THE DEVELOPMENT AND COMPARATIVE ANATOMY OF THE SYMPATHETIC SYSTEM IN VERTEBRATES.

THESIS

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Contents.

Introduction.

For several years I have investigated the process of development of the sympathetic chain and its peripheral branches in the chick. In the two papers which I have published on this subject the work of other investigators is referred to,but these references are necessarily short.In going over the literature of the sympathetic nervous system one is impressed with the fact that in no article or chapter in a textbook is anything like a fair account given of much of the work done on the subject.It is of course true that some of the earlier work is disproved by later investigation but much of it is substantiated,while in any case it is most interesting to follow out the gradual evolution of the present day conceptions on the development of the sympathetic system.

With this aim in view I have made a synopsis of work on the development of both the sympathetic chain and its peripheral branches and have illustrated it by photographs or copies in pen and ink of the diagrams used by the different writers in support of their views.These diagrams in many cases explain the meaning of the worker more clearly than the text.

As my own work is concerned with the development of the sympathetic in the chick I have devoted two chapters to the discussion of the results described by other workers on the sympathetic in the Bird, and the relation of these results to my own.

In addition to discussing the purely developmental aspect of the sympathetic I also give an account of the minute anatomy of the various ganglia and plexuses,in connection with which much interesting work has been done.Finally the gradual evolution of the sympathetic system from the primitive form in the Cyclostomata to the highly organized system in Birds and Mammals is followed out.

In this way I have attempted to give a concise account of the sympathetic system as regards its development,intimate structure, and its comparative development in the various orders of vertebrates.

I here take the opportunity of acknowledging my deep indebtedness to Professor D.Noel Paton,under whose guidance the work was done, for facilities,criticism,and unfailing encouragement.

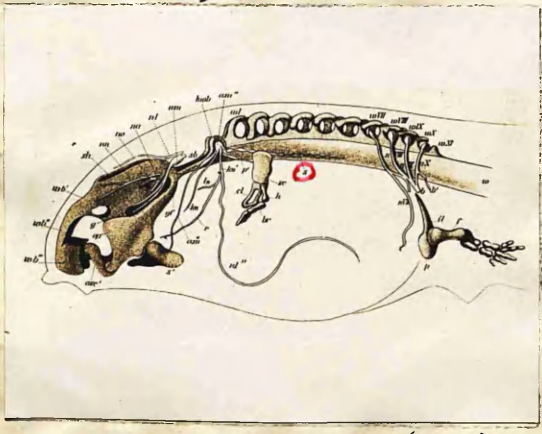
Chapter 1. -

A Historical Review of the Investigations on the Development of the Sympathetic Chain.

In all, or nearly all, papers dealing with the development of the sympathetic nervous system reference is made to the work of Remak(36), who is the first to describe the development of this structure in the chick. From his investigations he finds that the sympathetic chain arises as a series of small rounded swellings attached to the spinal nerves at the point of union of the anterior and posterior roots, and is derived wholly from the mesoderm. Further the sympathetic ~~is~~ chain is not connected with the peripheral portions of this system until the third week of incubation, when the "Mittelnerv" developes. For almost twenty years the teaching of Remak is accepted, no doubt as to the mesodermic origin of the sympathetic system being suggested. Hensen(13) writing in 1864 offers the suggestion, that all ganglionic cells in the body are ectodermic in origin. This is interesting as it is the first indication of what is now believed to be the correct description of the development of all nerve structures.

Goette(9) in his book on the development of the toad describes the sympathetic chain. He finds that it arises at the end of the first larval period as small groups of cells, closely resembling the cells of the spinal ganglion, situated at either side of the aorta. From the fact that those cells are not seen in all the cross sections of an embryo at this stage of development it is concluded that the sympathetic chain is at first a series of ganglia. At the middle of the second larval period these ganglia are found linked together~~and~~ and form a continuous chain which however is best developed in the anterior part of the body, as is shown in the reconstruction (fig. 1).

Fig. I



(Goette)

(S.) Sympathetic nerve.
p' Visceral branch of Vagus.
asn''' Ganglion of Vagus
asn'' Glossopharyngeal.
hn. nasal nerve
no - Oculomotor
na - Abducens.
asn - Ganglion of nerves to the jaw.
nl. Lateral nerve of head.
(other letters refer to bony structure)

At first the sympathetic chain is quite independent of both the vagus and the spinal nerves although the latter lie very near the chain (fig. 2).

Fig. II

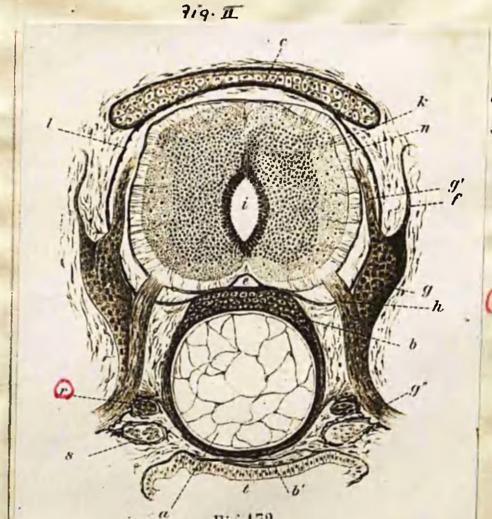


Fig. 172.

(Goette.)

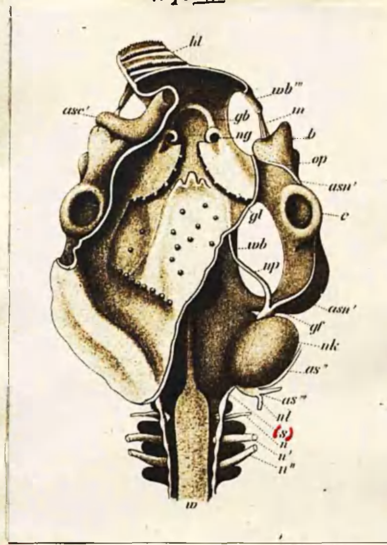
a. Notochord.
S. Ganglion of Posterior root.
H. Anterior root.
i. Central Canal spinal Cord.
(r.) Sympathetic.
T. Oesophagus.

(other letters refer to bony structure)

Later in development the anterior end of the chain is connected with the vagus immediately below the ganglion(fig.3).

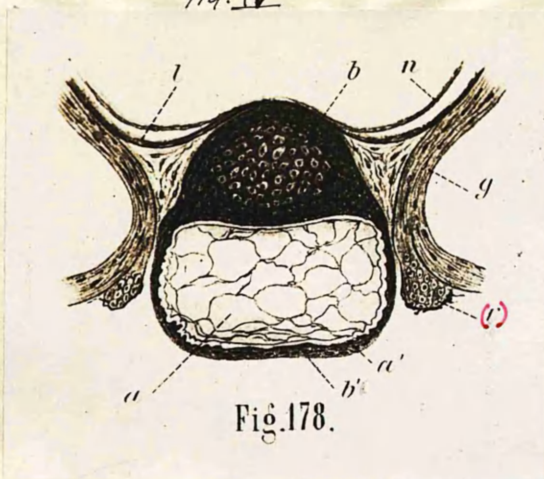
In the trunk the spinal nerves and the sympathetic chain are also linked together by means of fine rami communicantes(fig4).The whole structure is mesodermic in origin,the work of Goette being on this point in agreement with that of Remak.

Fig. III



(S)- Sympathetic (Goette)
n-n" - First three spinal nerves.
asn''' - Vagus
asn" - Glossopharyngeal
asn' - Facial nerve.
W - Spine.
(Other letters refer to bony structures)

Fig. IV



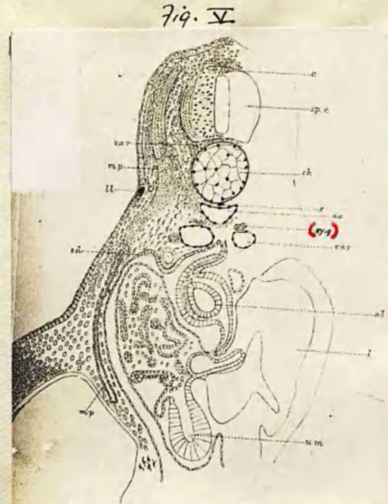
(Goette)

(1) Sympathetic
a.a'.b'. Notochord.
g. Spinal nerve
n. Pia mater.

Balfour(1)is the first to describe the sympathetic chain as an offshoot from the spinal nerves,and like all the cerebro-spinal system an ectodermic structure.In his first paper he describes the first stage of the sympathetic chain in Elasmobranch fishes as a series of short branches from the spinal nerves which take a medial direction and terminate in small irregular cellular masses immediately dorsal to the cardinal veins(fig.5).

As a result of more work on this subject Balfour(2)recognises that this is a second stage in the development of the chain.The ganglia are at first simply swellings on the main branches of the spinal nerves(fig.6)

Fig. V



Sp.C. - Spinal Cord. (Balfour)
ch - notochord.
(Sy.G) Sympathetic Ganglion
C.a.v - Anterior Cardinal Vein.
al - Alimentary Canal.
L - Liver.
m.p - muscle Plate.

Fig VI

(Balfour)

a.r. - anterior root
p.r - posterior root.
m.p. - muscle plate
(Sy.G.) - Sympathetic Ganglia

Schenk and Birdsall(38) describe the development of the sympathetic system in birds and mammals.They find that before the sympathetic chain appears the spinal ganglia show very irregular and indistinct ventral margins,and that cells may be traced along the spinal nerves from the ganglia.The sympathetic chain appears a little later as clusters of cells lying behind the aorta and connected to the spinal ganglia by cellular chains.The sympathetic chain is therefore derived directly from the spinal ganglia.

Kolliker(24) in the second part of his treatise on the development of man and the higher animals supports the view that the sympathetic chain is formed as a cellular outgrowth from the spinal ganglia.

In their textbook on embryology Foster and Balfour(6) note that although the development of the sympathetic system in birds and mammals is not thoroughly worked out there is little doubt but that the sympathetic chain is derived from, or rises in continuity with, the posterior spinal ganglia.

The next great worker is Onodi(32) who follows out the course of the development of the sympathetic chain in fish,birds,and mammals.

In fish he describes the process most fully in the embryo of the Scyllium canicula but confirms his observations in other types.

