

VI.—*On the Lateral Sense Organs of Elasmobranchs. II. The Sensory Canals of the Common Skate (Raia batis).* By J. C. EWART, M.D., Regius Professor of Natural History, and J. C. MITCHELL, B.Sc., University of Edinburgh. (Plate III.)

(Read 21st December, 1891.)

INTRODUCTORY.

In the paper on the sensory canals of *Læmargus*, communicated to the Royal Society in July last, it was pointed out that the arrangement of the sensory canals differed considerably in the Batoidei from that in Selachioidei, and it was mentioned that the sensory canals of the skate would be next described.

The skate has been selected chiefly because the sensory canals are more typical than in the torpedoes and the whip and sting rays. In the torpedoes some of the canals are in a vestigial condition; while in the rays proper they have in most species undergone great specialisation. But another reason is, that an account of the development of the lateral sense organs in the skate is likely ere long to be published; and, further, the skate will be more easily obtained and kept under observation than the rays, when physiologists eventually direct their attention to the lateral sense organs of Elasmobranchs.

In describing the sensory canals of the skate, an acquaintance with the papers on the sensory canals (1) and the cranial nerves (2) of *Læmargus* will be taken for granted.

THE GENERAL ANATOMY AND INNERVATION OF THE SENSORY CANALS.

The lateral sense organs in the skate consist of (1) sensory canals; (2) ampullary canals; and (3) sensory follicles or pit organs. As in *Læmargus*, the sensory canals may be said to consist of four main canals—viz., (1) a supra-orbital; (2) an infra-orbital; (3) a hyomandibular; and (4) a lateral canal. The ampullary canals radiate from five centres, their inner dilated ends giving rise to five groups of ampullæ. One, the most posterior (hyoid) group of ampullæ, lies at the outer end of the hyomandibular cartilage; a second (the superficial ophthalmic) group lies at the side of the rostrum; a third (the inner buccal) group lies in front of the nasal capsule; a fourth (the outer buccal) group lies in front of the antorbital cartilage; while the fifth (the mandibular) group lies near the outer end of the mandible. The sensory follicles ("spalt-papillen" of FRITSCH) consist of three rows of shallow pits, one of which lies internal to the canal of the lateral line, a second row lies under the orbit, and a third row near the auditory pores.

In the *Læmargus* paper it is pointed out that STENONIS discovered the openings of the mucous (ampullary) canals of the skate in 1664, and that both the ampullary and sensory canals were discovered some years later (1678) in the torpedo by LORENZINI, who,

in addition to distinguishing the simple (ampullary) from the branched (sensory) canals, noted and described the expansions, now usually known as the ampullæ of LORENZINI, at the inner ends of the simple canals. Reference was also made to the work of MONRO *secundus*, who, in his memoir "*On the Structure and Physiology of Fishes*" (1785), figures, without describing, several of the sensory as well as the more important ampullary canals. The most ambitious paper since the time of MONRO, dealing with the lateral sense organs of the skate, is one by SAPPEY (3). Unfortunately, SAPPEY's account of the sensory canals is far from complete, and there is no reference to their innervation. The groups of ampullæ are described as glands for secreting mucus, and the ampullary canals as ducts for conveying the mucus to the surface; and all the ampullæ are said to be supplied by the trigeminal nerve. It is difficult to make out which of the skates SAPPEY examined. From the drawings it appears to be *R. clavata*, but the arrangement of the canals in both *clavata* and *batis* very decidedly differs from SAPPEY's figures.

Three other investigators have considered at some length the lateral sense organs of the skate, viz., MERKEL, GARMAN, and FRITSCH. MERKEL (4) evidently failed to make out the arrangement of the sensory canals in the skate, more especially the hyomandibular canal, which is represented in one of his figures as springing from the great lateral canal, a condition which does not obtain in any Elasmobranch.

GARMAN (5), following AGASSIZ, studied the sensory canals mainly with a view to determining their value in classification. To admit of this, he examined and prepared outline figures of the canals of a large number of skates and rays. Necessarily, the descriptions are very short, and, as pointed out in the previous paper, there is no attempt to consider the canals either in reference to their development or innervation, with the result that a somewhat complex nomenclature has been introduced. Nevertheless, the figures and short descriptions of a large number of species cannot but be of service to the comparative morphologist as well as to systematists. Again and again we have found them most useful. FRITSCH (6), in addition to giving a short account of the canal system of the torpedo, has described a special form of sense-organ in the skate, to which he has given the name of "spalt-papille." FRITSCH's spalt-papillæ probably correspond to the minute pit organs of *Amia*, *Mustelus*, and *Squatina*.

The four main sensory canals are related to the same nerves as in *Læmargus*. The supra-orbital (S.O.<sup>1-5</sup>, figs. 6 and 7, Pl. III.), or canal of the ophthalmicus superficialis branch of the facial, runs forwards above the eyeball, pierces the snout, and then extends backwards external to the nasal capsule to communicate with the infra-orbital. The infra-orbital (I.O.<sup>1-8</sup>, figs. 6 and 7), or canal of the buccal nerve, passes downwards and forwards external to the eyeball, and then backwards along the ventral surface to bend inwards and forwards after communicating with the supra-orbital and the hyomandibular. The hyomandibular (HM<sup>1-6</sup>, figs. 6 and 7), or canal of the hyomandibular nerve, is far more extensive than in any of the sharks, though (as in sharks) the hyoid portion is absent and the mandibular portion is incomplete and disconnected. Beginning where the infra-orbital bends sharply inwards, it forms a long ventral loop, and then reaching the

dorsal surface it curves backwards, and eventually terminates by communicating with a long offshoot from the lateral canal.

The two lateral canals, or canals of the lateralis divisions of the vagus nerves, begin on a level with the spiracle (*sp.*, fig. 6), and extend backwards to the tip of the tail, giving off branches which unite and form the temporal commissure, and also two long (scapular) branches, the anterior of which communicates with the dorsal extension of the hyomandibular to form a wide dorsal loop.

I. *The Supra-Orbital Canal.*—This canal not only communicates by its proximal end with the infra-orbital canal as in *Læmargus*, but also with the anterior end of the lateral canal, as in *Chlamydoselachus*, *Acanthias*, and certain other sharks. Beginning on a level with the anterior margin of the spiracle, as shown in figure 6, it first arches inwards and then runs forwards parallel to the middle line as far as the nasal capsule; it then inclines inwards as it proceeds to the tip of the snout (S.O.<sup>2</sup>, fig. 6), which it pierces, and thus reaches the ventral surface, to run backwards and slightly outwards, as shown in figure 7. When some distance from the nasal aperture, it bends forwards and outwards to form a close loop (S.O.<sup>4</sup>, fig. 7), and finally runs outwards and backwards in front of the nasal capsule, to terminate by opening into the infra-orbital canal (S.O.<sup>5</sup>, fig. 7). Notwithstanding the great difference which obtains between the skate and *Læmargus*, the supra-orbital canal in the skate only really differs from that of *Læmargus* in being in direct connection with the canal of the lateral line, and in presenting a well-marked loop before it unites with the infra-orbital.

The supra-orbital canal, as above described, includes the cranial, rostral, and subrostral canals of GARMAN (5). The first (cranial) part of the supra-orbital lies immediately under the skin, and in some cases occupies a shallow but well-marked groove in the cranial cartilage. It has an internal diameter of 0.5 mm., while the entire canal is oval in form, measuring about 4 mm. by 2 mm. in thickness. Seven short, slender tubules spring from the first part of the canal (*t.-t.*<sup>7</sup>, fig. 6), and run inwards to open by minute pores about 1.2 cm. from the middle line. From the next part of the canal, nine slender tubules (*t.-t.*<sup>16</sup>, fig. 6), only one of which is over 3 mm. in length, extend directly outwards, and from the part of the canal that lies over the nasal capsule there are seven tubules (*t.-t.*<sup>23</sup>, fig. 6) which run outwards and forwards, the three anterior ones being over 2 cm. in length. Passing to the first section of the canal are sixteen nerves, the majority of which at once penetrate the canal, but the anterior ones break up and supply the sense organs corresponding to the anterior tubules. There are probably altogether twenty-three terminal branches.

