The Autonomic Nervous System of the Chimaeroid Fish

Hydrolagus colliei

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With two Plates

SUMMARY

The autonomic nervous system of the chimaeroid fish Hydrolagus colliei has been investigated by dissections and histological methods. It consists of a cranial parasympathetic portion and a sympathetic portion confined to the trunk. The latter extends from the level of the heart to the anus and consists of segmentally arranged ganglia on each side of the dorsal aorta. These ganglia are closely associated with small accumulations of suprarenal tissue. Two axillary bodies are the largest of the sympathetic and suprarenal structures. They lie about the subclavian arteries and are made up of a gastric ganglion and a relatively large mass of chromaffin tissue. The sympathetic ganglia lie in an irregular plexus of longitudinal and crossing sympathetic strands but there is no regular sympathetic chain or commissure between ganglia. There are white rami communicantes which connect the sympathetic ganglia with spinal nerves. A small pregastric ganglion lies on the rami communicantes to the gastric ganglion. The visceral nerves arising from the sympathetic ganglia proceed to blood-vessels, genital ducts, chromaffin tissue, and gut. The latter is supplied by large splanchnic nerves which originate in the gastric ganglia and proceed along the coeliac axis to the intestine, pancreas, and liver. Prevertebral ganglia are absent. A mucosal and a submucosal plexus are present in the intestine. The cranial component of the autonomic system comprises a midbrain and a hindbrain outflow. In the former there is a ciliary ganglion on the inferior oblique branch of the oculomotor nerve. Short ciliary nerves proceed from this branch to the eyeball. A radix longa is absent. Sensory fibres go directly to the eyeball from the profundus nerve as anterior and posterior long ciliary nerves. The hindbrain outflow comprises scattered nerve-cells and ganglia on post-trematic branches of the glossohyrgeal and vagus nerves. These autonomic fibres in the branchial nerves innervate smooth muscle in the pharyngeal region. A visceral branch of the vagus innervates the heart, oesophagus, and intestine; it also establishes a connexion with the pregastric ganglion. In general, the autonomic nervous system of Hydrolagus is very similar to that of selachians. It appears that the autonomic systems of these two groups have undergone little alteration since their origin in the Palaeozoic from some common form. Their autonomic systems reflect a simple and primitive level of organization from which more complex systems of the bony fishes and amphibians have evolved.

THE autonomic nervous system of selachians (sharks and rays) has been studied by several workers and detailed accounts are available for this group. In organization and function it shows a number of peculiar features of a primitive nature when compared with higher vertebrates. The selachians themselves are a primitive group and the arrangement of their autonomic system represents a simple level of organization from which the more complex systems of teleostomes and tetrapods could have evolved. There is another and quite distinct group of elasmobranchs, however, in which the autonomic system is very imperfectly known: these are the chimaeroid fishes or Holocephali. Since a representative of this group is common locally in British Columbian waters, namely the ratfish, *Hydrolagus colliei*, an investigation of its autonomic nervous system has been initiated. The object of this study has been to obtain sufficient data to determine the morphological organization of its autonomic nervous system. With this pattern established comparisons will be made with the autonomic systems of other recent elasmobranchs, and the evidence obtained will be discussed in terms of the phylogeny of the system.

Owing to unforeseen circumstances it has not been possible to pursue this investigation so as to reach all objectives that were set. However, it is believed that the information obtained is sufficient to warrant publication in its present form, and that it represents a useful whole.

Only a few authors have referred to the autonomic system of chimaeroid fishes. Leydig (1851, 1853) showed that the so-called axillary hearts on the subclavian arteries of *Chimaera* and selachians are not contractile structures, but comprise suprarenal tissue comparable to the adrenal medulla of mammals. Additional segmentally arranged suprarenal bodies occur on the segmental arteries and are closely related to the sympathetic ganglia. Chevrel (1887) had a single alcohol-preserved specimen available for examination. He stated that the sympathetic system resembles that of dogfishes and rays. The first suprarenal body is situated on the subclavian artery and is followed by 12 to 14 similar bodies which continue to the posterior end of the abdomen.
Chevrel also distinguished several visceral nerves. However, no details are available for sympathetic ganglia, connectives, distribution of visceral nerves, and relations with the parasympathetic system. Finally, Schwalbe (1879) and Cole (1896) have described the ciliary ganglion of *Chimaera monstrosa*.

**MATERIAL AND METHODS**

Specimens of *Hydrolagns colliei* (Lay and Bennett) were obtained from shrimp trawlers operating in the Gulf of Georgia in the vicinity of Vancouver harbour. It was only occasionally possible to obtain specimens of fish alive since they live for only a few hours after capture, even when placed in aerated sea-water. Specimens and tissues were preserved either at the time of capture, or soon after the return of the boat. Fresh specimens and formalin-preserved specimens were dissected and the course of nerves followed either by naked eye or under a binocular microscope. In order to facilitate observation the nerves were blackened by the application of a solution of osmium tetroxide.