In an embryo of the Scyllium canicula 15m.m. long the beginning of a three sided proliferation of the spinal ganglion is seen(fig.7)

Fig. VII

(Onodi)

E - Ectoderm.
M - Medullary column.
V - Abdominal artery
S - Posterior spinal ganglion
(Ss) - Sympathetic ganglion

THis ventral three sided proliferation is the first stage in the development of the sympathetic chain.The cells composing this proliferation are stained a darker colour than the surrounding cells of the mesoderm,while many of them are in process of division.

In a series of sections of an embryo 18 m.m. long the gradual separation of the sympathetic ganglia from the spinal ganglia may be followed (fig.8).

Fig VIII

M - Medullary Column.
sp. Spinal Ganglion
(X) - Proliferation of Cells
(S) Sympathetic Ganglion
ch - notochord

(Onodi)

As is seen from the figure the ventral proliferation gradually assumes an arched shape with the concavity directed ventrally.The outer portion of the arch rapidly increases in size due to proliferation of the cells,and is eventually separated off as the sympathetic ganglion.At 20 m.m.body length the sympathetic ganglia are independent of the spinal ganglia(fig.9).

Fig IX

(Onodi)

M_Medullary Column.
Sp-Spinal Ganglion
(X)—Proliferation of Cells.
(S)-Sympathetic Ganglion
Ch - Notochord.

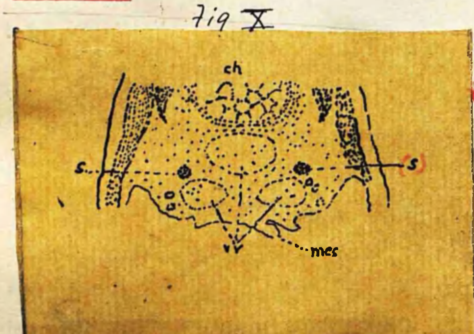
At 25 m.m. the sympathetic ganglia in the proximal part of the body are linked together and form the first part of the sympathetic chain proper.

In the Mustelus embryo at 18 m.m. body length the sympathetic is first recognised.It follows the same course as in the Scyllium and developes more rapidly in the proximal part of the body.

The Scymus embryo at 30m.m.shows well developed sympathetic ganglia which in the proximal part of the body are connected and form a definite chain.

In the Torpedo embryos the first stage of the sympathetic chain is not so clearly seen as in the other types,but as a well marked cellular connection between the sympathetic and spinal ganglia is seen in the earliest stages examined it is evident that they are derived from this source.In embryos 15 m.m. long the sympathetic chain is a bilateral structure the individual ganglia vary considerably in size (fig.10)..

Fig X



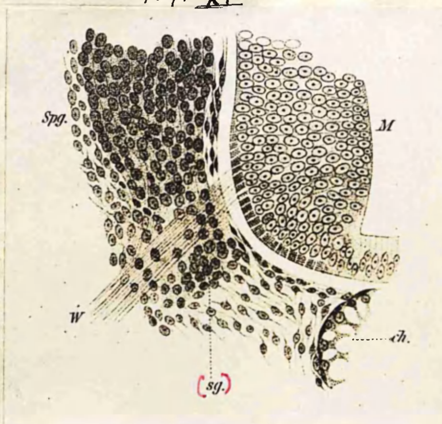
(Onodi)

Ch-Notochord
(S)-Sympathetic Ganglia
Mes. Mesentery
V.V_Blood Vessels.

It is evident therefore that ~~the~~ sympathetic chain is directly derived from the central nervous system and that the whole process is easily followed in fish.

In birds Onodi records investigations made on the embryonic chick and duck. At the second day of incubation the invertebral ganglia in the chick begin to form,at the third day they become more independent and extend ventrally as far as the point of exit of the anterior root.In a series of cross sections of a chick at this stage a band of cells is seen at different levels lying immediately under the anterior root bundle, They are distinguished from the surrounding mesodermic cells by their circular shape.Further careful examination of the intervertebral ganglia shows that their ventral margins are indefinite and blurred in outline,and it would seem that the band of cells lying immediately under the anterior root bundle is the ventral margin of an inter-vertebral ganglion.At the fourth day this band of cells is more pro-minent and cells from the intervertebral ganglia at different levels are found bridging the anterior root and thus clearly connecting it with the ~~with the~~ ganglia.This band of cells under the anterior root is the first stage of the sympathetic chain,and although its connection with the spinal ganglia is not so clearly seen as in fish,their is yet sufficient evidence to prove that as in the fish it is a derivative of these structures(fig.11).

Fig. XI



M_Medullary Column.
Sp.G_ Spinal Ganglion
W_Spinal root
(Sg) Sympathetic Ganglion in course of formation
Ch_Notochord.

(Gnodi)

At five days incubation the individual ganglia of the sympathetic chain are con-nected with the spinal nerves by cellular chains among which are a few fibres the precursors of the rami com-municantes.The cells are for the most part in a state of active division,and at the ventral margin of the ganglia they form a sharp point from which cells may be seen separating off (fig.12). In a duck embryo incubated six days the ~~the~~ same degree of development is seen.AT eight days incu- bation the relationship of the spinal nerves to the sympathetic chain is clearly seen while the migration of the sympathetic cells from the ganglia already referred to is well marked(fig.13).

Fig XII

(Gnodi)

Spg. Spinal Ganglion. N. Nerve trunk.
(Sg) Sympathetic Ganglion. (X) Migrating Cells.

Fig XIII

R- Spinal Cord.
C.C-Central Canal
gs-Grey Substance
W.S-White Substance
hw. posterior root
V.w. anterior root
Spg- Spinal Ganglion
(Sg) Sympathetic Ganglion
(p.sg.) peripheral sympathetic Ganglion
Va. Da- Ventral and Dorsal branches.

(Gnodi)

X. Connection between anterior root and sympathetic
(X_{II}) (X_{III}) Connection between posterior root and sympathetic and between the spinal and sympathetic ganglia.

In his work on mammals Onodi finds that in rabbits 10 m.m. long the sympathetic chain is represented by a series of connected ganglia ly-ing on the dorso lateral aspect of the aorta(fig.14)

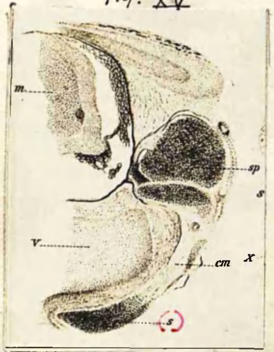
Fig. XIV

(S) Sympathetic Chain
V. Spinal Column
M. Medullary tube

(Gnodi)

In guinea pig embryos of 20 m.m. length the sympathetic chain is fully formed, while the migration from it of cells to form the peripheral sympathetic plexuses is well marked.
In human embryos Onodi finds that the sympathetic chain with its rami communicantes is fully formed from 18 m.m. body length (fig.15).

Fig. XV



M- Medullary Column. (Onodi)
sp.- Spinal Ganglion
Cm. Ramus Communicans
(S)- Sympathetic Ganglion

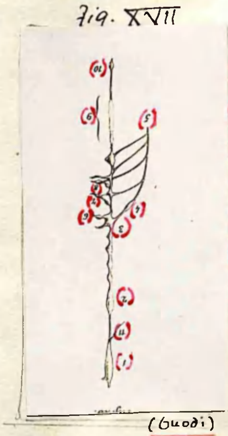
The development of the chain at later stages of embryonic life is referred to and illustrated in the accompanying diagrams (figs 16,17)

Fig XVI

(Onodi)

Human Embryo 10 C.M.
(1) Sup. Cervical Ganglion.
(2). Inf. Cervical Ganglion.
(3) Thoracic Ganglion
(4) Ganglia of the Splanchnics.
(5) Splanchnic nerves.
(6) Lumbar Ganglia
(7) Sacral Ganglia

Fig. XVII

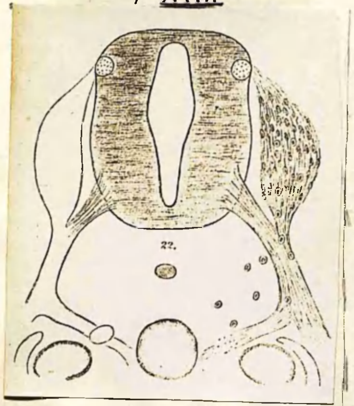


(Onodi)

Human Embryo 17 C.M.
(1)- Sup. Cervical Ganglion
(2) First Thoracic Ganglion
(3)- Ganglia which have become joined -
(4). Splanchnic Ganglia
(5) Splanchnic Nerves.
(6)(7)(8)- Ganglia of Rami Communicantes
(9) Lumbar Ganglia
(10)- First Sacral Ganglia
(11)- Rami Cardiacus.

As a result of his investigations Onodi concludes that the sympathetic chain is a secondary product and is formed by the union of the separate sympathetic ganglia which are derived from the ventral proliferating portion of the spinal ganglia. As a general rule the proximal portion of the chain developes rather in advance of the distal part. The process of development being slowest in fish they afford the best material for following out the course of development of the sympathetic chain, and they form a basis for comparison in the case of other vertebrates where the process is not so clearly seen.
In a textbook on embryology by Haddon(10) which appears about this time it is interesting to note that the later work of Balfour( ), already referred to is quoted as evidence for the ectodermic origin of the sympathetic ganglia.
Van Wijhe (40) agrees with Balfour in describing the sympathetic chain as originating in small cellular swellings on the spinal nerves.
He finds that they appear for the first time in Pristiurus embryos with 84 myotomes.
His sen.(14) in an article on the histogenesis and connection of nerve elements describes the development of the sympathetic chain in the human embryo. In an embryo 7m.m. long fibrous outgrowths are seen passing from the spinal nerves towards the aorta. These fibres are the rami communicantes, which therefore precede the ganglionic part of the chain in development (fig.18).

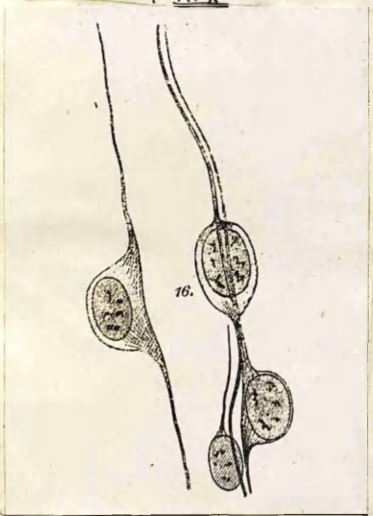
Fig. XVIII



(His)

The ganglia of the sympathetic chain appear at 10 m.m. body length, and are derived from the spinal ganglia. In the spinal ganglia are two types of cells, one of which is endowed with the power of movement. They migrate from the spinal ganglia and form the smpathetic ganglia. They are distinguished from the cells of the spinal ganglia by their size which is smaller, and their unipolar outgrowth (figs. 19;20). These cells migrate from the spinal ganglia along the course of the already developed rami communicantes (fig. 20).