The part of the supra-orbital canal which runs along the rostrum (rostral canal of GARMAN; S.O.<sup>1</sup>–S.O.<sup>2</sup>, fig. 6) differs from the part just described, and from the cranial canals in *Læmargus*, in giving off no tubules—in having no direct communication with the exterior. It lies about 2 mm. below the skin in the subcutaneous tissue, and has throughout the greater part of its length a diameter of 2.7 mm. It has thus a diameter fully five times that of the cranial portion, while the wall is only about 1 mm. in thick-

ness. As it approaches the tip of the snout it is reduced to 1.4 mm., and this diameter it retains for some distance as it extends backwards under the rostrum. The rostral part of the canal receives twenty branches from the superficial ophthalmic nerve as it proceeds to the tip of the snout.

The ventral part of the supra-orbital canal (subrostral canal of GARMAN; S.O.<sup>3</sup>, fig. 7) may be said to consist of three segments—(1) a part lying nearly parallel with the middle line; (2) the loop (S.O.<sup>4</sup>, fig. 7) already mentioned; and (3) a slightly curved part that runs outwards to the infra-orbital (I.O.<sup>4</sup>, fig. 7). The first part, as it runs backwards, increases slightly in diameter, and then expands considerably as it turns sharply forwards and outwards to form the loop. As the top of the loop is reached, the canal contracts and again expands slightly as it returns to bend backwards and outwards in front of the nasal capsule. It lies embedded in the gelatinous tissue of the snout, from 2 to 3 mm. from the surface. The first part opens to the exterior by ten extremely short tubules (*t.-t.*<sup>33</sup>, fig. 7), the first two being under 2 mm. in length. There are no tubules from the looped portion; there are, however, twelve regularly arranged but short tubules from the terminal portion (*t.-t.*<sup>45</sup>, fig. 7). Passing to the sense organs in the ventral part of the supra-orbital canal, forty-five nerves were counted—sixteen to the first part, seventeen to the loop, and twelve to the terminal portion. All the nerves to the sense organs of the supra-orbital canal spring from the ophthalmicus superficialis of the facial—a nerve which has almost universally been described as a branch of the trigeminal, and which is still apt to be confused with the superficial ophthalmic branch of the trigeminal or with the ophthalmicus profundus.

*Innervation.*—According to BEARD's scheme, referred to in the Læmargus paper (1), the three ophthalmic nerves—viz., the ophthalmicus profundus, the ophthalmic of the trigeminal, and the ophthalmic of the facial—are supra-branchial branches, and each should have sense organs in connection with it; in other words, all three nerves should take part in supplying sense organs in the supra-orbital region or in the snout. As to the ophthalmicus profundus, which lies in front of the trigeminus proper, we are satisfied that, as in Læmargus and *Amia* (7), it takes no part in supplying lateral sense organs. The superficial ophthalmic branch of the trigeminal so completely blends with the ophthalmicus superficialis division of the facial that it is all but impossible to trace its fibres. On the other hand, in the Elasmobranchs in which the ophthalmic division of the trigeminus is a separate nerve, it has not been found supplying any of the sense organs; while, even in the skate, the numerous branches for the sensory canals have been found springing directly or indirectly from the main trunk of the superficial ophthalmic division of the facial. This nerve (*s.o.f.*, fig. 6), on leaving the buccal division of the facial, escapes from the cranium along with the ophthalmicus profundus, leaving which it runs forwards superficial to the orbital muscles, and reaches the snout by traversing a canal at the junction of the nasal capsule and the cranium. On the way it gives off sixteen branches, which penetrate the roof of the orbit. These, after dividing, enter the first (cranial) portion of the supra-orbital canal, and terminate in sense organs, probably twenty-three in number.



As it runs along the side of the rostrum it gives off the twenty branches for the second (rostral) part of the canal; while, as it passes through the cartilage in front of the orbit, it gives off a large branch (*v.b.*, fig. 7) that curves outwards and downwards to break up into the forty-five twigs for the ventral portion of the supra-orbital canal—viz., sixteen for the inner part, twelve for the outer part, and seventeen for the looped part. This branch of the superficial ophthalmic comes into intimate relation with various branches of the buccal nerve.

II. *The Infra-Orbital Canal*.—This canal (I.O., figs. 6 and 7), which is continuous with the cranial portion of the lateral canal, and in communication with the supra-orbital canal, runs obliquely outwards between the eye and the spiracle, and then bending forwards runs for some distance nearly parallel to the supra-orbital canal. It next curves forwards and outwards to the margin of the snout, which it pierces to reach the ventral surface. It then runs backwards, communicating on the way with the supra-orbital, and on reaching the hyomandibular (H.M., fig. 7) turns inwards, to dip into the naso-buccal groove. Emerging from the groove it soon unites with the corresponding canal of the opposite side, and forms a very short median portion (I.O.<sup>7</sup>, fig. 7) from which two canals curve sharply outwards, and then running forwards in close contact with the suborbital canals again unite near the tip of the snout (I.O.<sup>8</sup>, fig. 7).

The infra-orbital canal includes the orbital, suborbital, orbito-nasal, nasal, half of the median, and the prenasal canals of GARMAN. The first (orbital) part of the infra-orbital canal seems to be a direct continuation forwards of the lateral canal. It has the same diameter and structure as the lateral canal. For the first 4 or 5 mm. of its course, it lies in a groove in the cartilage of the cranium, and afterwards is embedded in the fibrous tissue between the eye and the spiracle. As it bends forwards outside the eye it gives off a large tubule (*t*<sup>1</sup>, fig. 6),\* which runs backwards external to the spiracle, and opens by a terminal pore to the exterior. The portion of the canal which runs forwards in front of the eye (I.O.<sup>1</sup>–I.O.<sup>2</sup>) lies immediately underneath the skin, and slightly increases in size before passing to the ventral surface. The ventral portion may be said to consist of three parts:—(1) A straight part continuous with the hyomandibular canal, and in communication with the supra-orbital (I.O.<sup>4</sup>–I.O.<sup>5</sup>); (2) a looped part (I.O.<sup>5</sup>–I.O.<sup>7</sup>), which runs inwards to the middle line posterior to the nasal capsule; and (3) an inner part (I.O.<sup>7</sup>–I.O.<sup>8</sup>, fig. 6; I.O., fig. 6*α*), which runs forwards almost in contact with the inner ventral part of the supra-orbital (S.O.<sup>1</sup>, fig. 6*α*). These three ventral segments lie embedded in the gelatinous tissue of the snout from 2 to 4 mm. from the surface, and possess, as a whole, a considerably larger lumen than the dorsal portion of the infra-orbital.

As is the case with the supra-orbital, some parts are provided with, while other parts are without, tubules. The tubules in front of the eye (*t*.–*t*<sup>13</sup>, fig. 6), twelve in number, spring from the dorsal part of the canal. At first under a centimetre in length, they gradually increase up to two centimetres. Four of them (3–6) have a peculiar arrangement; they connect the infra-orbital canal with the dorsal part of the hyomandibular (H.M.<sup>5</sup>, fig. 6),

\* This tubule GARMAN considered a branch of the main canal—a view not supported by its structure.

which later unites with an offshoot from the lateral canal. The third and fifth tubules terminate in the hyomandibular canal; but the fourth and sixth, which are nearly 1.50 cm. in length, simply communicate with the canal as they pass obliquely outwards.

Passing to the ventral surface, the outer or straight part (suborbital and orbito-nasal of GARMAN) opens to the exterior by nine extremely short tubules (*t.-t.*<sup>22</sup>, fig. 7); the middle part (nasal of GARMAN) by seventeen tubules (*t.-v.*<sup>39</sup>, fig. 7), twelve short ones external to the naso-buccal groove, and five, slightly longer, internal to the groove; and the inner (prenasal) part gives off, from about its middle third, eleven tubules (*t.-t.*<sup>60</sup>, fig. 7). The direction of the tubules is indicated in the figure.

*Innervation.*—The first part of the infra-orbital canal is supplied by a slender nerve which springs from the buccal division of the facial as it separates from the superficial ophthalmic part of the facial. This nerve (*bu.*<sup>1</sup>, fig. 6) runs upwards posterior to the eyeball, and breaks up into six terminal branches, which enter the canal as represented in figure 6. For the next segment of the canal, two slender nerves spring from the buccal as it passes forwards under the eyeball. These nerves arch outwards, the first enters the canal nearly opposite the first tubule, the second by three branches opposite the origin of the three following tubules. To supply the middle portion of the canal on the dorsal surface a somewhat larger nerve springs from the buccal as it appears from under the eyeball. This nerve, as it turns outwards and forwards, breaks up into eleven branches, eight of which enter the canal opposite the eight remaining tubules, while three terminate in the canal immediately in front of the tubules.

