unite to form the chief portion of the vagus, there escape a number of fibres which unite to form the nerve (lateralis) which supplies the entire length of the lateral canal, the temporal commissure included. In Læmargus this nerve lies in intimate relation with the first division of the vagus (vagus I.). In the skate, it is from the first a distinct nerve, with an independent ganglion (*l.g.*, fig. 2), but it may receive fibres from the branchial divisions of the vagus. In Læmargus the three posterior branchial divisions of the vagus, together with the intestinal branch, are inseparably united, and in connection with one long ganglion, but they send no distinct branches to the lateralis nerve. In Raia, the three posterior branchial branches of the vagus, and the intestinal branch, are in contact with each other, but not blended, and each, like vagus I., has a distinct ganglion (I.-V., fig. 2), but, as in Læmargus, they send at the most very slender branches to the lateralis nerve. The condition in the adult thus seems to indicate that the lateral canal as above described has mainly arisen from the branchial sense organ above the first vagus cleft, and that the epidermic thickenings above the second, third, and fourth vagus clefts, while probably assisting in forming a long ganglion (Læmargus), or four separate ganglia (Raia), have taken little or no part in forming the "lateral line." The lateralis nerve behind the first branchial cleft consists entirely of special sensory somatic fibres; in front, it seems to be accompanied by a few ordinary sensory fibres which reach the skin.

If figure 2 is compared with the schemes previously published, it will be found to differ in several important points. It contains not only the dorsal but also the more important branchial and visceral branches, and in addition to the sensory canals, the various groups of ampullæ, and also the follicles or pit organs.

It is not intended to represent the arrangement in any given Elasmobranch, but rather to indicate the position, innervation, &c., of the lateral sense organs in a Selachian having these structures well developed. In the schemes hitherto constructed, the relation of the profundus nerve to the ciliary ganglion, and to the oculo-motor nerve, is not shown, and it is taken for granted that the profundus supplies a group of sense organs. This scheme represents (1) the dorsal branch of the profundus (*o.n.*) proceeding to the tip of the snout without supplying either sensory or ampullary canals; (2) the long ciliary nerves (*l.c.*) passing to the eyeball; and (3) the offshoot (*l.r.*) to the ciliary ganglion (*c.g.*); this offshoot may, perhaps, be looked upon as a visceral branch.

The trigeminal (*tr.*) agrees with the trigeminal of other schemes; but as in the case of the profundus, it is not represented as taking any part in innervating lateral sense organs. It gives off a dorsal branch (*s.o.t.*), and sends one branch (*m.x.*) in front of, and a second (*m.d.*) behind the mouth.

There is, however, a marked difference between the facial of this and other schemes. The facial was considered by MARSHALL (36) as a simple and typical nerve, and it has been represented as possessing a single root, a single root ganglion, and as breaking up into the three typical branches, *i.e.*, dorsal, pre- and post-branchial branches—the dorsal branch forking as it proceeds forwards. In my scheme the facial is represented as arising by five roots and possessing three large dorsal branches, each with a ganglion. One of the roots (*f.a.*) lies immediately in front of the auditory nerve. This root, which has an independent ganglion, and represents the facial of the higher vertebrates, breaks up into four branches—a dorsal (*d.f.*), which passes backwards towards the first branchial cleft; a small pre-branchial (*p.s.*) in front of the spiracle; a larger post-branchial (*p.b.*), which passes behind the spiracle round the hyomandibular cartilage to proceed to the mucous membrane of the mouth within the hyoid arch; and a pharyngeal (*p.l.*) which supplies the roof of the mouth. As the post-branchial branch bends forwards, it sends a few fibres to the muscles in the region of the hyoid cartilage and the jaw arches. These motor branches reach a large size in the torpedo, and they represent the main portion of the facial of higher vertebrates.

Two of the dorsal branches—the superficial ophthalmic (*s.o.f.*) and buccal (*bu.*)—result from the splitting of an originally simple branchial sense organ. The superficial ophthalmic passes above the eyeball to supply the supra-orbital canal, and the superficial ophthalmic group of ampullæ. The buccal passes below the eyeball and supplies the infra-orbital canal and the inner and outer buccal groups of ampullæ. The third dorsal branch—the segmental value of which is not yet known—runs outwards behind the spiracle and supplies the hyomandibular canal and the hyoid and mandibular groups of ampullæ. This hyomandibular nerve has not hitherto found its way into any of the schemes intended to show the general arrangement and distribution of the cranial nerves.

The glossopharyngeal in my scheme agrees in its arrangement with that of other schemes. It is represented as giving off the four typical branches. The dorsal one I have represented as supplying a short part of the great lateral canal as well as a row of pit organs; but I ought to mention that though this is the distribution of the glossopharyngeal in *Amia* (30), it has not yet been traced to sense organs in Selachians.