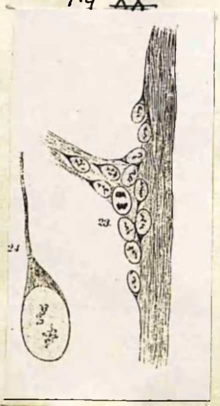
Fig XIX



(His)

Typical bipolar cells of Spinal Ganglia

Fig XX



(His)

(Typical unipolar Sympathetic Cell)
(Migration of those cells along Rami Communicantes)

Paterson (33) describes an investigation made by him on the development of the sympathetic chain in the rat, mouse, ~~andrabbit~~ rabbit, and human embryos. The sympathetic chain is first seen in the mouse embryo of about 8 days development. It arises on either side of the aorta as a solid unsegmented rod of fusiform cells which lie embedded in the mesoblast. This cord is formed by differentiation of the mesoblastic cells, and is at this stage quite unconnected with the spinal nerves (fig. 21).

Fig XXI

(Sy) - Sympathetic Cells. (Paterson)
Sp.C. Spinal cord with D.S. dorsal ganglion and anterior and posterior spinal nerves.

The junction between the spinal nerves and these columns of cells is effected by the gradual growth of the inferior primary division of the nerve and its final division at the junction of the somatopleure and splanchnopleure into somatic and splanchnic branches. The splanchnic branch goes to this rod of cells (fig. 22).

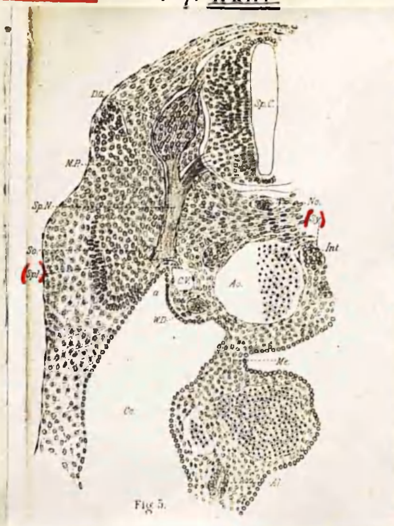
In the rat the process is the same but a little slower than in the mouse.At 8to 9 days the sympathetic chain is an isolated structure while the spinal nerves may be seen dividing into the somatic and splanchnic branches(fig.23).

Fig. XXII

(Paterson)

Sp.C. Spinal Cord with anterior and posterior nerve roots.
(Sy) Sympathetic Ganglion
(Spl.) Splanchnic branch from spinal nerve to sympathetic
So. Somatic branch of spinal nerve

Fig. XXIII



(Paterson)

Sp.C. Spinal Cord with anterior and posterior nerve roots and posterior ganglion
(Sy) Sympathetic
(Spl.) Splanchnic branch which does not reach sympathetic cells.

At 12 days the splanchnic branch of the spinal nerve is joined to the sympathetic chain(fig.24).

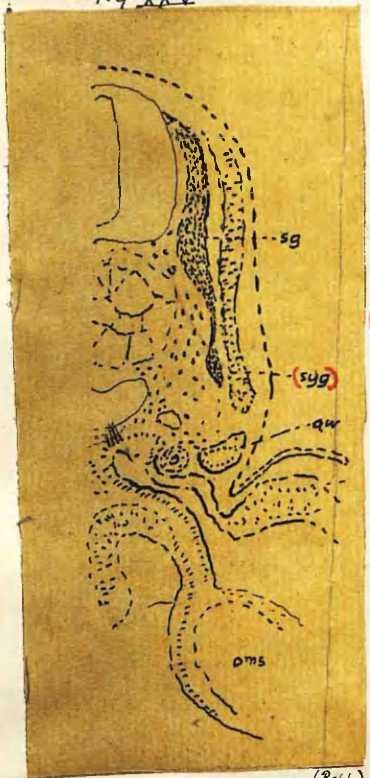
Fig. XXIV

(Paterson)

(Spl.) Splanchnic branch in which with Sympathetic (Sy)

The formation of the ganglia is a secondary process and is brought about partly by the junction of the splanchnic branches with the sympath-cord,and the consequent persistence of the ganglionic cells connected with the fibres of those nerves, and partly by the pressure of neighbouring structures.Paterson points out that according to this description the sympathetic chain is morphologically similar to the organs with which it is structurally and functionally connected in being mesoblastic in origin and primarily unsegmented. Fusari(8) differs from all other workers in his conception of the mode of development of the sympathetic chain.He describes it as a product of the protovertebrae,and consequently mesoblastic in origin. Carl Rabl(34,35) follows out the developmental process in the Pristiurus embryo.The first signs of the sympathetic chain are seen when the embryos show about 74 somites.The spinal ganglia are drawn out into a long narrow bands which terminate in a spindle shaped cluster of cells.This cluster of cells is the first stage of the sympathetic chain which is there fore in direct genetic connection with the spinal ganglia(fig.25).

Fig XXV

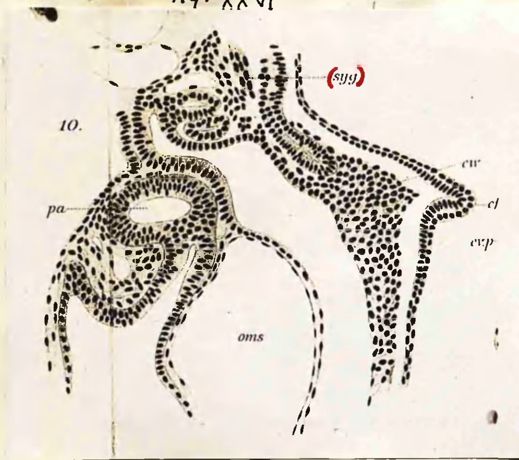


(Rabl)

Sg - Spinal Ganglion
(Syg) - Sympathetic Ganglion
O.M.S - Omphalo mesenteric Vein

At the next stage,83 somites,the sympathetic ganglia are prominent structuress standing out prominently from the surrounding mesoblastic tissue.At still later stages of development the ganglia increase in size and become more complicated in structure(fig 26).

Fig. XXVI

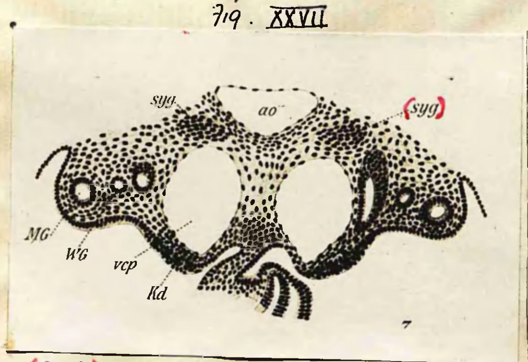


(Rabl)

(Syg) - Sympathetic Ganglion
pa - position of Pancreas
O.M.S. Omphalo mesenteric Vein

The rami communicantes which develope some time afte the ganglia are at first very scanty and are interspersed with numerous ganglion cells.In the embryo of the Torpedo marmorata at12 m.m. body length the sympathetic ganglia are quite distinct.In the posterior third they lie on the medial layer of the muscle plate,in the middle third they approach the cardinal veins,while in the anterior thir of the trunk they lie on the dorso lateral wall of the cardinal veins.As in the Pristiurus the rami communicantes are at first scanty and interspersed with ganglionic cells.At 18 m.m. the sympathetic chain is represented in the anterior two thirds of the body by a cluster of round or oval cells lying close to the dorsal walls of the cardinal veins(fig 27).

Fig. XXVII



(Syg) Sympathetic Ganglia
ao - aorta
vcp. Posterior Cardinal Veins.

(Rabl)

The sympathetic chain in the Torpedo is higher in type than that of the Pristiurus,but the mode of development is the same in both cases.

His jun. (15,16) gives an account of the development of the sympathetic chain in fish,birds,and mammals.He finds the development of the sympathetic ~~chai~~ chain in the fish somewhat difficult to follow as the number of nervous

elements is small and they show little difference from the mesoblastic cells. In a trout embryo 6 m.m. long the sympathetic chain is laid down in the upper part of the trunk and is connected with the spinal nerves by fibrous rami communicantes among which lie a few cells sympathetic in type(fig.28). These cells migrate from the spinal ganglia and are evi dently part of the general migration from those gang- lia to form the sympathetic chain. It is also seen from examination of somewhat earlier embryos that the rami com- municantes are formed prior to the cellular portion of the sympathetic chain. At 12 m.m. the chain begins to divide into fibrous and cellular parts and at this stage also the fifth, ninth and tenth cranial nerves send rami communi- cantes to the cervical portion*
(fig.29,30)

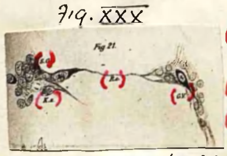
Fig XXVIII

(His 1r.)
Sg. Cells of Spinal ganglion
Ch. Chorda dorsalis
Ao. Aorta dorsalis
(R.C) Cells of Ramus Communicans.
M.Y. muscle fibres.

Fig. XXIX

(His 1r.)
Ao - Aorta
(R.C) Ramus Communicans
(G.V) Vagus Gang.
(S.G) Sympathetic chain.