The buccal, having given off this branch, divides into an internal and an external portion—the inner (*bu.*<sup>1</sup>, fig. 7) runs forwards above the palato-quadrate cartilage, and is mainly concerned in supplying the inner buccal group of ampullæ; while the outer (*bu.*<sup>2</sup>, fig. 7) runs obliquely outwards, and sends the most of its fibres to the outer buccal group of ampullæ. From this outer division of the buccal, a branch passes forwards and inwards to supply the remainder of the dorsal part of the infra-orbital canal, the branch penetrating the canal by six slender filaments. Supplying the ventral part of the infra-orbital canal, as far back as its junction with the supra-orbital (*S.O.*<sup>5</sup>, fig. 7), are nine twigs, which spring from a second branch from the outer division of the buccal that usually, at first, accompanies the one just described. The remainder of the outer part of the canal (orbito-nasal) is supplied by six slender nerves which also spring from the outer division of the buccal. The outer division of the buccal thus supplies the outer straight ventral portion, and the anterior part of the dorsal portion of the infra-orbital, *i.e.*, part of the suborbital and the orbito-nasal of GARMAN; the rest of the suborbital and the orbital of GARMAN being supplied by branches which spring from the main trunk of the buccal as it passes forwards under the eyeball.

The remaining ventral portion of the infra-orbital canal is supplied by the inner division of the buccal nerve. As the nerve reaches the anterior margin of the palato-quadrate cartilage it sends branches both outwards and inwards, while the main portion runs forwards to enter the inner buccal group of ampullæ, from which a few fibres escape

and run forwards all but in contact with the terminal portion of the ophthalmicus superficialis—the division of the facial with which the buccal was originally united. Two of the branches which proceed outwards from the inner division of the buccal supply the part of the canal lying between its junction with the hyomandibular canal and the inner margin of the naso-buccal groove. The part outside the groove receives seven twigs, the part which dips into the groove, six. Another branch breaks up into nine filaments for the part of the canal between the groove and the short commissure. This short expanded median portion receives as many as ten relatively large branches—five from the right and five from the left buccal nerve. The inner (prenasal) portion of the infra-orbital canal receives altogether twenty-six nerves from the inner division of the buccal as it runs along the rostrum; eleven of these, which reach the curved part of the canal behind the tubules, are relatively large, while the fifteen which pass to the anterior two-thirds are more slender and further apart. It thus appears that the buccal nerve innervates nearly one hundred sense organs—ninety-eight terminal twigs having been traced in the specimen examined.

The infra-orbital canal, though containing nearly one hundred sense organs only, opens to the exterior by forty-nine tubules. The two canals communicate with each other in front of the mouth, and also, as in *Amia*, at the tip of the snout, and by means of four of its tubules with the hyomandibular canal; while, by its proximal end, it is continuous with the lateral and supra-orbital canals. In communicating with the lateral, and in having a commissure at the tip of the snout,\* the infra-orbitals of the skate differ from those of *Læmargus*; they also differ in having a limited number of tubules—far fewer tubules than sense organs.

III. *The Hyomandibular Canal.*—The hyoid portion of this canal, as in *Læmargus*, is absent, but the distal part of the mandibular persists. The horizontal portion, on the other hand, has been greatly extended, forming a long loop under the pectoral fin; and, with the help of an offshoot from the lateral, a long wide loop on the upper surface. Beginning where the infra-orbital bends inwards, the hyomandibular (HM., fig. 7) runs backwards, external to the branchial clefts, as represented in figure 7, to form the long ventral loop (HM.<sup>1</sup>, fig. 7). The outer limb, when opposite the mouth (HM.<sup>2</sup>), curves inwards, and then runs forwards immediately outside the infra-orbital canal, to pierce the tissues inside the propterygium and reach the dorsal surface. Having gained the dorsal surface, it at once dilates, to form in some cases a club-shaped expansion (HM.<sup>5</sup>, fig. 6)—the end of which is connected, as already explained, by tubules with the infra-orbital canal. From this expansion the canal, now comparatively slender, curves outwards and backwards for some distance along the margin of the pectoral fin, and then bends inwards to join a branch (scapular; sc., fig. 6) from the lateral canal. This greatly extended hyomandibular corresponds to the angular, jugular, subpleural, and pleural canals of GARMAN.

The inner limb of the ventral loop gradually diminishes in size as far as the middle of

\* The union of the prenasals at the tip of the snout is said by GARMAN not to take place in *R. levis*.

the branchial region; throughout the remainder of the inner loop, and the entire length of the outer loop up to where it approaches the beginning of the canal, the same diameter (about 2 mm.) is maintained. The part which runs forwards side by side with the first part of the hyomandibular and the outer part of the infra-orbital has a diameter of 3.2 mm. The part in front of the gill region, like the part of the infra-orbital with which it is continuous, lies in gelatinous connective tissue, some 3 mm. beneath the surface; the rest of the ventral loop occupies a very superficial position. There are extremely few tubules given off from the ventral loop. Between the junction with the infra-orbital and the gill region there are ten tubules ( $t.-t.^{11}$ , fig. 7). Of these, the four anterior are very short and near each other, while the remaining six are from 1.7 to 5 mm. in length, and wider apart. From the outer limb of the ventral loop, only four tubules ( $t.-t.^{15}$ , fig. 7) arise: these tubules are wide apart, and they vary considerably in length and position, as shown in figure 7.

The dorsal extension of the hyomandibular canal is at first somewhat dilated, and at some distance (about 3.5 mm.) from the surface; the remainder, which is flattened and has a small lumen, occupies a superficial position, and takes an irregular course towards the outer angle of the pectoral fin before it bends inwards to join the scapular branch of the lateral canal. The expanded anterior portion does not open directly to the exterior, but it has two tubules from the infra-orbital opening into its wide inner end, and two infra-orbital tubules open into the canal as it leaves the dilatation. From the long part of the canal that runs backwards over the ampullary canals to eventually end in the offshoot from the lateral canal, thirty-nine tubules ( $t.-t.^{54}$ , fig. 6) were given off in the specimen figured. These, as the drawing indicates, are relatively numerous, and of varying lengths. They all run outwards, the majority outwards and backwards.

The two mandibular portions of the hyomandibular canals form a single canal behind the mouth. They lie immediately beneath the thin skin covering the mandible; and they together give off twenty-six short tubules ( $t.-t.^{67}$ , fig. 7) which open by a row of minute pores posterior to the openings of the mandibular ampullary canals.

*Innervation.*—The entire length of the hyomandibular canal (including the ventral loop, the long dorsal extension, and the mandibular part) is innervated by the hyomandibular branch of the facial nerve. This large nerve ( $hm.$ , fig. 6), as it approaches the hyoid group of ampullæ (H.A., fig. 6), breaks up into numerous branches, the majority of which terminate in the ampullæ. Some of the branches for the sensory canal leave the nerve before it enters the ampullary capsule, while others pass through between the ampullæ, and then radiate to the dorsal and ventral portions of the canal.

The part of the canal in front of the hyoid group of ampullæ is almost entirely supplied by branches which leave the nerve before it enters the ampullary capsule. From these branches nine nerves were given off to the anterior part of the hyomandibular canal (fig. 7). The whole of the long ventral loop, with the exception of the curve formed by the outer limb and the straight part that lies alongside the infra-orbital canal, is supplied by branches of the hyomandibular nerve, which penetrate the ampullary capsule

(fig. 7). The main branch runs backwards nearly parallel with the inner limb of the loop. From this branch (1) slender twigs reach and penetrate the middle third of the inner limb, and (2) longer delicate filaments proceed to the posterior third of the inner and posterior half of the outer limbs. The rest of the outer limb, as far forward as the point where it begins to bend inwards, is innervated by four branches, each of which has a separate exit from the ampullary capsule. The bend formed by the outer loop receives its nerves from the precapsular branches, which reach it by passing under the anterior portion of the canal. The straight, most anterior, ventral portion, and the dilated anterior portion on the dorsal aspect, are supplied from a large superficial precapsular branch which runs directly forwards and divides into two main branches (*hm.*<sup>2</sup>, fig. 6). The outer dips downwards and sends six twigs to the ventral part; the inner sends a long slender branch forwards which gives six twigs to the longitudinal part of the dilatation, and a short branch inwards, which sends several twigs to the transverse part of the dilatation. From the same precapsular branch three filaments proceed to supply the part of the canal immediately beyond its connection with the suborbital tubules. The next segment of the canal, the part from which the second to the fourteenth tubules are given off, is supplied by twelve twigs which radiate from a second precapsular branch. The rest of the dorsal portion of the hyomandibular canal is supplied by four branches, which escape from the capsule and break up into long, delicate filaments as they run outwards and backwards. This part of the canal gives off twenty-five tubules, and is penetrated by twenty-seven nerves, most of which enter near the origin of the tubules; the two last nerves enter the terminal part of the canal which runs inwards to communicate with the anterior (scapular) offshoot from the lateral canal.