For the study of microscopic anatomy and histology, material was fixed as a routine in 10 per cent. formol and in Bouin's fluid. Two determinations of freezing-point depression of whole blood (mean \( \Delta = 1.49 \)) and a study of haemolysis in saline solutions of different concentrations indicated that the blood of this species has an osmotic pressure equivalent to a 2:6 or 2:7 per cent. solution of NaCl. After these determinations 27 gm. of NaCl were added to each litre of fixing fluids whenever possible to improve cellular preservation (Young, 1933a).

Sections were stained with Harris’s haematoxylin and eosin, toluidine blue and safranin, or impregnated with silver. Two silver-on-the-slide methods were used with success and gave similar results, namely, Bodian's activated protargol and Holmes's buffered silver-pyridine method (Holmes, 1947). In preparing the incubating solution for Holmes's method, a pH of 8:4 and a silver concentration of 1/50,000 were used. Greater differentiation between nervous and connective tissues was obtained with formol-fixed material. After Bouin-fixation all fibrous and cellular elements tended to be equally darkened. Serial sections of specimens about 5 in. long were especially valuable for establishing details of micro-anatomy. These are later referred to as small specimens. In addition, some frozen sections were treated by the Gros-Bielschowsky method.

**OBSERVATIONS**

*Sympathetic Ganglia and Cells*

Sympathetic ganglia are confined to the trunk and form a bilaterally arranged series extending from the subclavian artery to the level of the anus. Generally there are two ganglia to each spinal segment but additional ganglia are often present (Text-fig. 1). The ganglia are intimately related to the suprarenal bodies, and are found near the latter structures or fused with them. The first ganglia of this series are the two ‘gastric’ ganglia which lie ventral to the
TEXT-FIG. 1. Outline drawing of the sympathetic nervous system of the ratfish. Dissection exposing the dorsal body wall of an adult \( \varphi \), \( \times \) about \( 1:1 \).
subclavian arteries near their origin from the dorsal aorta. These ganglia are closely associated with the first suprarenal bodies, and the whole complex of gastric ganglion and suprarenal body is termed the axillary body (Pl. I, fig. 1). This complex is organized in a similar manner to, and is homologous with, the axillary body of selachians (Chevrel, 1887; Leydig, 1851, 1852; Young, 1933a). In selachians, the axillary body supplies visceral nerves to the anterior viscera, including the stomach. In chimaeroids, however, a stomach is wanting. The absence of a stomach is probably a secondary feature, and the term 'gastric' ganglion is retained for reasons of homology and convenience.

The gastric ganglion lies in the wall of the posterior cardinal sinus. Posterior to this level the details differ somewhat for the two sexes but the fundamental pattern is similar. The mesonephros extends far forwards in the male. Between the level of the gastric ganglion and the mesonephros there are about three small sympathetic ganglia on each side of the median axis (Text-fig. 2). In the female the mesonephros lies more posteriorly and there are many more sympathetic ganglia in the interval between the gastric ganglia and the kidney (Text-fig. 1). They lie in the dorsal wall of the posterior cardinal sinuses, near the outer angle of the haemal ridges of the vertebrae. The ganglion cells are situated in discrete groups or they are conjoined to the suprarenal bodies. The segmental arrangement of anterior sympathetic ganglia and suprarenals is revealed by their association with segmental arteries proceeding to the body-wall.

In the kidney region the sympathetic ganglia and suprarenals shift ventrally and come to lie in the inferior wall of the posterior cardinal veins above each kidney (Pl. I, figs. 3, 4). The ganglia maintain their segmental arrangement, one or several ganglia corresponding to each spinal nerve. Renal ganglia and suprarenals tend to be larger than more anterior sympathetic ganglia, with the exception of the axillary body. They continue to the posterior abdominal region and stop at the level of the anus. No ganglion occurs in the small post-anal mesonephros which extends into the beginning of the tail, or in the haemal canal. In the posterior kidney region the ganglia become very small.

The arrangement of ganglionic and suprarenal tissues in *Hydrolagus* is very similar to that found in selachians. Chevrel (1887) distinguished two groups of ganglia, one group lying in front of the kidney, and a second group lying above the kidney. The latter group is also characterized by its more segmental arrangement according to this author. Young (1933a), however, has shown that such a distinction is a very difficult one to maintain, the ganglia of both groups forming part of one continuous segmental series. The same arrangement obtains in *Hydrolagus* where all the ganglia constitute a homogeneous system. *Hydrolagus* also agrees with other elasmobranchs in the absence of a caudal sympathetic system. Ganglia, longitudinal cords, and ganglion cells are definitely absent from the haemal canal both of adults and of the smallest specimens that we have been able to obtain (5 in. in length). Hoffmann (1900) and Young (1933a) identified caudal sympathetic ganglia in embryos of *Scyllium*, *Squatus*, and *Torpedo*, but they disappear in the adult.
The sympathetic ganglia frequently bulge into the cavity of the posterior cardinal veins. In the kidney region the ganglion cells lie in the median portion of the suprarenal mass, or occur as discrete ganglia separate from the suprarenal. They are also closely related to the segmental and renal arteries.
dorsal aorta. These groups are connected with the ganglia by small sympathetic nerves (Text-fig. 3). Young (1933a) has figured a similar arrangement in selachians, where one or several ganglia lie median and ventral to the segmental ganglia on the proximal course of the visceral nerves. These secondary ganglia are rather infrequent in *Hydrolagus* and may be regarded as fortuitously segregated components of the main ganglia.