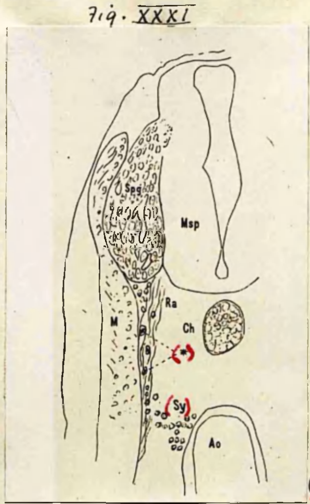
Fig. XXX



(His 1r.)
(R.C) Ramus Communicans
(G.V) Vagus Ganglion.
(S.G) Sympathetic Chain
(K.Z) Germinal Cells in Chain

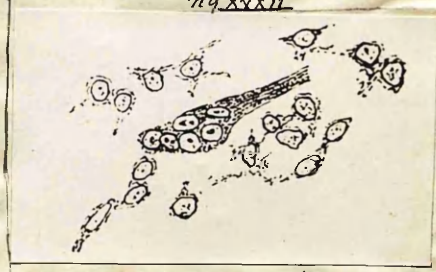
* The chick is the subject of very careful examination by His who recognises the first stage in the development of the sympathetic chain in a cellular migration from the spinal ganglia at the end of the third day(fig.31). These cells which form tiny clusters behind the carotid in the neck and at either side of the aorta in the trunk, are com- posed of cells a very little larger than the mesoblasts. They are distinguished by their col- our which with the ordinary Haematoxylin and Eosin stain is darker than the mesoblastic tissue. The more important characteristic is however the presence of uni- polar outgrowths(fig.32). Many of these cells on their course from the spinal ganglia are in process of active division. At the end of the fourth day the sympathetic chain is much more prominent, and presents different appearances at different levels. In the cervical and thoracic regions it is a closed band girt round by a mesoblastic sheath. About the level of the heart however there is a well marked ventral migration

Fig. XXXI



(His 1r.)
Spg - Spinal Ganglion
(Sy) - Sympathetic Ganglion
(*) - migrating cells -
Ao - Aorta
Ch - Notochord -

Fig XXXII

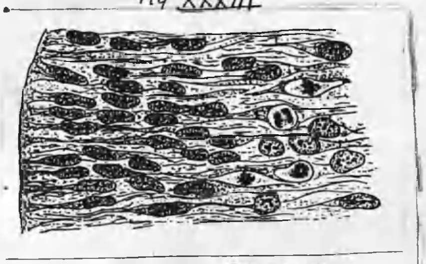


(His 1r.)

In the abdominal region there are several points from which swarms of cells migrate ventrally.
At the sixth day the secondary sympathetic chain appears.This is the permanent chain and lies close to the anterior root.It is formed in the same way as the primary chain from the migration of special cells from the spinal ganglia.It is a stronger structure than the primary chain,which it almost entirely supersedes,except in the uppermost cervical region and in the pelvic region.In the upper part of the neck there is a double sympathetic supply derived from the primary chain which persists as the superior cervical ganglion,while a second superior ganglion is formed by the migration of sympathetic cells from the vagus ganglion.The two ganglia are united by a fibrous band and they form the most proximal portion of the secondary sympathetic chain.The rami communicantes are developed secondarily in contrast to the mode of development in fish.
As ~~the~~ regards the development of the sympathetic chain in mammals the process is essentially the same but there are several minor points of difference.The first portion of the chain to appear is the ramus communicans the cells migrating later from the spinal ganglia along the course of the fibres.There is no secondary sympathetic chain, in this the mammals resemble the fish.
As a result of an extensive series of investigations His concludes that the sympathetic system as a whole is the product of the cerbro spinal system.In the formation of the sympathetic chain all the spinal ganglia,and the vagal and possibly the glossopharyngeal ganglia take part.The participation of the vagal ganglion in the formation of the sympathetic is most clearly seen in the bird but it highly probable that the condition is the same in the mammal.
Mazzarelli(30) in his discussion on the development of the sympathetic chain in Selachians and Birds describes an active migration of special cells from the spinal ganglia to form the sympathetic chain. This is in complete agreement with the work of His.
Sedgwick(39) describes the sympathetic chain in Elasmobranch fishes as arising in swellings on the posterior roots of the spinal nerves. At a slightly later stage of development these swellings become removed from the nerves but remain connected with them by means of a fine fibrous band.Later the individual clusters or ganglia become linked together to form a chain.
The work of Schaper(37) on the mode of development of the cell components of the central nervous system is included in this section since reference will be made later to his work,although it does not

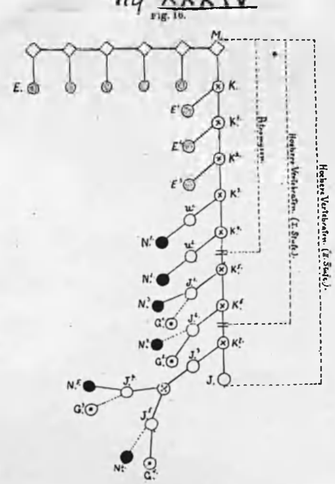
deal directly with the development of the sympathetic chain.He traces the gradual development of the cells forming the central nervous system from a common origin the primitive epithelium.He regards the Keimzellen of His as an embryonic and proliferating stage of the epithelial cells,and demonstrates the gradual evolution of the Keimzellen situated round the internal limiting membrane of medullary canal to the marginal epithelial cells(fig.33). He therefore differs from His who regards them as specialized types of cells having an ecto dermic origin.Further the course of development of the cells of the central nervous system**- is represented in a schematic manner(figs.34,35)For following out the schema reference must be made to the accompanying key(fig.36)

Fig XXXIII



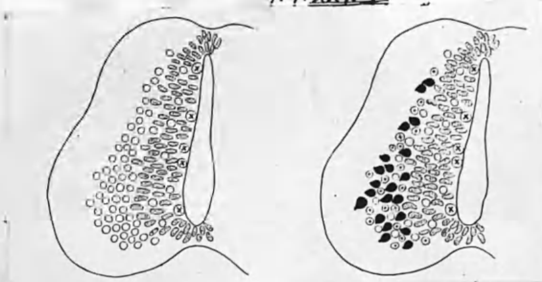
(Schaper)

Fig XXXIV



(Schaper)

Fig. XXXV



(Schaper)

Fig. XXXVI

◉ Ependymzellen.
⊗ Keimzellen.
○ Indifferente Zellen.
● Nervenzellen.
⊙ Gliazellen.
⊛ Mitosen der indifferenten Zellen (Keimzellen zweiter Ordnung).

(Schaper)

According to this scheme the primitive epithelial cells form the base.In some of the lower types such as the Amphioxus these cells become either ependyma cells or nerve cells.In the higher vertebrates the process is more* complicated .In Petromyzon these primitive epithelial cells may go through several stages of evolution.The first stage is the development of the Keimzellen which in turn gives* rise to a second series of Keimzellen and ependyma cells.This process is repeated several times and finally a stage is reached when the Keimzellen give rise to an indifferent cell instead of an ependyma cell.From this indifferent cell evolves the nerve cell.This process is repeated and forms the whole scheme of development in Petromyzon.In higher vertebrates the next stage is represented by the development of an indiffer ent cell which has the power of forming either a nerve or glial cell. In the highest form of vertebrate the indifferent cell may give rise to a Keimzell which in turn forms indifferent cells which as before evolve into glial or nerve cells. According to Schaper therefore the potentiality of the indifferent cell is enormous and it is possible that it comes into play in processes of repair.

Hoffmann (17,18) describes the development of the sympathetic in Selachians Taking the Acanthias vulgaris as a type he finds that the first sign of the sympathetic ganglia is sees about 15 m.m. body length. At this stage the evidence derived from sections goes to prove that the sympathetic ganglia originates as a swelling on the ramus ventralis (figs. 37-38.

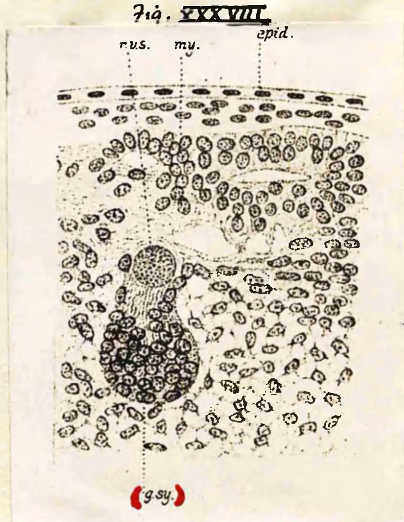
Fig. XXXVII

(Hoffmann)

my – Myotome
4gs – Fourth spinal ganglion
m.w – motor root
s.w – sensory root
r.v4 – ramus ventralis of fourth nerve
(4 g.sy) Fourth sympathetic ganglion
bg – Blood vessel.

Fig 38.
epid – Epidermis
my – myotome
r.v.s – ramus ventralis
(g. sy) Sympathetic ganglion

Fig. XXXVIII



(Hoffmann)

A sympathetic ganglion is formed when the anterior and posterior spinal nerves join. The cranial nerves do not show junction between the anterior and posterior nerves of a segment except in the case of the Nervus opthalmicus profundus and the Nervus oculomotorius, the dorsal and ventral nerve roots of the anterior cranial segment The ciliary ganglion formed in connection with those nerves is therefore the sole cranial sympathetic ganglion.

The sympathetic ganglia are at first small cellular thickenings on the ramus ventralis but they soon incease in size and differentiate into a central cellular portion and a peripheral fibrous portion which joins the beginning of the ramus anastomosticus which connects the sympathetic ganglia with the spinal nerves. The cellular portion or sympathetic ganglia proper also differentiates into two portions. In one the cells are large with well marked nuclei and lie mostly on the medial side of the ganglion.In the other part the cells are more numerous,and are much smaller in size(fig.39).

Fig. XXXIX.

Sympathetic ganglion showing large sympathetic cells, and small sympathetic or Chromaffine cells.

(Hoffmann)

The sympathetic ganglia in the trunk and tail are all laid down when the embryo reaches24 to 25 m.m. body length.In the later stages of development some of the ganglia vanish while most of the others fuse in groups of four or six.

In a later investigation on Urodelphibians Hoffmann finds many points of contrast.Instead of the cellular thickenings on the rami ventrales as seen in Selachians a very few and isolated cells are seen breaking away from the rami.These cells are only recognisable by their very slender outgrowths which connects in a rather vague manner with the ramùs ventralis.They are found scattered round the aorta and in some parts it is quite impossible to trace all the cells from the ramus ventralis.It is difficult to decide at this stage to what tissue the cells belong,but from evidence supplied by embryos at a later stage of development it is probable that they are all derived from nerve cells which have migrated along the rami ventrales.

In the Salamander embryo of 30 to 33 m.m.lèngth the sympathetic appears as a continuous partly cellular partly fibrous trunk extending downwards from the level of the first spinal nerve to the caudal region. At the level of the first spinal nerve it forms a connection with this nerve.At the level of the eleventh or twelfth spinal nerves the two chains blend separating again a little lower down

In the Triton the sympathetic chain developes in the same way and is seen first when the embryo is about 9 to 10 m.m. long.