The vagus complex, as shown in my scheme, differs very considerably from the vagus of other writers. I have found it far more simple and primitive than I expected. The usual plan has been to represent the vagus as made up of (1) one separate nerve with a ganglion for the first vagus cleft, and (2) of a compound nerve with one large ganglion made up of fibres for the three or four remaining clefts. The first nerve (vagus I.) has been described as having a dorsal branch for the supra-temporal commissure, while the nerve for the lateral line of the trunk has been described as springing from the large

compound nerve, and made up of four sets of dorsal fibres—the dorsal branches of vagus II., III., IV., and V. In my scheme, which represents the arrangement in *Raia* and *Lamna*, the lateralis nerve is represented as springing by a special set of fibres on a higher level and partly in front of the glossopharyngeal, and it supplies not only the lateral line (the lateral canal of the trunk), but also the temporal commissure and a portion of the great lateral canal in front of the commissure. The lateralis either receives from or gives slender branches to the four or five divisions of the vagus as it proceeds backwards; but whether this implies that all the divisions of the vagus have contributed to the formation of the lateralis, I am not yet in a position to say. Strangely enough, the lateralis has a special and distinct ganglion.

Vagus I., II., and III., in the case of the skate, are all separate nerves, and each has a ganglion, visceral, pre- and post-branchial branches. Vagus IV., which has also the usual branches, is intimately connected with the intestinal division, but the ganglia are partly or completely separate. In the skate there are thus in connection with the vagus six ganglia. The value of these, and especially the origin of the ganglion of the lateralis, whether it arises independently or from vagus I., or from all the branchial divisions of the vagus, are points well worth further investigation.

It is worthy of note that all the groups of ampullæ—the superficial ophthalmic (S.O.A.), inner (I.B.A.) and outer (O.B.A.) buccal, hyoid (H.A.) and mandibular (M.A., fig. 2)—are supplied by dorsal branches of the facial, and that the lateralis, in addition to supplying the entire length of the lateral canal, innervates (*e.g.*, in *Mustelus* and *Raia*) a row of pit organs (*p.o.l.*, fig. 2).

CONCLUDING OBSERVATIONS.

Although from a morphological point of view there seems no doubt that the sensory canals subserve some important function, it has not yet been discovered by actual experiment what this function is.

GARMAN (29) thinks that it has been pretty well established that the function of the sensory canals is “that of very delicate tactile organs receiving and carrying the slighter vibrations of the water, noting changes of density, currents, &c.”

It is now most desirable that experiments should be instituted, under favourable conditions, to test the various suggestions made as to the function of both the sensory and ampullary canals. In view of further experiments being undertaken, I cannot do better, in concluding this paper, than point out some of the more striking modifications of the sensory canals found in Elasmobranchs.*

In the first place, in some of the sharks, as already noted, a furrow takes the place of the greater extent of the lateral canal. In *Chlamydoselachus*, *e.g.*, the lateral canal, with the exception of a small part behind the temporal commissure, is represented by a groove, guarded by overlapping scales. In *Heptanchus maculatus*, the canal opens into a groove

* For outline figures showing the arrangement of the canals, see GARMAN (29).

on a level with the anterior part of the pectoral fin ; while in *Acanthias*, the canal is closed except for a short distance in the caudal region. In as far as these species have furrows, they agree with *Chimæra*, in which grooves take the place of canals in the head as well as in the trunk, but differ from *Callorhynchus*, which has canals like the skates and rays, and the majority of the sharks. The difference, however, between canals and furrows is, in most cases, more apparent than real, as the sense organs which lie in the furrows are protected by overlapping scales or folds of skin, which practically convert the furrows into canals.

In some sharks, the arrangement of the canals is simpler and the tubules less numerous than in others. In *Læmargus* and *Heptanchus*, the arrangement of the canals is very simple. Their length has not been greatly increased by the formation of loops, and the tubules are short and never break up into branches before opening on the surface. But in the extremely active thresher shark *Alopias*, there is a loop on the infra-orbital under the eyeball ; and the mandibular part of the hyomandibular is well developed and provided with long branching tubules. But *Alopias* is especially noticeable for the remarkable development of the lateral canal and its tubules, which are not only extremely abundant, but are of unusual length, and give off numerous branches.

It is extremely probable that the remarkable development of the tubules in *Alopias* is related to the active pelagic habits of the fish, which in this respect differs strikingly from *Læmargus*, which, from its being frequently taken in the beam trawl, seems to move about in a leisurely manner, near the bottom.

Further evidence of a relation between the development of the sensory canals and the habits of the fish is especially found among the skates and rays (Batoidei). In the common skate (*Raia batis*) the expansion of the pectoral fins has been accompanied with a great extension of the hyomandibular canal ; and the appearance of long, dorsal offshoots or branches from the lateral canal.

That there is a relation between the extent of the sensory canals and the size of the pectorals is placed beyond doubt by comparing the condition of the canals in the more specialised Batoidei with such shark-like forms as *Rhinobatis* and *Pristis*. In these, although the ventral loop so characteristic of the Batoidei has made its appearance, it is very short and narrow, not reaching as far as the first branchial cleft.

As fully explained in a paper in process of preparation, the hyomandibular in the skate has extended backwards external to the branchial region to form a long, wide, ventral loop, one end of which passes to the upper surface to form, with a branch from the lateral, a long and still wider dorsal loop over the pectoral fin ; while a second branch from the lateral extends over the fin behind the loop.