The gastric ganglia are preceded by several diffuse 'pregastric' ganglia. The pregastric ganglia occur on the course of the rami communicantes leading from anterior spinal nerves to the gastric ganglia. They may be found in the superficial dorsal wall of the oesophagus, just beneath the posterior cardinal sinus. Each visceral vagal nerve, on entering the oesophageal wall, also sends a short branch dorsally to the ipsilateral pregastric ganglion. Similarly arranged pregastric ganglia and vagal connexions have been described in other elasmobranchs. In *Scyllium*, Chevrel (1887) observed several small ganglia on the rami communicantes supplying the gastric ganglion, and Young (1933a) found that there is often a small ganglion on the course of the anterior rami communicantes at the front end of the cardinal sinus. Both these authors have also described a connexion between the gastric ganglia and the visceral vagus in selachians. Chevrel claimed that sympathetic fibres proceed anteriorly into the oesophagus to reach the vagus nerve. Young found a similar connexion in some specimens of *Scyllium*, but regarded it as a contribution of preganglionic fibres from the vagus to the gastric ganglion. In *Hydrolagus* the connexion of the pregastric ganglia with the vagus is comparable to the similar junction between sympathetic and parasympathetic in selachians.
The exact relationship is uncertain: it may represent a vagal contribution of pre-ganglionic fibres in the nature of a ramus communicans to the pregastric and gastric ganglia, but the possibility cannot be excluded that these vagal fibres are discrete and run through sympathetic pathways to the end-organs.

A detailed cytological study of the sympathetic nerve-cells was not completed, but within certain limits it was observable that these cells in the rat-fish display the characters typical of such neurones. All ganglionic neurocytons are encapsulated and surrounded by satellite cells (Text-fig. 4). They are about 35μ in diameter (in the adult animal), but occasionally they are very large and of bizarre shape (Text-fig. 4b). They are usually uninucleate, but binucleate cells are frequent, and some are even multinucleate; one or two large nucleoli are present. Multipolar cells can be observed with one large axonal process; possibly all cells are of this category. Within the ganglia extra-capsular dendrites and pre-ganglionic fibres ramify in an intricate network among the nerve-cells. Large pre-ganglionic fibres appear to be wrapped about the cell bodies, and other fine fibres—subcapsular dendrites—encircle their cells. The picture is one of considerable complexity, but there are obvious opportunities for contact and trans-synaptic transmission, without invoking a neurosyncytial hypothesis (cf. Nonidez, 1944). Young (1933) has described and figured the autonomic neurocytons of selachians in greater detail. Besides encircling whirls of dendrites and axons, he found dense extra-
capsular glomeruli permitting association between pre- and post-ganglionic fibres, and extra-capsular boutons on amphibocytes. Diamare (1901) also has described multinuclear sympathetic nerve-cells in selachians.

**Connectives and Commissures**

Not only do the sympathetic ganglia display considerable irregularity in arrangement but there is also a great deal of variation in the sympathetic connectives. There is no definite transverse commissure between ganglia of the same segment. Posterior to the axillary body longitudinally arranged sympathetic strands occur in the dorsal abdominal wall near the median axis (Text-figs. 1, 2, 5, 6). In the anterior abdominal region these nerves are rather scanty, but in the posterior half of the abdomen, above the kidney, they become numerous and conspicuous. The longitudinal strands interconnect with one another to form an irregular plexus which lies lateral and ventral to the dorsal aorta, and which contains the sympathetic ganglia. Longitudinal nerves may link together two successive sympathetic ganglia, or may bypass one or several ganglia. Some nerves do cross the mid-line, but they usually interconnect nerve strands, not ganglia.

The efferent fibres in the sympathetic nerves are small in diameter, and are lightly myelinated or unmyelinated. Occasional sensory fibres occur: these are conspicuous by virtue of their larger diameters and thicker myelin coverings. Many of the fibres in these strands are post-ganglionic axons which travel some distance longitudinally before entering visceral nerves and proceeding to the end-organs.