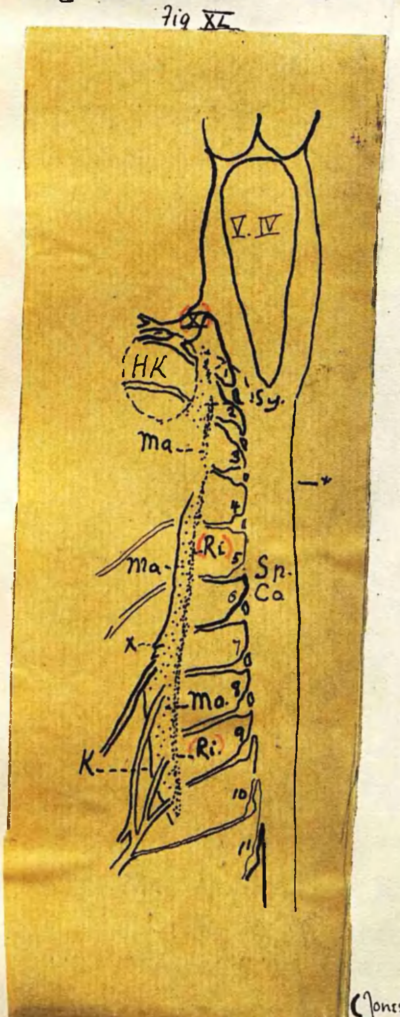
It is interesting to note that early in development the sympathetic chain is connected with the vagus,while the ciliary ganglion ,the cranial sympathetic ganglion is connected with the ramus anastomosticus by a complicated network which might be known as the cranial sympathetic.

Harrison(11)working on theSalmo salar points out that nerve cells leave the spinal cord along the motor fibres somewhat late in the course of development.He suggests that very probably they form the motor neurones of the sympathetic.

Kolliker(24) agrees with Balfour as to the method of development of the sympathetic chain describing it as originating in swellings on spinal nerve trunks.

Jones(19) describes the development of the sympathetic nervous system in the common toad. He finds in the region between the vagus ganglion and the second spinal nerve cells probably of epiblastic origin lying scattered in the mesoblast. These gradually become aggregated to form a cord (fig. 40). All the sympathetic chain posterior to this region arises from an antecedent structure, which is bilaterally symmetrical and lies closely applied to the dorsal and external side of the aorta. This antecedent structure consists of an irregular ridge of cells extending back to the region between the ninth and tenth nerves, but interrupted at the level of the third nerve. The cells of this ridge are continuous throughout with the mass of cells lying between the aorta and the Wolffian duct and at a lower level between the kidney and the aorta. The ridge is continuous anteriorly with the sympathetic cord, already referred to between the vagus ganglion and the second spinal nerve. The cells of the anterior portion of the sympathetic are round or slightly elliptical and are devoid of processes. They are distinguished from the connective tissue cells by the fact that they stain more deeply. In the region posterior the cells of the ridge-like elevation mingle freely with the nerve fibres and although there is no definite clue as to their origin this fact suggests that they are epiblastic in origin.

Fig XL



(Jones)

Sp. Co - Spinal Cord.
(Ri) - Sympathetic ridge.
HK - Head Kidney.
(X) Vagus ganglion
1, 2 etc. - ganglia of spinal nerves.

Later in development, after metamorphosis the sympathetic cord is completely separated from its antecedent structures and is removed dorsally and somewhat laterally from the aorta. The rami communicantes are prominent structures, while differentiation into ganglia and commissure is now almost complete.

Kohn(2/22) describes the development of the sympathetic chain in mammals. Working on rabbits he finds the first unmistakeable trace of the sympathetic chain at eleven days six hours incubation.

At this stage the appearance presented is strongly suggestive of an elongation of the spinal ganglia downwards into the nerve trunk. Numerous cells accompany the anterior and posterior nerve trunks coming respectively from the medullary cord and the spinal ganglia, but it is impossible to distinguish the two sets in the mixed spinal nerve.These cells or neurocytes according to Kupffer,are in the state of active division and are massed at the point of exit of the anterior root,at the medullary end of the posterior root,and at the peripheral end of the ingoing nerve.Such a collection is seen at this stage at the ventral end of the mixed nerve,but the cells differ somewhat from the neurocytes in the nerve trunk as they are round and not elongated in shape.From this cluster of cells a chain of cells leads to the dorso-lateral aspect of the aorta and terminates in a small collection of cells which constitute the first stage of the sympathetic chain(fig.41). The sympathetic chain is therefore formed from a medially directed outgrowth of neurocytes.Kohn points out that his theory does away with the difficult problem as to why certain cells should assume the position occupied by the sympathetic chain,for one recognises in this structure merely the medial branch of the spinal nerve.

Fig. XLI

N.Z. – neurocytes
N – nerve.
(r.c) – Ramus communicans
b.k – Blood Corpuscles.
(Kohn)

At twelve days development nerve fibres a appear between the spinal nerve and the sympathetic chain replacing the primary cellular connection.

At thirteen days the sympathetic is built up of thick unbroken groups of nerve cells and nerve fibres,while the rami communicantes are wholly fibrous

At fourteen days the formation of ganglia begins

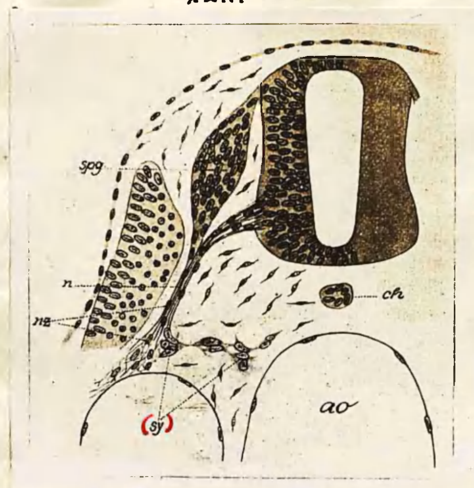
At fifteen days the adult condition is clearly foreshadowed,the relationship of the fibrous rami communicantes and the developing ganglia of the chain is well seen(fig.42).

Finally Kohn emphasizes that the sympathetic chain is a derivative of the central nervous system,but it is not formed from some part of it which is pushed off,or loosened off,or to the migration of a special type of cell,but it is by a medially directed migration of the neurocytes which accompany the mixed spinal nerve.The neurocytes are therefore the foundation stones of the chain.A schematic diagram illustrating the whole process of development is given below(fig 43).

Fig XLII

(Rc) Ramus Communicans
N.Z – Neurocytes
(Sy) – Sympathetic
Ao — Aorta
(Kohn)

XLIII



spg – Spinal Ganglion
n – nerve
NZ – neurocyte
(sy) – sympathetic
ao – aorta
ch – notochord
(Kohn)

Carpenter(4) finds in the chick embryo that some of the cells of the ciliary ganglion are derived from the ventral wall of the mid-brain by migration of indifferent cells (Schapers nomenclature) along the oculomotor nerve.As this ganglion is generally recognised as a sympathetic structure this fact opens up a new field for the potentialities of those indifferent cells.

Carpenter and Main(5) investigating the question of migration of nerve elements from the ventral nerve root come to the conclusion that in mammals at least the migration at this region of the medullary cells is greater than is generally recognised.In these medullary cells escaping from the spinal cord they recognise the indifferent cells of Schaper(fig 44).As to their ultimate fate it is more difficult to speak with certainty.They may form nerve cells for the sympathetic ganglia but this is not definitely known.

Fig. XLIV

(Carpenter and Main)

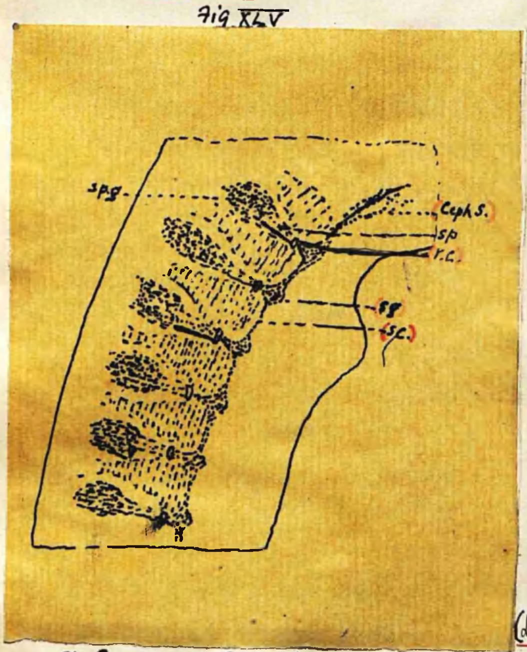
Spinal cord, showing cells passing out along anterior root.

Neumayer(31) working on Lacerta (Spec?) and chick embryos describes the sympathetic chain as originating in a ventrally directed outgrowth of cells from the mixed spinal nerve.The cells of which it is formed are derived from the cells which accompany the anterior and posterior nerve roots,which are differentiated in situ.

Froriep(7) working on Torpedo and rabbit embryosdescribes a migration of cells from the spinal cord along the ventral nerve roots.These cells he regards as the main source of supply for the formation of the sympathetic system,although some cells may come from the spinal ~~gan~~ ganglia also.In his opinion the ventral half of the neural tube supplies all the sympathetic neurones.

Lillie(28) in his book on the development of the chick gives a brief account of some of the theories on the development of the sympathetic chain.He finds the first clear evidence of the chain at the end of the third or beginning of the fourth day.At this stage it is represented by small masses of cells lying on each side of the dorsal aspect of the aorta.These cellsform a continuous cord extending from the upper part of the vagus to the beginning of the tail.Cells similar in structure are found along the course of the nerves up to the* spinal ganglia,and careful examination of the earlier stages indicates that the cells composing the cord have migrated from the spinal ganglia(fig45).At the sixth day of incubation the secondary or permanent chain appears.It consists of groups of neuroblasts situated just median to the ventral roots of the spinal nerves.The number of these secondary sympathetic ganglia is originally ~~thirty,one opposite the main vagus~~ thirty,one opposite the main vagus ganglion,and each spinal ganglion to the twenty-ninth.They are connected to the corresponding nerve root by the fibrous rami communicantes,and with one another by longitudinal bundles of fibres.

Fig XLV



(Lillie)

Sp.G. - Spinal Ganglia
(S.C.) Sympathetic Cord.
(S.G.) Sympathetic Ganglion
(r.c.) Ramus Communicans
Sp - Spinal nerve
(Cph.S.) Cephalic Continuation of the Sympathetic Trunk.