The mandibular canal is supplied by a branch (*hm.*<sup>1</sup>, fig. 7) of the hyomandibular nerve, which leaves it and passes downwards between the first branchial chamber and the jaw muscles. This branch, after parting with the majority of its fibres to the mandibular ampullæ (*M.A.*, fig. 7), runs along the posterior border of the mandible, and sends thirteen filaments to the sense organs of the canal.

The hyomandibular canal, with its remarkable ventral loop (subpleural of GARMAN) and its long dorsal extension (pleural of GARMAN), has many points of interest. In the first place, these pleural or pectoral extensions are characteristic of the Batoidei. In all of them the dorsal extension, which bends backwards to join the scapular branch of the lateral canal, is invariably present; and, except in the torpedoes, the ventral extension is also present, though in some of them, *e.g. Raja ocellata*, the outer limb of the loop is absent. SAPPEY's description of what may be called the pectoral portions of the hyomandibular canal is in many respects remarkable. Having failed, apparently, to establish a connection between the ventral and dorsal portions of the canal, he describes the ventral loop as forming the external and internal branches of the ventral mucous canal, which he describes as beginning near the front of the snout and extending backwards and then forwards to terminate near its origin. The inner limb is thus made to include the ventral part of the infra-orbital, which he evidently failed to discover was continuous

with the dorsal part, *i.e.*, with what he calls the anterior part of the dorsal longitudinal canal. The dorsal portion of the hyomandibular he represents accurately enough as connected with the infra-orbital—his dorsal longitudinal canal. He makes no reference to the innervation of any of the cranial canals, and, like MONRO, considers the hyomandibular division of the facial as a branch of the trigeminal.

GARMAN, after pointing out that "the manner in which the Batoidei became possessed of the 'pleurals' is a question of considerable interest," states that the "clue to the solution of the problem is to be seen in *Chlamydoselachus*" (5). He considers that the dorsal portion (pleural canal) was derived from the spiracular, and the ventral loop (subpleural canal) from the jugular. Elsewhere he says, "No doubt the pleural originated as a branch of the orbital." Why GARMAN should suppose the "pleurals" originated from the "orbital" (*i.e.*, the first portion of the infra-orbital) canal, it is difficult to understand. Some of the tubules of the infra-orbital open into the dorsal extension, and in some cases, *e.g.* *R. ocellata*, this dorsal portion is disconnected from the ventral portion. But, on the other hand, both the ventral loop and the long dorsal extension are supplied by the hyomandibular nerve; and when the canals are examined in embryo skate, and in the less specialised members of the Batoidei group, it becomes evident that the ventral loop (subpleural) has been formed by a backward extension of the hyomandibular canal, which turned upon itself (in some cases before reaching the level of the first branchial cleft), and grew forwards to penetrate the snout and then proceed backwards along the margin of the pectoral fin, thus forming, first, the ventral, and afterwards the dorsal loop.

IV. *The Lateral Canal*.—This canal has been frequently figured, and more or less accurately described. Hitherto, it has usually been looked upon as beginning in the skate at or near the temporal commissure. The commissure has been said to consist of two canals (the aurals), and the part between the end of the commissure and the supra-orbital canal has been described as a separate canal (the occipital.) But, as the commissure and the whole of the longitudinal canal, including its branches, from the beginning of the supra-orbital to the tip of the tail, is innervated by one nerve, *viz.*, the lateralis division of the vagus, we shall consider the lateral canal as including in addition to the trunk portion, the commissural portion and the part immediately in front of it.

The first precommissural portion (occipital of GARMAN; *lp.*, fig. 6) runs backwards and inwards to the outer end of the temporal commissure. It has the same diameter as the cranial part of the supra-orbital, and lies for the most part in a groove in the cranial cartilage.

The commissure (*lc.*, fig. 6), formed by the union of two branches, one from each lateral canal, runs right across the cranium, immediately behind the auditory pores. It lies immediately beneath the skin and firmly adheres to it. Neither of those portions give off any tubules, nor do they open to the exterior by means of pores.

The first part (*L.*, fig. 6) of the lateral canal of the trunk, after running for a short distance directly backwards, forms a sigmoid curve, and reaches the supra-scapular

prominence. At the anterior margin of the supra-scapula, it gives off a long (scapular) branch (*sc.*, fig. 6), which runs backwards and outwards towards the margin of the fin, communicating on the way with the dorsal extension of the hyomandibular canal. A second (post-scapular) branch (*p.sc.*, fig. 6) springs from the canal opposite the posterior margin of the scapula, and runs backwards in a similar direction to the first (scapular) branch. The main canal having given off the posterior scapular, curves inwards, and runs along first the trunk, and then the side of the tail, terminating at or near its tip. The lateral canal and its scapular branches are flattened, and have a small lumen—the diameter diminishing as the tip of the tail is reached.

From the part of the canal in front of the scapular branch there spring eleven tubules (*t.-t.<sup>11</sup>*, fig. 6); ten of these, which are of about the same length, curve inwards, and one, longer than the others, bends forwards and outwards. The part of the canal lying on the supra-scapula gives off no tubules, but from the origin of the post-scapular branch to the tip of the tail tubules are regularly given off. These tubules, which first run backwards and outwards, and afterwards backwards and inwards across the canal, gradually diminish in length from before backwards. The scapular branch gives off twelve tubules before, and fourteen after, communicating with the dorsal part of the hyomandibular canal. The inner tubules, which are of considerable length, run outwards and forwards, while those beyond the junction run almost directly outwards. The latter gradually diminish in length, and lie nearer each other than the former.

The post-scapular branch gives off twenty tubules, which arch outwards; the last eight rapidly diminish in length as the end of the canal is reached.

*Innervation of the Lateral Canal.*—The precommissural and commissural portions, and the part of the trunk portion of the canal up to near the origin of the scapular branch, are supplied by a special nerve which springs from the lateralis division of the vagus at or near its ganglion. This branch passes upwards behind the auditory capsule, and as it approaches the surface breaks up into three bundles. One runs forwards to innervate the precommissural, another bends inwards to the commissural part of the canal, the third passes backwards at some distance below and to the outer side of the first part of the trunk portion of the canal, which it supplies as far as its eighth tubule (fig. 6). For the part of the canal immediately in front of the scapular branch, the two scapular branches, and the short part of the main canal between them, the lateralis gives off two special branches. The first, a fairly large nerve, springs from the lateralis in front of the shoulder-girdle, and, after approaching the surface, runs backwards and outwards immediately behind the scapular branch of the canal. It sends three twigs to the main canal in front of, and a similar number to the main canal behind, the scapular branch; and, as it accompanies the scapular branch outwards, it gives off thirty-two twigs, the majority of which enter the canal opposite the tubules (fig. 6). The second, or post-scapular nerve, springs from the lateralis as it reaches the posterior border of the shoulder-girdle. Having sent a twig to the main canal, it proceeds outwards behind the post-scapular offshoot, to which it contributes twenty-four twigs, the greater number of which enter

opposite the tubules (fig. 6). No other large branches proceed from the lateralis nerve. As it proceeds backwards, first at some distance from the canal, but afterwards in close contact with it, the lateralis gives off slender branches which either directly, or after dividing, enter the canal to terminate in the sense organs.

#### THE HISTOLOGY OF THE SENSORY CANALS.

Many investigators have studied the minute structure of the lateral sense organs of fishes, but to LEYDIG (8), MERKEL (4), SOLGER (9), and FRITSCH (6) we are most indebted for information on this subject. In this paper it will only be necessary to give a short account of the minute structure of the canals of the skate.