In dogfishes and rays a similar diffuse and irregular arrangement of sympathetic strands has been noted by several workers. Chevrel (1887) considered that a true sympathetic cord is absent in selachians (Scyllium and Acanthias). In general all the sympathetic ganglia are united among themselves in a coarse network. However, a connecting cord may be absent between two successive ganglia or, when present, it may be divided into two or three fine strands and have an irregular course. Hoffmann (1900), in a study of the development of Acanthias, concluded that longitudinal connectives between ganglia are either absent or are extremely tenuous. Müller (1920) observed longitudinal connectives in the Squalus embryo, but noted that they are very thin. In Raja, Müller and Liljestrand (1919) found that although ganglia are bound together by longitudinal anastomoses, such connexions vary considerably. Young (1933a), in Scyllium, &c., noted that ganglia of succeeding segments are sometimes joined together by longitudinal nervous strands, but often no such connexion is present. He concluded that a definite sympathetic chain, such as occurs in teleosts and tetrapods, is certainly lacking.

Fine rami communicantes extend from the spinal nerves to the sympathetic system. Only white rami of lightly myelinated fibres have been observed but, owing to the extreme tenuity of the rami communicantes, the possibility exists that fine grey rami are present and have been overlooked. The rami are segmentally arranged: they arise some distance laterally from the ventral
rami of the spinal nerves, and extend medially to terminate in sympathetic ganglia or the longitudinal sympathetic strands. The large gastric ganglia are composite structures and are connected with a number of anterior spinal nerves. In *Chimaera monstrosa*, Chevrel (1887) found that these ganglia receive at least five rami communicantes from anterior spinal nerves.

The axillary bodies in selachians are similarly of composite origin, as evidenced by their embryonic history and their connexions in the adult. The
the Chimaeroid Fish Hydrologus colliei

gastric ganglia receive a variable number of rami from anterior spinal nerves, the exact number varying with the individual animal and the species (Young, 1933a). Chevrel (1887) observed from 10 to 15 rami in Scyllium, Raja, and Torpedo. That the multiplicity of rami results from fusion of a corresponding number of ganglia is shown by the fact that, in embryo Squalus, the gastric ganglia are formed by union of sympathetic anlagen of segments 1 to 14 (Müller, 1920). Similarly, in Acanthias, sympathetic anlagen of segments 6 to 15 fuse together in varying degrees to form the gastric ganglia during development (Hoffmann, 1900).

The nature of the rami communicantes in selachians has been investigated in some detail by Young (1933a). He found that only white rami of pre-ganglionic fibres occur in these forms; such post-ganglionic fibres as do extend to the body-wall accompany the segmental arteries. In some teleosts at least (Young, 1931a), and in tetrapods (Gaskell, 1920; Langley, 1921), as is well known, post-ganglionic fibres reach peripheral blood-vessels and dermal structures via recurrent grey rami and the spinal nerves.

Visceral Nerves and Post-ganglionic Pathways

The sympathetic system supplies post-ganglionic fibres to the walls of blood-vessels. These fibres arise from the sympathetic ganglia and proceed to the dorsal aorta or accompany the segmental and visceral arteries. Other nerves leave the sympathetic ganglia and proceed to the abdominal viscera.

The alimentary tract of chimaeroids is peculiar in that there is no stomach, and in that the dorsal mesenteries are reduced to small strands enveloping the

![Text-fig. 6. Semi-diagrammatic representation of the sympathetic system as seen in longitudinal sections. Dorsal body wall of a young specimen, in the region of the kidney. Based on superimposed tracings of microscopic projections of serial sections. × 14.](image-url)
coeliac axis and the two mesenteric arteries. The oesophagus passes directly into the duodenum; the wall of the former contains only striated muscle. Following the short duodenum there is a long ileum containing a spiral valve. Behind the ileum there is a short rectum which ends at the anus. The walls of the rectum contain smooth muscle. The urogenital apertures are separate and there is no cloaca.

The coeliac axis supplies the posterior oesophagus, duodenum, liver, and pancreas, and sends branches to the anterior ileum. The anterior mesenteric artery crosses the right face of the pancreas, to which it sends branches, gives rise to the splenic artery, and provides arteries for the dorsal and ventral surfaces of the ileum. The posterior mesenteric artery runs to the dorsal surface of the posterior ileum. Accompanying these several visceral arteries are cords or bands of smooth muscle, particularly between the pancreas and ileum where the muscle forms two flat bands of considerable magnitude. The muscular bands act as slings, suspending the ileum and neighbouring viscera within the abdominal cavity.

Post-ganglionic neurones and a myenteric plexus occur just within the serosa in the duodenum and ileum, but not in the oesophagus or rectum. A submucosal plexus is also located in the ileum. The vagal supply to the oesophagus may be classified as a special visceral efferent. The innervation of the rectum presents certain peculiarities which are discussed below.

The gastric ganglia give rise to the anterior splanchnic nerves in the following manner. Two or three main nerves and several smaller twigs originate from the median face of each gastric ganglion, and these nerves extend to the coeliac axis, where they form a plexus or network in the wall of the artery. Although the right and left splanchnic nerves combine in a complex manner, there is no direct connexion or commissure between the bilateral gastric ganglia. Occasional nerve-cells occur along the course of the splanchnic nerves near their origin. The splanchnic nerves resolve themselves further distally into two main trunks lying in the wall of the artery. After giving off fibres to the ductus choledochus and anterior pancreas, the splanchnic nerves accompany the coeliac artery to the duodenum and ileum (Text-fig. 2; Pl. I, fig. 6).