Bryce(3) in the embryological section of Quains Anatomy discusses some of the most important work on the development of the sympathetic system In the human embryo the sympathetic chain first appears as groups of cells closely applied to the ventral branches of the spinal nerves.Each of these soon becomes a cellular cord which is the rudiment of the ramus communicans.The ramus communicans soon becomes fibrillar,and the ganglion is produced by proliferation of a terminal group of cells(fig46).In the neck the vagus and sympathetic are very closely

Fig. XLVI

(Bryce)

N.C. neural canal.
n.a. neural arch
sp.G. Spinal Ganglion
S.r. Sensory root
m.r. motor root.
d.b. dorsal branch
v.b. ventral branch
w.b. Wolffian body
(Sy.) Visceral branch with Sympathetic Ganglion
St. Stomach
Sp. Spleen.
Ad. Adrenal
g.g. Genital Gland
L. liver - p. pancreas - A - Aorta

united. According to the work of His Jr. the superior cervical ganglion may be derived from the vagus and glosso-pharyngeal ganglia.

Held(12) records observations made by him on several types of vertebrates In Petromyzon** an outgrowth of cells is seen from the sensory and probably from the motor roots. This outgrowth which is in all probability the first stage of the sympathetic chain, is first seen at eighteen to nineteen days development

In Selachians the sympathetic chain is developed as a spindle shaped mass of cells attached to the posterior spinal ganglion(fig.47).

In trout embryos of eighteen days twenty hours development a short cellular chain from the spinal nerves towards the aorta represents the first stage of the sympathetic chain

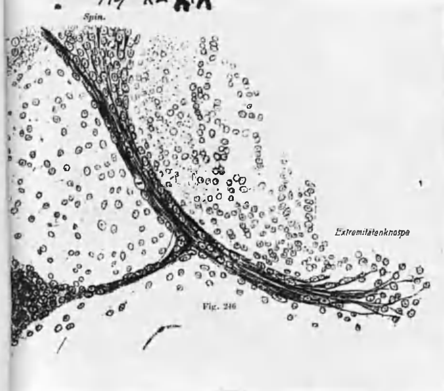
In the frog Rana esculenta the first trace of the sympathetic chain is seen at or about 5 to 6 m.m. body length, and consists of a small thickening on the spinal nerve(fig.48). The development differs in the frog from the Selachian in the fact that in the Selachian all the sympathetic cells are derived directly from the spinal ganglion while in the frog they pass down the motor nerve root as well. It is highly probable however that all the cells in the case of the frog originate in the spinal ganglia.

Fig. XLVII

Me. Medullary Column. (Held)
Ch. Noto chord.
A - Aorta

At about 7 m.m. body length the rami communicantes develope, while at 8 to 9 m.m. the cells of the sympathetic ganglia may be divided into neuroblasts and intervening cells.

Fig XLIX

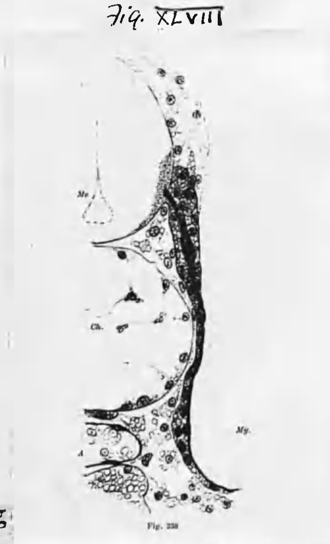


Medullarrohr - Medullary Column - (Held)
Aorta - with (sympathetic)

In reptiles taking the Emys europaea as a type the sympathetic chain is formed by an outgrowth of cells from the spinal nerves.This outgrowth is seen in embryos of thirty somites(fig.49). Slightly later in development the rami communicantes develope.

In the Turtle the sympathetic chain is seen very clearly to be an outgrowth of the spinal nerves.

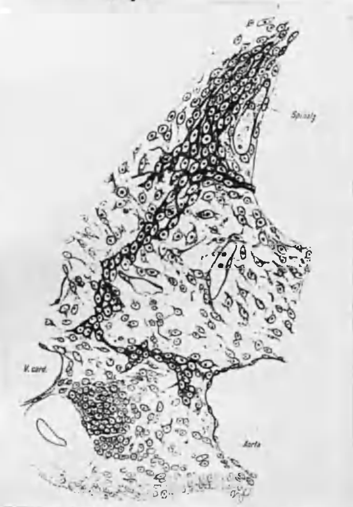
Fig. XLVIII



Me. Medullary Column (Held)
A - Aorta
My - Myotome
Ch - Notochord

In the chick and duck embryos cell chains are seen extending from the spinal nerves towards the aorta.These cell chains constitute the first ~~stag~~ stage in the development of the sympathetic chain,and is seen in the chicks after three days incubation,and in ducks slightly later(fig.50).

Fig. L



(Held)
Spinalg - Spinal ganglion
Aorta -
V. Card - Cardinal vein

In mammalian embryos taking the rabbit as a type the sympathetic chain is also developed from an outgrowth of cells from the spinal nerves.

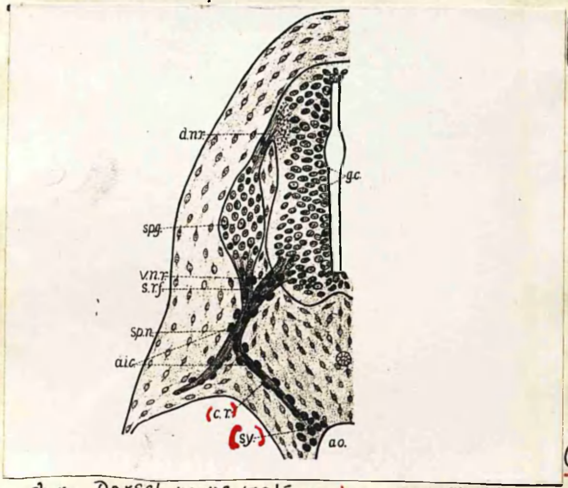
As a result of his investigations Held concludes that while a few cells are seen migrating from the ventral roots in embryonic chicks and ducks,and there is some doubt as to the exact condition in amphibians the balance of evidence is in favour of the view that the sympathetic chain is derived from the dorsal nerve root.Further the cells migrating from the spinal nerves to form the sympathetic are of two varieties,neuroblasts and aneuroblasts.The aneuroblasts accompany the neuroblasts and their outgrowths and may act as supporting cells.

Kuntz(25-27) discusses the development of the sympathetic chain in mammals birds and turtles.

In mammals,his observations were made on pig and cat embryos,

In embryos of 4 ~~59~~ to 5 m.m. the earliest signs of cellular migration from the neural tube are seen. At 7 m.m. the spinal ganglia are differentiated, rows of cells may be traced through the mantel layer to those ganglia, at that part of the neural tube where the dorsal root emerges. At 9 m.m. this migration into the spinal ganglia is evidently finished. At 6 to 11 m.m. cells are seen migrating from the medullary tube into the ventral nerve root. These migrant medullary move along the course of the spinal nerves and branching off form the sympathetic chain (fig. 51). All the accompanying cells do not leave the spinal nerves and may be seen along the course of the spinal nerves. Kuntz further points out that these accompanying cells do not correspond with the neurocytes of Kohn but are either neuroblasts or indifferent cells, both varieties being seen in almost any good section. Kuntz adopts the nomenclature of Schaper and furnishes a diagram (fig. 52) illustrating the relationship of the different cells.

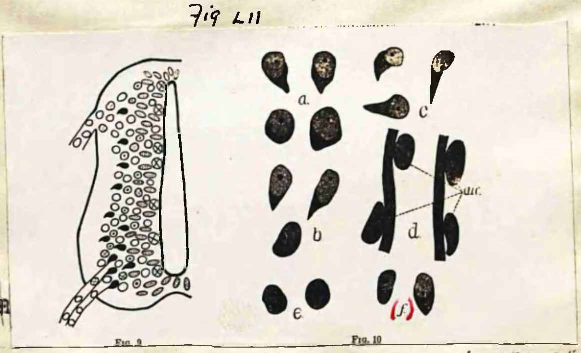
Fig LI



(Kuntz)

d.n.r. - Dorsal nerve root
spg - spinal ganglion
v.n.r - Ventral nerve root
g.c - germinal cells
(sy) - sympathetic
ao - aorta
(c r) - ramus communicans
sp n - spinal nerve.

Fig LII



(Kuntz)

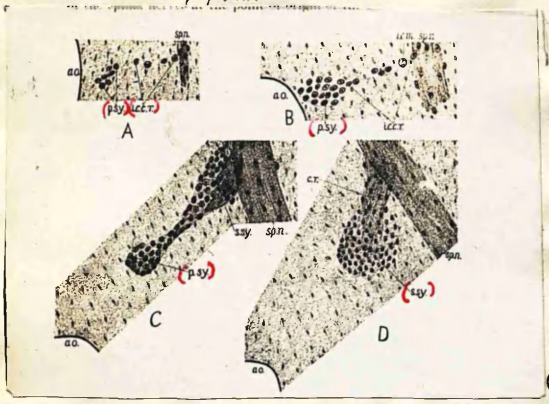
b - neuroblasts a - Cells in spinal ganglia
c - neuroblasts in spinal nerve trunks
d. Fibres with indifferent cells fr. spinal nerve.
e. Neuroblasts in communicating rami (f.) Sympathetic Neuroblasts

He suggests a wider application of Schapers conception of the developmental relationship of the neuroblasts and the indifferent cells in the central nervous system, pointing out that the neuroblasts and indifferent cells of the sympathetic chain are developmentally similar to those of the central nervous system. This theory taken in conjunction with the fact that both sensory and motor nerve elements pass directly into the chain from the cord serves to bring the sympathetic chain into line with the central nervous system, and to emphasize the fact that it is not a separate unit but a part of this system.

In birds the chick is the subject of investigation, and here also the sympathetic chain is developed from cells which migrate from the medullary tube along both nerve roots. The cells as in the mammals correspond to the neuroblasts and indifferent cells of Schaper.

The first evidence of the sympathetic chain is seen at the end of the third day.This is the primary chain and is replaced by the secondary chain about the sixth day.As however there is little or no migration of cellular elements from the anterior part of the sympathetic chain it is highly probable that in this area at least the primary chain is incorporated with the secondary.A diagrammatic representation is given of the whole process of development(fig.53).

Fig LIII



(Kuntz)

A.
sp.n. spinal nerve.
(ic.c.v.) Indifferent cells ramus communicans
(p.sy.) Primary sympathetic
ao. – Aorta
B – (P.sy.) Primary Sympathetic
C. (P.sy.) Primary Sympathetic Later in development.
D
(s.sy.) secondary sympathetic.
c.v. – ramus communicans
sp.n. spinal nerve.