By these extensions and folds an extremely sensitive apparatus has been arranged over the surface of the pectoral fin. Though, in the meantime, it is impossible to account for these complex arrangements of the sensory canals, it may be taken for granted that they are far from meaningless.

In the rays there seems to be, as in the sharks, a relation between the development

of the sensory canals and the habits of the fish. In the sluggish members of the Batoidei, the canals are in a more or less vestigial condition; while in the active forms they are amazingly complex. For example, in *Narcine braziliensis*, a small inactive torpedo found often in brackish water on the east coast of Central America, in the Caribbean Sea, and on the coasts of the West Indian Islands, the whole of the ventral canals are absent, and the supra-orbital stops short on a level with the nasal capsule; and while the dorsal loop is present, the post-scapular branch is undeveloped. Moreover, the tubules are few in number, short and simple, and the number of the sense organs is limited.

In the torpedoes, a similar state of matters prevails. They are all, apparently, in the habit of resting long on the bottom; and with the possible exception of one or two species, they seldom seem to move, save in the most sluggish fashion. As the sluggish habits were gradually acquired, the extent of the sensory canal system, it may be presumed, has been gradually reduced. The ventral sensory canals having become useless, natural selection has made no effort to preserve them, with the result that only vestiges are left in the form of small vesicles—the follicles of SAVI—one for each of the sense organs that persist in connection with the ventral branches of the facial nerve. At the same time, the dorsal sensory canals are, compared with the skate, less highly developed; the canals are simpler in their arrangement; the post-scapulars are entirely absent; and the tubules in most species are simple, short, and few in number.

If, from the sluggish electric rays, we turn to the active Mylobatidæ, e.g., to *Dicerobatus*, the difference in development is most striking; the area covered by the tubules and their numerous branches being far more extensive than in the common skate; the openings of the tubules being especially numerous on the ventral surface, and on the dorsal surface near the margins of the pectoral fins, and at each side of the middle line of the trunk. The ventral loop, which even in the skate is almost destitute of tubules, has in *Dicerobatus* reached an extraordinary development, and throws numerous branching tubules backwards towards the pelvic fin; and there is a row of tubules along the entire length of the anterior border of the pectoral fin. On the dorsal surface, the branching tubules from the lateral canal are so numerous that they seem to form a network at each side of the middle line—some of them even meet in the middle line, and thus form trunk commissures; and a large number of branching tubules occupy the area enclosed by the dorsal pectoral loop.

Judging from the complexity of the sensory canals, and especially from the abundance of the tubules—the feelers of the canals—which they throw out in all directions, it may be concluded that whatever their function, they are of the utmost importance.

It may be presumed that they take up and transmit various kinds of impressions other than those which are taken cognisance of by the sense organs of the auditory apparatus. Whether they enable the fish the better to obtain its food, or the better to escape from its enemies, or both, remains to be made out. In comparing *Dicerobatus* with the skate (*Raia batis*) and the torpedo (*T. marmorata*), one is especially struck with

the difference in the condition of the sensory canals of the ventral surface. In the torpedo the ventral loop is entirely absent, and there are only a few follicles under the snout, representing the anterior canals. In the skate, the ventral loop and the various ventral portions of the cranial canals are well developed, but the tubules are extremely few in number—the long loop only possessing nine in all. In *Dicerobatus*, as pointed out above, the ventral loop and its tubules have reached a state of great elaboration. These differences might very well be accounted for by the differences in the mode of life of the three forms. The torpedo moves about little, and trusts both for its defence and its food to its batteries ; and the sensory canals are, as it were, only sufficiently developed to enable it to appreciate ordinary disturbances in its immediate vicinity.

The skate moves about more than the torpedo, but less than *Dicerobatus* ; but in its movements it usually keeps close to the bottom, and apparently it has comparatively few enemies. It is far less often captured by other fish than one would naturally suppose ; and it seems to have little difficulty in obtaining its food. Hence, though the ventral loop is present, it possesses few tubules ; and, though the dorsal canals are well developed, the tubules are simple and less numerous than in *Dicerobatus*.

As to the habits of *Dicerobatus*, little is known ; but it undoubtedly differs from both the torpedo and the skate. Instead of resting almost constantly on, or merely skimming along the bottom, it is in the habit of taking long flights through the water. This probably accounts for the great development of the tubules of the ventral loop. Why the dorsal tubules are so enormously complex is more difficult to account for ; but their development may have some relation to the unprotected condition of the tail, which is not only devoid of a spine, but comparatively short and powerless.

Taking into consideration the marked difference between the sensory canals of the sharks and those of the skates and rays, it will be well, before dealing further with the sharks, to give an account of the sensory canals in one of the Batoidei—this I hope to do in a subsequent communication.

(For Explanation of Plates see page 102.)

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* A more complete list of works on the Lateral Sense Organs will be found in GARMAN's paper (29).

Fig. 1.

Fig. 2.

Fig. 4.

Fig. 3.