The intestine, liver, pancreas, and spleen appear to receive their sympathetic innervation nearly or entirely from the anterior splanchnic nerves which accompany the coeliac artery. No comparable splanchnic nerves arise from more posterior sympathetic ganglia to accompany the anterior and posterior mesenteric arteries. On the other hand there are occasional groups of nerve-cells and stout bundles of nerve-fibres along the lower course of the anterior mesenteric branches, towards the ileum. These nerves probably proceed from the wall of the ileum to the bands of smooth muscle about the anterior mesenteric artery. There are no distinct visceral nerves along the course of the posterior mesenteric artery.

A comparable arrangement of splanchnic nerves occurs in selachians. In Scyllium and Raja there are two gastric ganglia which are independent of
the Chimaeroid Fish *Hydrolagus colliei*

Each gives rise to about three anterior splanchnic nerves which bear scattered nerve-cells on their proximal course and which continue to form a plexus about the coeliac artery. They run with the coeliac artery to supply the oesophagus, stomach, pylorus, duodenum, anterior ileum, liver, bile passages, and spleen (Babkin *et al.*, 1935; Chevrel, 1887; Müller and Liljestrand, 1919; Young, 1933a). But in addition there are middle splanchnic nerves which arise from the sympathetic ganglia of several segments, and which accompany the anterior mesenteric artery to the ileum, spleen, and possibly the pancreas (op. cit.). Posterior splanchnic nerves run as separate strands in the mesentery and along the posterior mesenteric artery to the colon and rectum (Müller and Liljestrand; Young).

The splanchnic nerves of *Hydrolagus* thus reveal some distinctive features in organization and distribution, when compared with those of selachians. Apart from the absence of a stomach and of corresponding gastric nerves, the most noteworthy feature is the absence of middle and posterior splanchnic nerves at the levels of the mesenteric arteries. Probably the explanation of these differences is to be sought in the loss of the stomach, reduction of dorsal mesenteries, and shortening of the gut and abdominal cavity (Barrington, 1942; Dean, 1906). It is noteworthy, in both *Hydrolagus* and selachians, that there are no coeliac and mesenteric ganglia on the course of the splanchnic nerves, which contain only post-ganglionic fibres.

The sympathetic supply to the kidney is confined to nerve-fibres which pass from the sympathetic ganglia along the renal arteries. No nervous termination has been demonstrated on renal tubules or glomeruli. There is some histological evidence for innervation of renal units in mammals (Maximow and Bloom, 1944), but not for selachians (Young, 1933a). The sympathetic also innervates the Müllerian ducts and vasa deferentia. The visceral nerves to these structures arise medially from the segmental ganglia; they proceed between the kidney and the subcardinal veins across the ventral face of the kidney, and terminate in a plexus in the walls of the ducts. Similarly, in *Scyllium*, Young (1933a) found that the sympathetic ganglia send nerves to the oviducts and vasa deferentia in each segment.

There are no sympathetic fibres to the heart.

At the posterior end of the abdominal cavity several small twigs arise from the ventral rami of three or four spinal nerves. These twigs contain small myelinated fibres which enter the wall of the posterior rectum near the anus, at the level of the pelvic cartilage. Sections show that these nerve-fibres proceed directly to smooth muscle in the rectal wall. In *Scyllium* and *Torpedo* the walls of the cloaca are innervated directly from several spinal nerves in the posterior abdomen (Young, 1933a). This innervation of the posterior extremity of the abdominal canal is essentially the same in both chimacroids and selachians. In neither group are there post-ganglionic cells in the nervous pathway; this feature excludes it from the autonomic system *sensu stricto*. Young has suggested the possibility that it may correspond to the anal sphincter nerves of *Uranoscopus* (Teleostei), and perhaps to the pudendal.
J. A. Colin Nicol—The Autonomic Nervous System of

nerves of tetrapods, but an homology is difficult owing to the absence of autonomic ganglia and peripheral neurones.

Relation between Sympathetic and Suprarenal Tissues

It is well known that in lower vertebrates the cortical and medullary portions of the adrenal glands are separate from one another and the medullary tissue is closely associated with the sympathetic system (Kendall, 1947). In Hydrologus the cortical or interrenal tissue forms a long median block lying beneath the dorsal aorta and between the two mesonephroi in the posterior half of the kidney. Besides the main interrenal mass there are several smaller aggregations of interrenal tissue lying more anteriorly (Text-fig. 3; Pl. I, figs. 2, 3). The interrenal tissue receives no sympathetic supply. The suprarenal tissue occurs as segmentally arranged bodies associated with the sympathetic ganglia from the axillary body to the level of the anus (Pl. I, figs. 1, 2, 3, 5; Pl. II, fig. 7).