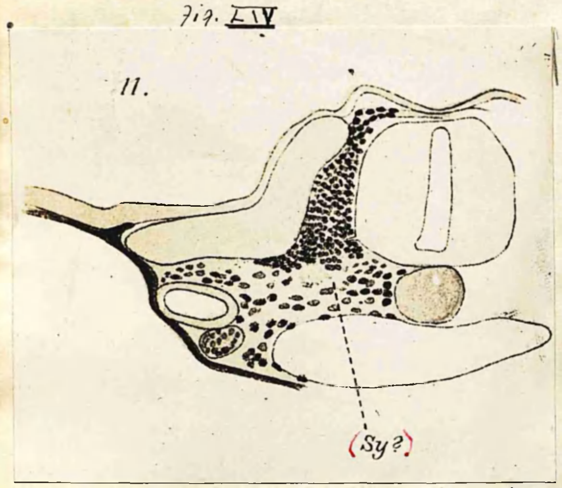
In the turtlethe embryos of the Thalassochelys caretta and the Chelydra serpentina are selected for examination.The earliest traceo of the sympathetic chain is seen at the eighth day of incubation.At this stage it is represented by loose *collections of cells lying along the lateral aspects of the aorta.These cells are connected to the distal ends of the spinal ganglia and are distinguished from the surrounding cells by their deeper reaction to the stain ~~stain~~,the iron haematoxylin,and the chromatin structure of the nuclei.At the end of the ninth day the chain is laid down from the cervical to the sacral regions,while the presence of a few fibres in the cellular bands connecting the sympathetic chain with the spinal nerves indicates that the fibrous rami communicantes are beginning to develope.At this stage also cells may be seen migrating from the ventral nerve root,and it is highly probable that they too take part in the formation of the sympathetic chain.At the eleventh day the migration of cells from the ventral nerve root is probably at its maximum,while the sympathetic chain shows distinct improvement in development.It is interesting to note that although a few fibres are seen among the cells leading from the spinal nerves to the sympathetic,the bulk of the fibres of the future rami communicantes are formed alongside those cellular chains.The two chains fuse about the twentieth day.

Comparing the conditions found in the turtle with those in the chick it is seen that although there is no secondary sympathetic chain formed in the turtle yet there is a rearrangement and regrouping of the elements.The earliest stages of the sympathetic chain are the same in both but in the adult form the chain is at some distance from the spinal nerves,while in the chick it is closely applied to ~~thos~~ those nerves.

As in the case of mammals and birds the cells migrating from the medullary tube to the spinal nerves and thence to the sympathetic chain correspond to the neuroblasts and indifferent cells of Schaper. In the turtle however the majority of the cells are of the indiffeent type so that the numerous neuroblasts seen later in the sympathetic chain must arise from mitosis of those cells.

Marcus(29) describes the sympathetic chain in Gymnophionia as arising from medially directed clusters of cells which branch off from the spinal nerves. These cells are not derivatives of the spinal ganglia but are neurocytes directly connected with the neurocytes of the neural crest. In other words the sympathetic ganglia are sister formations to the spinal ganglia. This is shown by the fact that the sympathetic ganglia begin to develope when the spinal ganglia are extremely primitive in structure(fig.54). Further it is found that a sympathetic ganglion is developed in connection with the first spinal nerve which in the Gymnophionia possesses neither a posterior root or ganglion(fig.55). This obviously refutes the old theory that the sympathetic ganglia are derivatives of the spinal ganglia, and also the other theory that the union of the anterior and posterior is necessary for the development of a sympathetic ganglion. No evidence is obtained of the ventral migration of cells along the anterior root for the formation of the sympathetic chain.

Fig. LIV

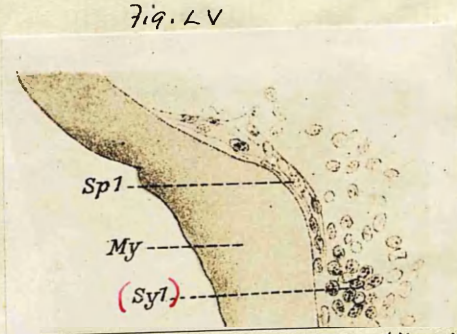


(Marcus)

(Sy?) Probably the first stage of the Sympathetic Chain.

Marcus also points out the close relationship which exists in the early stages of development between the cells of the sympathetic chain and the lymph spaces round the aorta. Keibel and Mall(20) in their Manual of Human Embryology describe the sympathetic system, its development and relationship to the central nervous system. They describe the sympathetic chain as arising in common with the spinal ganglia from that portion of the ectoderm which forms the lateral border

Fig. LV



sp1 - first spinal nerve (Marcus)

My - myotome

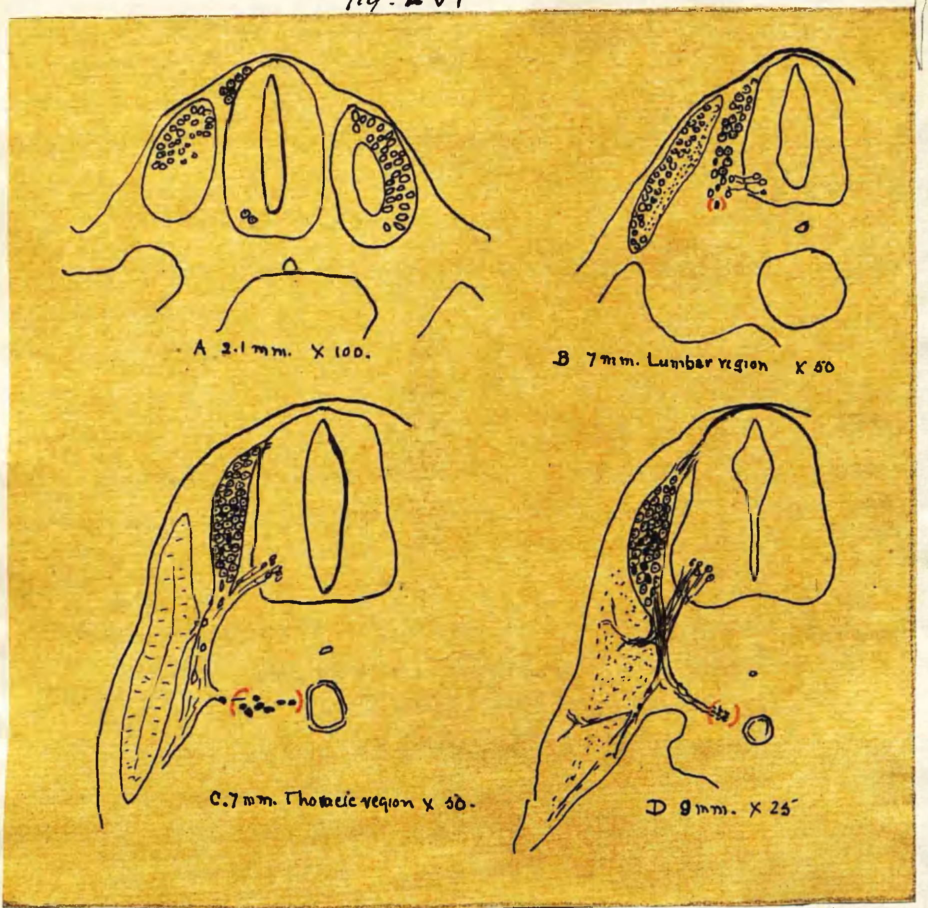
sp1 - first spinal "nerve ganglions)

My - myotome

(Sy1) - first sympathetic ganglion.

of the neural plate, and like the spinal ganglia takes part in the formation of the neural crest (fig.56). From the diagram it is seen that the sympathetic is an outgrowth from the spinal ganglia. The cellular migration begins at 7mm. and at 9mm. the sympathetic chain is clearly outlined. It is interesting to note that some of the sympathetic cells in the spinal ganglia never wander out but remain stationary in it (fig.D). The conception of the development of the sympathetic chain here described is the same as that given by His Jr. (15.16) except that the time of cellular migration is described at a slightly earlier period of development.

Fig. LVI



(Black cells) = sympathetic cells, Dotted circles = spinal ganglion cells, Sheath cells = white rings (Kribel and Mall)

From the account given of the most important work on the development of the sympathetic chain the various theories with their chief exponents may be briefly summarised as follows:

(1). Remak(36) teaches that the sympathetic chain is a mesodermic structure developed in common with the spinal nerves which are also derived from the mesoblast.

(2). Paterson(33) describes the sympathetic chain as a mesodermic structure developed separately from the spinal nerves with which it is connected later.

(3). Fusari(8) describes the sympathetic chain as a product of the protovertebrae.

(4). Jones(19) finds in the toad that the anterior part of the sympathetic chain probably arises from epiblastic cells, while the posterior portion is developed from an irregular bilateral ridge of cells which may be epiblastic. This assumption is based on the connection whichh exists between the posterior ridge and the anterior part of the sympathetic chain which is in turn connected with the first and second spinal nerves.

(5). Balfour(1,2) describes the sympathetic chain as an outgrowth or offshoot from the spinal nerves which begins as a series of small swellings on the main branches of those nerves.

(6). Onodi(32) finds that the sympathetic chain arises as a proliferation of the cells at the ventral portion of the spinal ganglia.

(7). His sen(14) and jr.(15,16) both agree in regarding the sympathetic chain as the result of the migration of a special type of cell from the spinal ganglia.

(8). Kohn(21,22) describes the sympathetic chain as formed from neurocytes which migrate from the medullary column along both the anterior and posterior nerve roots.

(9). Marcus(29) describes the sympathetic ganglia as formed from the neurocytes of the neural crest at the same time as the spinal ganglia, to which they therefore are "sister structures".

(10). Carpenter and Main(5) and Kuntz(25-27) suggest that the sympathetic chain is formed partly from cells which correspond to the neuroblasts and indifferent cells of Schaper(37), and which leave the spinal cord by the anterior as well as by the posterior root.

(11). Froriep(7) considers that the ventral half of the neural tube supplies all the sympathetic neurones.

The divergence of opinion is as shown here very marked.

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Chapter 2.

Methods.