Hitherto it seems to have been taken for granted that the cranial canals differed in structure from the lateral canal. This, however, is not the case; for in the skate, for example, some parts of the cranial canals exactly agree in structure with the canal of the trunk. It would be more accurate to say that the canals of the dorsal surface differ in structure from the canals of the ventral surface; but even to this statement there are exceptions, for the anterior (rostral) part of the supra-orbital canal and the anterior dorsal part of the infra-orbital canal, as well as the dilated dorsal portion of the hyomandibular canal, all differ from the canal of the lateral line, and agree with the canals of the ventral aspect. Apparently the difference in structure depends on the relation of the canals to the skin; for the canals which are imbedded in, or lie immediately in contact with, the skin, differ from those that lie more or less deep in the subcutaneous tissue. The canals intimately related to the skin, *i.e.*, the lateral canal, and, with the exceptions just mentioned, all the dorsal cranial canals, are flattened, have a small lumen, and are to a large extent composed of fibro-cartilage.

The ventral canals and the portions of the supra-orbital, infra-orbital, and hyomandibular already specified, have, on the other hand, a rounded form; the lumen is often five to six times greater than that of the lateral canal, and there is little or no fibro-cartilage in the wall. Further, while the wall of the ventral canals is of nearly the same thickness all round, the wall of the lateral canal, and of the cranial canals which resemble it, while presenting thick fibro-cartilaginous sides, have only a thin roof and floor. It may here be mentioned that FRITSCH (6) gives a figure of a "trunk canal" of the torpedo, and states that while the trunk canals are fibrous, the head canals bear a fibro-cartilaginous character. This may be true of the torpedo, but it does not hold for the skate.

*The Dorsal Canals.*—The lateral canal may be taken as an example of what might be known as the dorsal or cutaneous type, while the ventral part of the infra-orbital may serve as an example of the wide, thin-walled ventral or subcutaneous type. The lateral canal, which lies either in or immediately beneath the skin, is flattened, and somewhat resembles a long narrow slightly tapering ribbon, having one of its surfaces parallel with the surface of the skin. The small lumen occupies less than a third of the width of the ribbon; and, while it is bounded at each side by a thick fibro-cartilaginous wall, the floor



and roof agree in consisting of a thin layer of fibrous tissue with at the most a few cartilage cells. The roof is translucent; hence, when a canal is exposed, the position of the lumen is at once evident, presenting quite a different appearance from the dense lateral walls.

The thin, fibrous roof and floor, and the thick, fibro-cartilaginous lateral walls, and the sense organ, are shown in figure 8. The sense organ (*s.o.*), it will be observed, stretches almost right across the inner wall. Usually the tubules run obliquely through the wall, and the fibro-cartilage extends along each tubule to within a short distance of the external aperture. Beyond the cartilage the tubule consists of epidermal cells, with pigment cells interspersed; these pigment cells, by forming a dark ring, often indicate the position of the terminal pore.

The sense organs throughout the greater part of the lateral canal do not, as might be expected, lie in the floor; but, as shown in figure 8, in contact with the inner lateral wall. In front of the shoulder-girdle they are either on the side of the canal or on the roof.

The canals (with the exception of the parts occupied by the sense organs) and the tubules are lined with two layers of epithelial cells. The deeper layer consists of rounded and somewhat irregular cells which rest on a basement membrane, and are often separated by intercellular spaces containing leucocytes.

The superficial cells are columnar in form; in most cases they are short and broad, having the free outer end non-granular, and the deep end occupied by the nucleus. These columnar cells, though resembling mucin-forming cells, were never seen assuming the goblet form, or giving evidence of being actively concerned in the production of mucus. They contrasted strongly with the goblet cells which exist in great numbers in the epithelium of the skin (fig. 8); and, undoubtedly, produce the abundant coating of mucus always present in the skate.

In longitudinal and transverse sections through the areas occupied by the sense organs, it is observed that, as the sense organ or hillock is approached, the deeper layer of cells disappears, while the superficial layer assumes the form of long narrow columns, each with a nucleus near the middle of its length. These columnar cells form a well-marked zone around the sense organ proper—a zone sometimes fifteen cells wide. The sense organ which lies within this zone consists of sense cells, supporting cells, and of highly refractile processes, which project into the hillock from the basement membrane.

The sense cells, which are of a cylindrical form, lie within and between the supporting cells. Each has a large nucleus near its deep, inner end, and a hair-like process projecting from its outer end. These hair cells are less numerous than the supporting cells, which lie between and around them. The supporting cells, especially towards the centre of the hillock, are long and narrow, and thus differ from the short and comparatively broad cells which line the canal and the hair cells already mentioned. The processes which project into the hillock from the basement membrane SOLGER describes as "zwischen-pfeiler" (9). They seem to extend from between the inner ends of the support-

ing cells to the top of the hillock, and thus they in a way resemble the Müllerian fibres of the retina.

Resting on the top of the hillock there is often what SOLGER terms the "cupula-bildung." This seems to consist of mucin. In some cases we have seen long threads of mucin extending from the hillock into the cupula or across the canal, the threads having frequently leucocytes entangled between them.

Each sense organ has a nerve passing to it. The nerves, usually accompanied with one or more capillaries, enter the canal a short distance from their respective sense organs, and run obliquely through the canal to break up under the hillock into a number of terminal fibres which seem to end in close connection with the hair cells.

With the exceptions already mentioned, the dorsal canals have the same structure as the lateral canal.

But, while the sense organs and tubules have a metameric arrangement in the trunk, there is no relation between the sense organs and segments in the head region; and, as already pointed out, some portions of the cranial canals, though possessing numerous sense organs, have no tubules connecting them with the exterior.

In all the cranial canals, both dorsal and ventral, there are far more sense organs than segments, *e.g.*, in the supra-orbital canal there are nearly ninety sense organs, and in the infra-orbital there are over ninety. Why the sense organs of the head are so numerous, may be understood should we in course of time discover the function of the lateral sense organs.

The writers who assert that the sense organs and tubules agree in number have probably only directed their attention to the sensory canals of sharks; for certainly, as figures 6 and 7 clearly show, there are long stretches of canals with few or no tubules. As to whether in the embryo the tubules are more numerous than in the adult we have no information. If there are more tubules in the embryo than in the adult, it may be inferred that the parts of canals that have lost their tubules are in process of degenerating—of being reduced to vesicles, such as take the place of the ventral sensory canals in the torpedo.

*The Ventral or Subcutaneous Canals.*—In these canals, which have usually a lumen five or six times greater than that of the dorsal canals, the wall is of uniform thickness, and composed of a thin layer of fibrous tissue (fig. 9). Like the dorsal, they are lined by two layers of cells, except at the sides of the sense organs. The sense organs only differ from those of the dorsal canals in being slightly larger, and in having a wider zone of columnar cells surrounding them.

It may be mentioned that in a very young skate we had the opportunity of examining the lining cells, and to a certain extent the sensory cells differed from those of the adult. The two layers of cells which line the canals closely resemble each other; and, as the sense organ is reached, the layers separate, the deeper one passing under the hillock, while the superficial becomes continuous with the supporting cells. The sensory cells are pear-shaped, and have oval nuclei, while the supporting cells are long and narrow.

## THE SENSORY FOLLICLES OR PIT ORGANS.

The sensory follicles ("spalt-papillen" of FRITSCH), as already indicated, lie in relation to the lateral and infra-orbital canals. Those related to the lateral canal form a row which extends from the region of the supra-scapula as far as the first dorsal fin—one for every two segments. The follicles lie between the lateral line and the middle line of the trunk and tail (*p.o.*, fig. 6).

The second group consists of two follicles (*p.o.*<sup>1</sup>, fig. 6) which lie in front of the auditory pores; while the third group consists of five follicles (*p.o.*<sup>2</sup>, fig. 6) which lie external to the eye, immediately within the infra-orbital canal. The follicles though small are quite visible without the assistance of a lens in fresh specimens, especially when the epidermis is removed with the edge of a scalpel from the slight papillæ by which they open on the surface. With the help of a lens, the groove or split which runs across the papilla, and leads into the pit, becomes evident. In those related to the lateral canal, and the two in front of the auditory pores, the split is at right angles to the long axis of the fish; while in those lying within the infra-orbital canal, the split is nearly parallel to the long axis.