The axillary bodies contain the largest mass of suprarenal tissue in the body. They completely envelop the subclavian arteries and are suspended in the posterior cardinal sinuses. Each body is made up of densely packed suprarenal cells which are irregular or stellate in shape and which bear long processes. The cytoplasm is basophilic and the nuclei are rather small and densely staining. Nerve-fibres entering this body proceed among the suprarenal cells. The smaller gastric ganglion is attached to the medio-ventral face of each suprarenal mass. Occasional sympathetic cells are also distributed about the periphery of the suprarenal body, and within the latter structure (Text-fig. 2; Pl. I, figs. 1, 5; Pl. II, fig. 7).

Small aggregations of suprarenal tissue are associated with the anterior sympathetic ganglia. Within the kidney region the suprarenal bodies and the sympathetic ganglia are inextricably fused, forming conjoined gangliomedullary units. The suprarenal (chromaffin) cells are rather small with fairly regular cell boundaries. They have basophilic cytoplasm, and small densely staining nuclei. Besides post-ganglionic fibres to the blood-vessels and viscera, the ganglionic cells send numerous nerve-fibres into the suprarenals where they terminate on or among the medullary cells.

Cranial Autonomic System

Midbrain Outflow. The first autonomic (parasympathetic) pathway in Hydrologus is represented by pre-ganglionic fibres which run in the oculo-motor (IIIrd cranial) nerve to the ciliary ganglion. Since a cranial sympathetic system is absent, the ciliary ganglion receives no sympathetic contribution. The oculomotor is a motor nerve, containing both somatic efferent and general visceral efferent fibres. General visceral afferent fibres destined for the same peripheral region are contained in the ramus ophthalmicus profundus. The latter is relatively large in this fish and extends anteriorly across the lateral wall of the orbit below the oculomotor branch to the anterior rectus muscle. It constitutes a dorsal root corresponding to the same cranial segment as the oculomotor.
The ciliary ganglion lies on the ventral branch of the oculomotor nerve proceeding to the inferior oblique muscle, and it is so closely applied to this nerve that no separate radix brevis is distinguishable (Text-fig. 7; Pl. II, figs. 10, 11). The ganglion itself is situated distally towards the insertion of

the nerve into the inferior oblique muscle, but there are also scattered nerve-cells elsewhere on the course of the nerve. Fine non-myelinated nerves arise in the vicinity of the ganglion and pass to the wall of the eyeball: these are motor ciliary nerves (short ciliary nerves). There are no ganglion cells on the root or other branches of the oculomotor nerve.

The profundus nerve crosses the root of the oculomotor where the latter pierces the lateral wall of the orbit, and it lies on top of the oculomotor root.
and the origin of the common ventral ramus to the inferior rectus and inferior oblique. There is a large sensory ganglion on the profundus at this level. The profundus nerve and ganglion and the ventral ramus of the oculomotor nerve are actually fused together at this point by common connective tissue, and it is impossible to separate them cleanly in a dissection. However, the profundus sends no nerve-fibres to the oculomotor, and a radix longa is absent. This point has been checked carefully both by dissections and by serial sections of the entire orbital region.

The profundus gives off two sets of medullated sensory nerves to the eyeball. These are the posterior and anterior long ciliary nerves (Text-fig. 7; Pl. II, fig. 9). The posterior arise as a set of small nerves from the region of the profundus ganglion, and extend over the posterior surface of the eyeball. The anterior arise from the profundus well forwards towards the superior oblique muscle and pass to the wall of the eyeball. These nerves pierce the sclera through small apertures in the cartilage investing the eyeball. In Hydrolagus, therefore, the visceral sensory and motor fibres follow an independent course to the eyeball. Young (1933a) has described similar anterior and posterior long ciliary nerves in Mustelus.

In Chimaera monstrosa there is a ganglion or small group of nerve-cells on the ventral ramus of the oculomotor and a ciliary nerve is given off to the eyeball from this point (Cole, 1896; Schwalbe, 1879). But in addition to this ganglion Cole has figured a discrete ciliary ganglion, which lies near the proximal course of the ventral ramus, and which is connected both with this ramus and with the profundus by a distinct radix brevis and r. longa, respectively. Ciliary nerves proceed to the eyeball from the ciliary ganglion and the profundus nerve. The first (Schwalbe's) ganglion corresponds to the ciliary ganglion described in Hydrolagus; but a second distinct ciliary ganglion, connected with oculomotor and profundus nerves by radices, as described by Cole, is absent in Hydrolagus.