In uninjured specimens, each follicle is seen to present externally a slight rounded projection, divided into two by a fissure which leads into the pit or follicle proper.

The elevation consists chiefly of layers of epithelial cells, amongst which are many goblet cells. In vertical sections the epithelial layer, still containing goblet cells, is seen to extend well into the follicle. The bottom of the follicle is occupied by a large rounded sense organ (fig. 10), which in many respects resembles a taste-bud. The sense organ consists of pear-shaped sensory cells, with large oval nuclei and hair-like processes at the outer end of each cell. The sensory cells are surrounded by columnar supporting cells, in which the nuclei are deeper than in the hair cells. Passing to the sense organ of each follicle are several nerve fibrils. These fibrils pass obliquely upwards through the epidermic cells which underlie the follicle, and terminate in the sense organ. The nerves for the trunk follicles seem to come from the lateralis, those for the infra-orbital group from the buccal, while those for the two follicles in front of the auditory pore may either arise from the lateralis nerve or from the glossopharyngeal—this is a point we have not been able to settle. We look upon these follicles as homologous with the pit organs of *Amia*. MERKEL states they have been found in *Mustelus* and *Squatina*.

## BIBLIOGRAPHY.\*

- (1) EWART, "The Sensory Canals of *Læmargus*," *Roy. Soc. Trans. Edin.*, vol. xxxvii. part i. p. 59.
- (2) EWART, "The Cranial Nerves of Elasmobranch Fishes," *Roy. Soc. Proc.*, vol. xlv., 1889.
- (3) SAPPEY, *Étude sur l'appareil mucipare*, &c., 1879.
- (4) MERKEL, *Ueber die Endigungen der sensiblen Nerven in der Haut der Wirbelthiere*, Rostock, 1880.
- (5) GARMAN, "On the Lateral Canal System of the Selachia," *Bull. Mus. Comp. Zool.*, Cambridge, Mass., vol. xvii. No. 2.
- (6) FRITSCH, *Die Electricischen Fische Die Torpedineen*, Leipzig, 1890.
- (7) ALLIS, "The Anatomy and Development of the Lateral Canal System of *Amia calva*," *Journal of Morphology*, vol. ii., 1889.
- (8) LEYDIG, *Lehrbuch d. Histologie des Menschen u. d. Thiere*, 1857.
- (9) SOLGER, "Neue Untersuchungen zur Anatomie der Sectenorgane der Fische," *Arch. für mikro Anat.*, 1879-80.

## EXPLANATION OF PLATES.—PLATE I.

Fig. 1. The sensory canals of the head and part of the lateral canal of the trunk, and the nerves which innervate their sense organs. The position and relations of the various canals and nerves have been represented as accurately as possible from actual dissections.

S.O.—S.O.<sup>4</sup>, The supra-orbital canal. S.O., where the canal begins on the dorsal surface in connection with the infra-orbital; S.O.<sup>1</sup>, the middle of the great dorsal outward curve; S.O.<sup>2</sup>, where the canal dips into the snout to reach the under surface; S.O.<sup>3</sup>, the canal as it arches over the nasal capsule; S.O.<sup>4</sup>, the end of the supra-orbital canal communicating with the infra-orbital. The tubules by which the canal communicates with the exterior are shown on the right side; the ventral part of the canal is represented by dotted lines.

s.o.f., The superficial ophthalmic branch of the facial nerve. On the right side it is represented as giving off numerous branches which enter the canal and terminate in the sense organs (hillocks); s.o.f.<sup>2</sup>, the deep or ventral branch which supplies the distal portion of the supra-orbital canal. The ophthalmic branch is represented as being intimately related at its origin with the buccal (*bu.*) and hyomandibular (*hm.*) branches. The fibres which supply the ampullæ of the ophthalmic group of ampullary canals are not figured. s.o.f.<sup>1</sup>, the ganglion of the superficial ophthalmic branch of the facial.

I.O.—I.O.<sup>5</sup>, The infra-orbital canal. I.O., the infra-orbital in contact with the supra-orbital; I.O.<sup>1</sup>, where the canal, after it has reached the ventral aspect, communicates with the hyomandibular (*HM.*); I.O.<sup>2</sup>, where it communicates with the supra-orbital; I.O.<sup>3</sup>, the ventral loop; I.O.<sup>4</sup>, where the two infra-orbitals meet in the middle line; I.O.<sup>5</sup>, the infra-orbital terminating at the front of the snout. The tubules are as far as possible represented on the left side of the figure; the ventral tubules have been represented as running obliquely outwards, but in reality the majority of them project directly downwards from the under surface of the canal. *ot.*, the (otic) part of the infra-orbital canal continuous with the lateral canal (*lp.*); *bu.*, the buccal branch of the facial; on the left side, the buccal branches to the infra-orbital canal are shown; *ot.n.*, the branch to the otic portion of the infra-orbital springing from the buccal ganglion (*bu.gl.*); *bu.<sup>1</sup>*, the inner branch of the buccal which supplies the greater part of the canal beyond its connection with the supra-orbital, and also the inner buccal group of ampullæ; *bu.<sup>2</sup>*, the outer branch of the buccal which sends the most of its fibres to the outer buccal group of ampullæ.

HM.—HM.<sup>1</sup>, The Hyomandibular canal. *hm.*, the hyomandibular branch of the facial with its ganglion (*hm.gl.*). It sends most of its fibres to the hyoid group of ampullæ, but a slender branch, *hm.<sup>1</sup>*, supplies the sense organs of the hyomandibular canal.

\* A more complete list will be found appended to the paper on *Læmargus*.

*L.lp.lc.*, The lateral canal. *lp.*, the most anterior part continuous with the otic portion of infra-orbital; *lc.*, the commissure connecting the two canals; *L.*, the anterior portion of the trunk canal—the tubules are shown on right of figure; *l.*, the lateralis nerve arising above the level of the glossopharyngeal nerve; *l.gl.*, the ganglion of the lateralis; *l.<sup>1</sup>*, the first branch passing to the sense organs of the commissure and the precommissural part of the lateral canal—this branch may contain some glossopharyngeal fibres; *l.<sup>2</sup>*, the second branch supplying sense organs of anterior part of trunk canal; *n.a.*, nasal aperture; *E.*, eye; *sp.*, spiracle; *mo.*, mouth; *lf.*, labial fold; *a.p.*, auditory pores; *fa.*, facial nerve—the homologue of facial in higher vertebrates; *pl.*, its palatine branch; *ps.*, pre-branchial, and *p.b.*, post-branchial branches; *s.f.*, the most superficial root fibres of facial, some of which pass to all three supra-branchial nerves—these fibres probably innervate the ampullæ of the ampullary canals; *v.gl.*, large ganglion of vagus with which the branchial branches (*b.<sup>1</sup>–b.<sup>4</sup>*) and the intestinal branch are connected.

## PLATE II.

Fig. 2. Diagram to indicate the distribution of the dorsal branches of the cranial nerves. *Pr.*, Ophthalmicus profundus, springing from brain in front of the trigeminal (*Tr.*); *o.n.*, root of profundus (oculo-nasal); *o.n.g.*, ganglion of profundus; *o.n.<sup>1</sup>*, dorsal branch of profundus; *lc.*, long ciliary branches; *or.*, orbital branch; *l.r.*, long root of ciliary ganglion; *o.m.*, deep branch of oculo-motor giving off short root (*s.r.*) of ciliary ganglion (*c.g.*); *s.c.*, short ciliary nerves passing to eyeball.

*Tr.*, Trigeminus. *t.r.*, trunk of trigeminus near Gasserian ganglion (*G.*); *s.o.t.*, dorsal or superficial ophthalmic branch of trigeminus; *mx.*, maxillary (pre-branchial) branch; *md.*, mandibular (post-branchial) branch; *mo.*, mouth.

*Fa.<sup>1</sup>*, Four roots, the fibres of which are rearranged to form the three supra-branchial branches of the facial (the superficial ophthalmic, buccal, and hyomandibular), which innervate the five groups of ampullæ, and the supra-orbital, infra-orbital, and hyomandibular sensory canals.

*Fa.*, Root of the nerve which corresponds to the facial of higher vertebrates. It lies in contact with, and receives a communicating branch from, the auditory nerve (*Au.*).