The ciliary complex has been studied in some detail in other elasmobranchs. In Mustelus and Squalus a ciliary ganglion lies on the oculomotor just within the orbit. Additional nerve-cells and groups of cells occur on the ventral ramus of the oculomotor and on the short ciliary nerves. The latter take their origin from the oculomotor nerve and ciliary ganglion, and form a ciliary plexus which proceeds to the eyeball. The profundus sends a branch to the ciliary plexus, and separate sensory nerves to the eye (Norris and Hughes, 1920; Young, 1933a). In Scyllium, on the other hand, sensory and motor roots from the profundus and oculomotor join to form two mixed ciliary nerves which supply the eyeball, in part. The ciliary ganglion is represented by three groups of cells on ventral branches of the oculomotor and on the short ciliary nerves which form a ciliary plexus (Schwalbe, 1879; Young, 1933a).

A ganglion has been found on the trochlear nerve in some small specimens of Hydrolagus. When present it lies closely joined to the nerve shortly after the latter pierces the dorso-lateral cranial wall. This ganglion possibly repre-
the Chimaeroid Fish *Hydrolagus colliei*

sents an ephemeral feature of ontogeny, since it is absent in the adult, and may not even be present bilaterally in the same immature specimen. No nerve-cells are present on the course of the abducens nerve.

A transient trochlear ganglion has been reported in *Squalus*. Neal (1914) found a group of cells at the point of union of anlagen of the trochlear and superficial ophthalmic nerves: this group of cells appeared to be a rudimentary autonomic ganglion comparable to the ciliary ganglion which develops on the oculomotor. The trochlear ganglion disappears in the adult. No ganglion develops on the abducens in this form.

**Hindbrain Outflow.** Ganglionic cells occur in post-trematic rami of the glossopharyngeal and vagal nerves. These cells lie scattered among the nerve-fibres, or are aggregated into small ganglia along the course of the nerves. The cells are encapsulated and are associated with bundles of fine nerve-fibres (Pl. II, fig. 12). They constitute post-ganglionic autonomic neurones concerned with innervating smooth muscle in the branchial and pharyngeal regions. A careful search of serial sections was made for autonomic ganglia on other cranial nerves. Ganglionic autonomic cells are not present in pre-trematic branches of the glossopharyngeal and vagal nerves, in the hyomandibular or hyoidean branches of the facial, in the mandibular branch of the facial, or in the trigeminal nerve.

Autonomic ganglia have been identified on post-trematic rami of the branchial nerves in *Squalus, Mustelus,* and *Scyllium,* but not on the trigeminal (V). Scattered cells and small ganglia occur on the hyomandibular branch of the facial, on the ramus hyoideus, and on the post-trematic branches of the glossopharyngeal and first three branchial rami of the vagus. Autonomic ganglia are absent from the fourth branchial vagal nerve. From the ganglia arise bundles of small non-medullated fibres which have a somewhat diffuse arrangement (Allis, 1901; Norris and Hughes, 1920; Young, 1933a).

In *Hydrolagus* the visceral branches of the right and left vagi supply the anterior alimentary canal and the heart. From each visceral vagal nerve a cardiac branch descends ventrally in the wall of the duct of Cuvier to the sinus venosus. The cardiac nerves give rise to a network of fibres in the walls of the ducts of Cuvier, sinus venosus and at the sino-atrial junction, but both nerve-cells and fibres are lacking in the ventricle (Pl. II, fig. 8).

The visceral vagal nerves extend from the dorso-lateral body-wall into the wall of the oesophagus, where they immediately subdivide into numerous branches passing anteriorly and posteriorly. Some anterior branches pass dorsally to reach the pregastric ganglia, or extend forwards into the pharynx. Posterior branches form discrete bundles which course longitudinally in the pigmented layer of the serosa; at intervals they give off fascicles which descend into the muscular layers of the oesophagus, where individual nerve-fibres terminate on striated muscle-fibres by motor-end plates. The vagal fibres continue posteriorly in the gut, and are distributed to the wall of the intestine. A vagal contribution to the sympathetic system has been described above (p. 385).
The course of the visceral vagus in the ratfish corresponds closely with that found in selachians. In *Scyllium* and *Raja* the vagus innervates the oesophagus, the corpus, and the pyloric region of the stomach (Babkin *et al.*, 1935; Young, 1933a). According to Müller and Liljestrand (1919), the vagus reaches the ileum in *Raja*, and Müller (1920) traced it to the intestine in developing specimens of *Squalus*.

**Discussion**

All the facts assembled in this investigation demonstrate an essential similarity between the autonomic nervous systems of chimaeroids and selachians (Text-fig. 8). In both groups the sympathetic ganglia are segmentally arranged in the abdominal region, and are connected with the spinal nerves by white rami communicantes, but segmental correspondence is not strict in the adult, and there may be more than two ganglia to each segment. Of greater interest is the absence of definite sympathetic trunks and commissures, with the result that the sympathetic system has a rather diffuse organization. Axillary bodies and gastric ganglia are peculiar to these two groups, and the anterior splanchnic nerves are similarly arranged. A system of sympathetic ganglia and connectives is absent from the tail of both groups, although transient ganglia do appear ontogenetically, in the caudal region of selachians at least. Other primitive features are the absence of a cephalic sympathetic component, of sympathetic cardiac nerves, and of collateral sympathetic ganglia. A sacral outflow (parasympathetic) is also wanting.