*s.o.f.*, The first dorsal branch of facial—the ophthalmicus superficialis—which supplies the supra-orbital canal (*S.O.*), the superficial ophthalmic group of ampullæ (*S.O.A.*). *s.o.f.<sup>1</sup>*, the ganglion; *s.o.f.<sup>2</sup>*, the ventral branch passing to the terminal portion of the supra-orbital canal (*S.O.*).

*bu.*, The second dorsal branch of facial—the buccalis—which supplies the infra-orbital canal (*I.O.*), and the inner (*I.B.A.*) and outer (*O.B.A.*) buccal groups of ampullæ. *bu.*, the ganglion on the buccal nerve, from which a branch springs to supply the proximal part of the infra-orbital canal; *bu.<sup>1</sup>*, the inner division of the buccal which innervates the inner buccal group of ampullæ (*I.B.A.*) and the greater part of the infra-orbital canal beyond its connection with the supra-orbital; *bu.<sup>2</sup>*, the outer division of the buccal which supplies part of the infra-orbital canal and the outer buccal group of ampullæ (*O.B.A.*); *hm.*, the third dorsal branch of facial—hyomandibularis—which innervates the hyoid and mandibular groups of ampullæ, and the hyomandibular canal, including the ventral loop, the dorsal extension, and the mandibular part, when present; *h.g.*, the ganglion of the hyomandibular lying in contact with the ganglion of the facial proper (*fa.*); *hm.<sup>1</sup>*, the large branch for the hyoid group (*H.A.*) of ampullæ; *hm.<sup>3</sup>*, the branch which supplies the mandibular group of ampullæ (*M.A.*), and the mandibular canal (*m.c.*)—the mandibular offshoot and the mandibular group of ampullæ are both absent in *Læmargus*; *sp.*, spiracle.

*fa.*, The homologue of the facial of higher vertebrates. *pl.*, palatine which passes from the ganglion to roof of mouth; *p.s.*, pre-branchial fibres to the spiracle; *p.b.*, post-branchial branch which passes behind spiracle, and eventually reaches the mucous membrane over the hyoid arch; *m.f.*, motor fibres which leave this nerve to supply some of the jaw muscles.

*Au.*, The auditory nerve passing to the auditory apparatus (*A.A.*). *a.*, auditory pore; *Gl.*, glossopharyngeal nerve arising under cover of the lateralis; *gl.*, its ganglion, beyond which are the pharyngeal pre- and post-branchial branches; *gl.*, the dorsal branch represented as supplying

- (1) a short segment (T.T.) of the great longitudinal canal immediately behind the infra-orbital canal, and (2) a row of pit organs (*p.o.*). That the dorsal branch of the glossopharyngeal innervates sense organs and pit organs in Selachian as in *Amia* has not yet been demonstrated.
- T.T., The part of the longitudinal canal which the glossopharyngeal might be expected to innervate in a typical Selachian. This might be known as the glossopharyngeal or temporal canal. 1 *br.*, first (glossopharyngeal) branchial cleft.
- La., Lateralis nerve. *lg.*, lateral ganglion; *l.*<sup>1</sup>, first branch passing to the temporal commissure (*lc.*), and the anterior part of the lateral canal (*L.*).
- l.*<sup>1</sup>, Branch springing from the ganglion to supply part of the canal and the anterior follicles or pit organs (*p.o.l.*). *ln.*, the lateral extending backwards, nearly parallel with the lateral canal (*L.*).
- V.<sup>1</sup>–V.<sup>3</sup>, The first three branchial branches of the vagus, each with a ganglion (II.–IV.), pharyngeal pre- and post-branchial branches.
- V.<sup>4</sup>–V.<sup>5</sup>, The united fourth branchial and intestinal branches of vagus. V., ganglion of vagus IV.; *igl.*, ganglion at root of intestinal branch (*in.*); 2 *br.*–5 *br.*, second to fifth branchial (vagus) clefts.
- Fig. 3. The Cranial Canals of *Amia*. This figure has been introduced to admit of a comparison between *Amia* and Selachians, and to indicate the new system of grouping the canals. The details are from a figure by ALLIS (30), with which it should be compared.
- S.O., Supra-orbital canal. *s.o.f.*, superficial ophthalmic of facial supplying the canal and a row of pit organs (*s.p.*).
- I.O., Infra-orbital canal. *ot.n.*, the otic branch of facial which supplies the sense organs 15 and 16 of the first segment (*ot. ot.*<sup>1</sup>) of the infra-orbital; *bu.*, the buccal nerve supplying the infra-orbital canal, with the exception of the otic part. H.M., the hyomandibular canal extending downwards from the proximal end of the infra-orbital to run along the mandible; *hm.*, the hyomandibular nerve supplying the hyomandibular and four rows of pit organs.
- T., Temporal canal lying between infra-orbital and lateral. *gl.*<sup>1</sup>, glossopharyngeal nerve supplying the single sense organ of the temporal canal and a row of pit organs; *gl.*, ganglion of glossopharyngeal nerve.
- L., Lateral canal beginning at the posterior end of the temporal and extending on to the trunk. *lc.*, supra-temporal commissure; *l.*, lateral nerve; *l.*<sup>1</sup>, first branch supplying commissure, a line of pit organs, and two sense organs of the main canal; *l.*<sup>2</sup>, second branch supplying a sense organ and a row of pit organs (*p.o.*); *l.*<sup>3</sup>, a third branch supplying the sense organ (21), which, according to ALLIS, lies at the junction of the infra-orbital and lateral canals.
- Figs. 4 and 5. Sensory Canals of *Chlamydoselachus* (after GARMAN). *cr.*, *r.*, *sr.* = supra-orbital canal; *orb.*, *on.*, *n.*, *pn.* = infra-orbital; *oc.*, *au.* = precommissural and commissural parts of lateral canal (*l.*); *ang.*, angular; *j.*, jugular; *o.*, oval; *g.*, gular; *sp.*, spiracular—part of hyomandibular canal.

## PLATE III.

- Figs. 6 and 7. Sensory Canals of *Raia batis*. S.O.–S.O.<sup>3</sup>, Supra-orbital canal. S.O., proximal part; S.O.<sup>1</sup>, beginning of rostral portion; S.O.<sup>2</sup>, point where canal penetrates snout to reach ventral aspect; S.O.<sup>3</sup>, S.O.<sup>4</sup>, ventral loop; S.O.<sup>5</sup>, canal joining infra-orbital; *t.*<sup>7</sup>, *t.*<sup>23</sup>, *t.*<sup>33</sup>, *t.*<sup>45</sup>, tubules.
- s.o.f.*, Superficial ophthalmic branch of facial with ganglion on root. It supplies supra-orbital canal and the ophthalmic group of ampullæ. *v.b.*, ventral branch passing to sense organs of ventral portion of canal; S.O.A, position of superficial ophthalmic group of ampullæ.
- I.O.–I.O.<sup>8</sup>, Infra-orbital canal. I.O., canal continuous with lateral canal and communicating with supra-orbital; I.O.<sup>1</sup>, sub-orbital portion; I.O.<sup>2</sup>, canal passing to ventral surface; I.O.<sup>3</sup>, beginning of ventral portion; I.O.<sup>4</sup>, its communication with supra-orbital; I.O.<sup>5</sup>, canal communicates with hyomandibular and bends inwards; I.O.<sup>6</sup>, part of canal which dips into buccal groove; I.O.<sup>7</sup>, union of two infra-orbitals in front of mouth; I.O.<sup>8</sup>, union of two infra-orbitals at tip of snout; *t.*<sup>1</sup>, *t.*<sup>13</sup>, *t.*<sup>39</sup>, *t.*<sup>50</sup>, tubules of canal; *bu.*, buccal nerve with ganglion on its root, supplying infra-orbital canal and inner and outer buccal groups of ampullæ; *bu.o.*, branch for first part of canal—this branch probably supplies the sub-orbital row of pit organs, *p.o.*<sup>2</sup>; *bu.*<sup>2</sup>, outer division of buccal

passing to outer buccal group of ampullæ; O.B.A., part of the dorsal and part of the ventral portion of the infra-orbital canal; *bu*.<sup>1</sup>, inner division of buccal passing to inner buccal group of ampullæ and the infra-orbital canal from its junction with the hyomandibular.