The close correspondence of autonomic organization in these fish points to a basic pattern derived from a common ancestral form. The Holocephali are an ancient group which have had an evolutionary course separate from
the Chimaeroid Fish Hydrolagus colliei 397

the Selachii since the Devonian, and probably are derived from early selachian stock through the palaeozoic brachydonts. Modern forms, the Euselachii and the Chimaeridae, occur from the Jurassic (Woodward, 1932; Moy-Thomas, 1939; Berg, 1947). Extant chimaeroids show many peculiar anatomical features, such as holostylic jaw suspension, operculum, cephalic clasper in the male, lack of a spiracle, peculiar dentition, absence of a stomach, &c. All these characters are probably secondary, and not primitive in nature (Dean, 1906), although Fahrenholz (1915) regarded the absence of a stomach as a primitive character. The autonomic system, in contrast, appears to have undergone remarkably little alteration, except with regard to secondary changes such as disappearance of a stomach and reduction of mesenteries in chimaeroids. Its basic character in these two groups, chimaeroids and selachians, seems well attested by these dual lines of evidence, and it constitutes a simple and primitive level of organization.

The organization of the autonomic system in elasmobranchs (Selachii and Holocephali) stands in an interesting position to that found in teleostomes and tetrapods. Chevrel (1894) has described this system in the sturgeon (Acipenser). In this fish there is an irregular sympathetic plexus in the abdomen. The plexus contains segmentally arranged ganglia, and it is connected at regular intervals to the spinal nerves by rami communicantes. Sympathetic ganglia are absent from the head and tail. From this account it appears that the sympathetic system is no more highly organized in Acipenser than it is in elasmobranchs.

In teleosts the sympathetic ganglia are segmentally arranged in a definite chain with connectives and commissures. Both white and grey rami communicantes are present. Sympathetic ganglia are present in the tail, and the sympathetic system extends into the head to connect with the parasympathetic system (Chevrel, 1887; Young, 1931a). Thus in teleosts, as in Amphibia, the autonomic system shows considerable advances in complexity and regularity of organization over the same system in elasmobranchs. Moreover, it is probable that the relatively diffuse systems of elasmobranchs and Chondrostei represent a simple level of organization from which the more highly organized systems of higher teleostomes and Amphibia evolved.

Gastric physiology of lower vertebrates has been reviewed by Barrington (1942), and further accounts of autonomic functioning in fish have been given by Lutz (1930), Young (1931b, 1933b, 1933c), and Babkin (1946). No information is available for chimaeroids, but in selachians it has been shown that both the sympathetic and parasympathetic systems are motor to the gut, and that there is no functional antagonism between these two components. In teleosts there is an increase in the field of autonomic innervation (air bladder, chromatophores), and of double innervation (cephalic structures), and evidence for some functional antagonism (eye) (Bohr, 1894; Young, op. cit.; Waring, 1942, review). Autonomic functioning is on a relatively simple level in elasmobranchs and parallels simplicity of structure. With increase in morphological complexity in teleosts and tetrapods there is,
pari passu, development of greater physiological diversity in the autonomic system.

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—— 1894. Ibid., 2, 401.
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EXPLANATION OF PLATES

PLATE I

**FIG. 1.** Transverse section of the body at the level of the oesophagus. The paired axillary bodies are shown adjoining the subclavian arteries. Young ratfish. Holmes's silver.

**FIG. 2.** Transverse section of the body in the posterior kidney region. Young ratfish. Holmes's silver.

**FIG. 3.** Transverse section through the dorsal body-wall in the posterior abdominal region. Young ratfish. Haematoxylin and eosin.

**FIG. 4.** Transverse section through the dorsal body-wall in the middle abdominal region. Young ratfish. Haematoxylin and eosin.

**FIG. 5.** Longitudinal section through axillary body (transverse to body axis). Young ratfish. Holmes's silver.

**FIG. 6.** Transverse section of the dorsal body-wall in the anterior abdomen. Young ratfish. Holmes's silver.

PLATE II

**FIG. 7.** Transverse section through axillary body of an adult ratfish. Holmes's silver.

**FIG. 8.** Transverse section through the wall of the sinus venosus to show a branch of the cardiac vagal nerve, and cardiac nerve-cells. Young ratfish. Holmes's silver.

**FIG. 9.** Transverse section through the orbit of a young ratfish. Holmes's silver. Legend: gang p, profundus ganglion; III, ventral ramus of the oculomotor nerve; Vp, ramus ophthalmicus profundus.

**FIG. 10.** Longitudinal section through the oculomotor branch to the inferior oblique muscle (III). Adult ratfish. Holmes's silver.

**FIG. 11.** Transverse section through the orbit of a young ratfish. Holmes's silver.

**FIG. 12.** Section cut longitudinally along the post-trematic branch of the second branchial vagal nerve (XII). Adult ratfish. Holmes's silver.