HM.-HM.<sup>7</sup>, Hyomandibular canal. HM., canal communicating with the infra-orbital (I.O.<sup>5</sup>); HM.<sup>1</sup>, end of ventral loop; HM.<sup>2</sup>, outer limb of loop bends inwards; HM.<sup>3</sup>, canal passing to dorsal surface; HM.<sup>4</sup>, canal as it reaches dorsal surface; HM.<sup>5</sup>, expanded part communicating with tubules of infra-orbital; HM.<sup>5</sup>-HM.<sup>6</sup>, long dorsal extension which terminates in scapular offshoot from lateral canal; HM.<sup>7</sup>, mandibular portion of hyomandibular canal; *t*.<sup>11</sup>, *t*.<sup>15</sup>, *t*.<sup>54</sup>, *t*.<sup>67</sup>, tubules; *hm*., hyomandibular nerve; *hm.g.*, its ganglion; *hm*.<sup>2</sup>, branches passing in front of or through the hyoid group of ampullæ (H.A.) to innervate the sense organs of the various parts of the hyomandibular canal, with the exception of the mandibular portion; *hm*.<sup>1</sup>, branch for the mandibular group of ampullæ (M.A.) and the mandibular portion (HM.<sup>7</sup>) of the hyomandibular canal.

L.-L.<sup>3</sup>, The lateral canal. *l.p.*, the precommissural part, and *l.c.* the commissural part, of lateral canal; *sc.*, scapular offshoot; *p.sc.*, post-scapular offshoot; *p.o*.<sup>1</sup>, lateral row of pit organs; *p.o.*, pit organs near the auditory pore (*a.*).

*l*.-*l*.<sup>2</sup>, Lateralis nerve. *l.g.*, its ganglion; *l.t.*, branch which innervates half of commissure (*l.c.*), part of lateral canal in front of commissure (*l.p.*), and anterior part of main canal; *l.sc.*, branch for scapular offshoot (*sc.*); *l.p.sc.*, branch for post-scapular offshoot; *l*.<sup>1</sup>-*l*.<sup>2</sup>, lateral giving off branches to sense organs of lateral canal posterior to shoulder girdle.

Fig. 6a. Transverse section through snout of young (just hatched) *R. batis*. S.O., supra-orbital canal (rostral part); S.O.<sup>1</sup>, ventral part of the same canal (subrostral); I.O., infra-orbital canal (prenasal part); *r.*, cartilage of rostrum; *a.c.*, ampullary canals from superficial ophthalmic group of ampullæ; *g.c.*, goblet cells of skin.

Fig. 8. Transverse section through lateral canal of a young (just hatched) *R. batis*, showing the thick cartilaginous lateral walls, and thin roof and floor. *s.o.*, the sense organ on inner wall of canal; *g.c.*, goblet cells of skin.  $\times 120$ . From a photograph.

Fig. 9. Transverse section through a ventral subcutaneous canal (ventral part of supra-orbital), showing the large sense organ (*s.o.*) lying in the roof of the canal, and some of the connective tissue in which the canal is embedded.  $\times 300$ . From a photograph of a section of a *R. batis* 16.5 cm. long.

Fig. 10. Transverse section through a pit organ, showing the sense organ at the bottom of the involution. From near root of tail of a young *R. batis*.



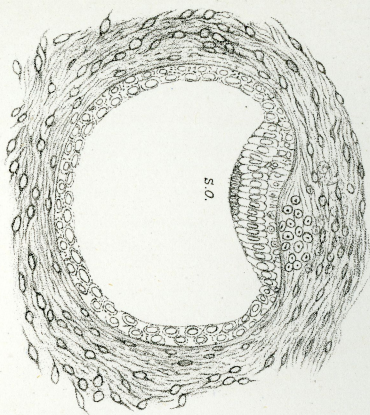


Fig. 9.

Fig. 8.

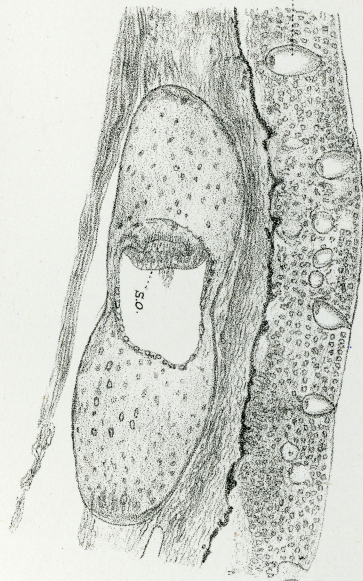


Fig. 10.

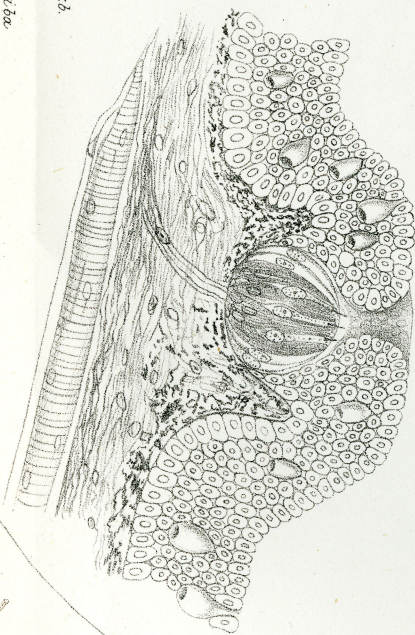


Fig. 7.

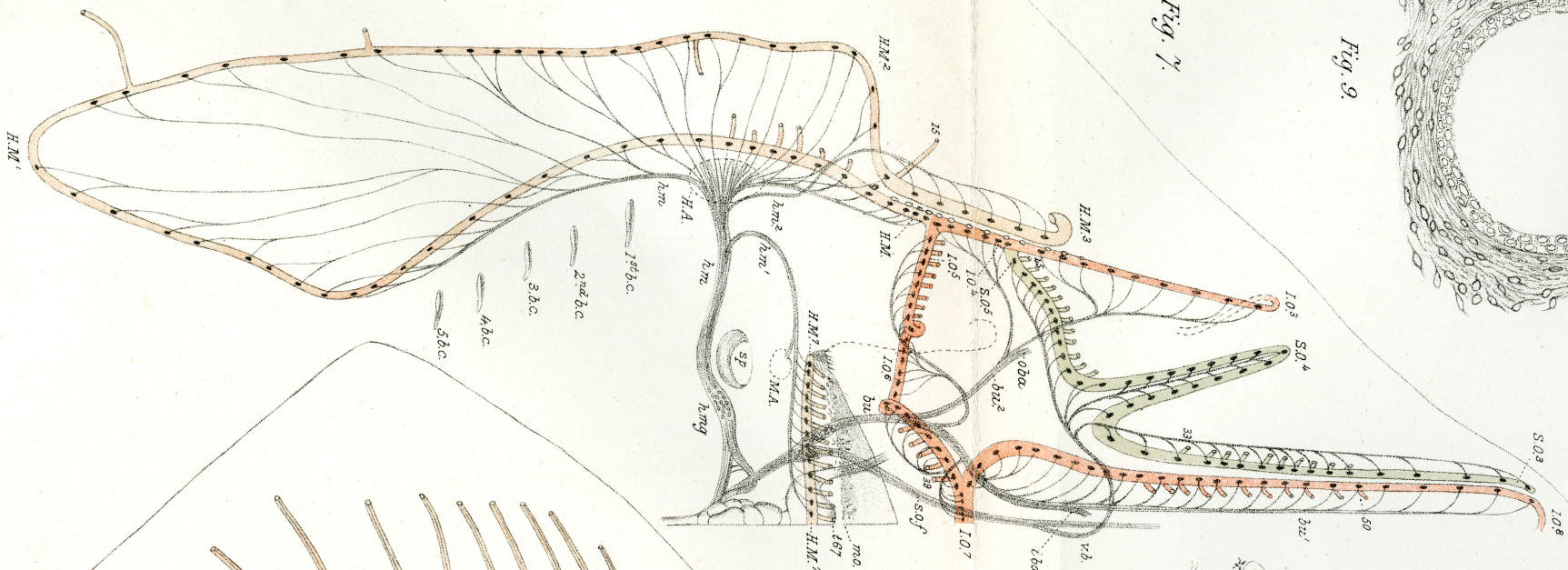


Fig. 6.



Fig. 6a.