METHODS

The staining method used in this investigation is the Silver Nitrate method of Ramon y Cajal(1). There are several modifications of this method, and a little experience is required in selecting the modification most suited for a particular type of tissue. It is found that where the tissue is very delicate as in the case of chicks incubated for varying periods up to seventy-two hours, the best results are got when the original method is used. With chicks incubated for a longer period the first modification is best. This modification is the most reliable for staining adult tissue. In the case of chicks incubated for seven days or longer the second modification is the most satisfactory. Descriptions of the method and its modifications are to be found in many textbooks, but there exists a certain degree of variation in the descriptions, I therefore give an account of the methods as they are applied in this investigation.

A. The original method:

The tissue is placed in a 1% solution of silver nitrate and kept in the dark at a temperature of about 35 centigrade. The tissue is examined from time to time in a red light until it assumes a golden brown colour. It is next washed in distilled water and placed in the following developing fluid:

Pyrogallic Acid	1 gramme.
Alcohol	10 c.c.
Formalin	5 c.c.
Distilled Water	ad 100c.c.

The tissue is kept in this fluid for twenty-four hours under the same conditions as those just described for the silver nitrate bath. It is again washed in distilled water and then dehydrated in the usual way. It is important to note that all manipulation of the tissue after it is placed in the silver solution to the final washing in distilled water prior to dehydration must be done in a red light.

B. The first modification.

The fresh tissue is placed in the following solution for twelve hours

Alcohol	65c.c.
Ammonia	·5 to 1c.c.
Distilled Water	ad 100c.c.

It is next placed for twelve hours in absolute alcohol to which 5 to 1c.c. of ammonia is added. Finally it is washed thoroughly in distilled water and transferred to the silver solution after which it is carried through in the ordinary way.

C.The second modification.

The fresh tissue is placed for twenty-four hours in the following solution

Formalin	25c.c.
Ammonia	1c.c.
Distilled Water ad	100c.c.

It is then washed for twelve hours in running water,and after a precautionary bath of a few minutes in distilled water,placed in the silver solution.

This method with its modifications shares the characteristic of many of the metallic stains and gives the best results where the tissue is not quite fresh.In the case of embryos incubated for more than four days the eggs are removed from the incubator several hours before the chicks are placed in the stain so as to allow of a certain degree of post mortem change.

The embryos are embedded in paraffin and afterwards cut in sections of from 5 to 7 micra.

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Chapter 3.

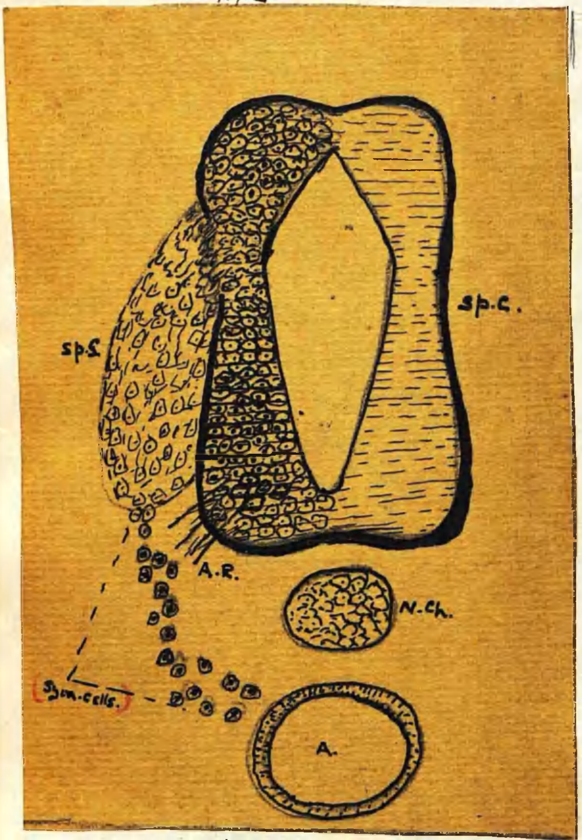
The Process of Development of the Sympathetic Chain as shown in the present Investigation.

Development of the Sympathetic Chain.

In the chick the earliest definite evidence of the sympathetic chain is seen at seventy-two hours incubation. Prior to this period a few cells are seen amongst the mesoblastic tissue lying in front of the neural tube which strongly suggest by their appearance and colouration that they are of ectodermic origin. They stand out from the mesoblastic cells partly on account of their size, which is a little bigger, but more on account of their colour which is golden brown while the mesoblastic cells are yellow. These cells are however very scanty and as they do not occur in every section they are easily overlooked. From their position and also from the fact that they correspond very exactly with the cells which at a somewhat later date form the sympathetic chain these cells must be regarded as the very earliest stages of this chain. In a very few instances they are found as early in the third day as the sixtieth hour of incubation, but more frequently at stages between this and the end of the third day.

At the seventy-second hour of incubation the central nervous system has already attained to a considerable degree of development. The spinal ganglia are differentiated while in the ventral part of the neural tube a few fine fibrils are seen emerging from the site of anterior nerve root. From the ventral extremity of the spinal ganglia a delicate chain of nerve cells is seen passing ventrally across the position occupied later by the anterior nerveroot to terminate in the mesoblastic tissue lying near the aorta in the trunk, and the carotids in the neck. These cells correspond to the description given of the stray cells found at the earlier stages of development in the tissue ventral to the neural tube, but as they are more numerous they are easier of recognition. It must be remembered that even at this stage when the migration of cells from the spinal ganglia is clearly seen the number of cells is comparatively small and in some sections they are almost if not completely absent. The diagram which is here given is therefore prepared from a reconstruction of the trunk of a chick and is not an illustration of the condition found at all points along the spinal ganglia (fig. 1) At this stage no exact observations can be made on the intimate structure of those cells but many of them have a granular appearance. At this stage therefore the sympathetic chain is in process of formation its cells being derived wholly from the spinal ganglia.

Fig. I

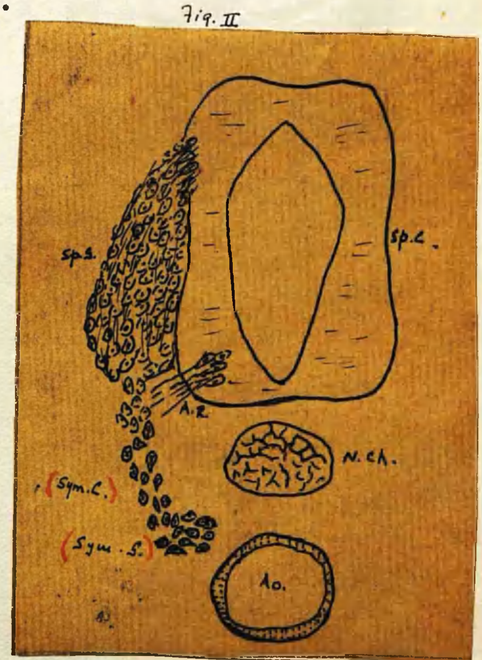


Sp.c. Spinal cord.
Sp.S. Spinal ganglion
A.R. Fibres of anterior root
(Sym cells) Sympathetic cells
N.Ch. Noto chord
A – Aorta –
(abel)

At eighty hours incubation the number of cells migrating from the spinal ganglia have increased and chains of nerve cells may be seen at almost any level in the trunk leading from the spinal ganglia to the dorso lateral aspect of the aorta or the dorsal wall of the carotids.Clusters of sympathetic nerve cells now appear in those positions and the sympathetic chain is now a comparatively prominent structure,more especially in the proximal part of the trunk(Fig.2).
At this stage careful examination of the anterior root shows that amongst the nerve fibres cells may be seen which are passing out from the neural tube.This migration varies in different chicks in some it is much more striking than in others but it is always present to some extent.Compared with the migration from the neural tube to the posterior nerve root it is very scanty.

.The cell chains are easily identified in their course from the spinal ganglia to the sympathetic chain.They are larger than the surrounding mesoblasts and stain even more characteristically than at earlier stages,their granularity is even more marked.A few of them are seen to be already provided with a very short unipolar outgrowth,but the majority of the cells are roughly circular in outline and depend for identification on the three points noted. In these early stages of development the excellence of the Silver nitrate stain is demonstrated in the differential colouration of the nerve elements which is appreciable at the initial stages of nerve development and which improves with the progress of development.

Fig. II



Sp.c. Spinal cord. (abel)
Sp.G. Spinal ganglion
A.R. Anterior root
(Sym.c.) Sympathetic cell chain
(Sym G) Sympathetic ganglion
N.Ch. Noto chord.
Ao – Aorta

One drawback to the method is that while the differentiation of nerve cells is comparatively easy in the early stages, the degree of difference in the colour of the nerve cells and of the mesoblasts is not sufficient to allow of successful photography. Attempts have been made repeatedly but it is not until the development of the nerve tissue is somewhat advanced that successful photographic pictures are obtained.

From eighty to ninety-six hours development the migration of nerve cells takes place from both the spinal ganglia and the anterior nerve root. These cells are now definitely seen to consist of two varieties. The greater number have large nuclei, are generally rounded in contour, and show very granular protoplasm~~ic~~. These cells are very frequently seen in the condition of mitosis(fig.3).

Fig. III

(Abel)

The other variety is characterised by a unipolar outgrowth, a well marked nucleus, and the shape of the cell which is roughly triangular. They are very much scantier than the cells of the first variety(fig.4).

Fig. IV

(Abel)

In the anterior root the nerve cells may be followed in an embryo of some ninety hours incubation from the neural tube through the limiting membrane to the fibres of the nerve root(fig.5)

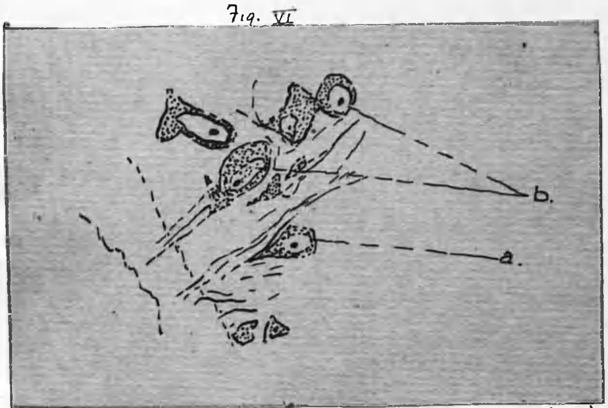
Fig. V

(Abel)

1. 2. 3. - shows gradual migration of cells from the spinal cord along the anterior nerve root.

Examination of the anterior nerve root at ninety-six hours incubation shows that both varieties of cells lie amongst the nerve fibres (fig 6). The cells migrating from the posterior nerve are also composed of the two varieties both of which are however far more numerous than at the anterior root (fig.7).

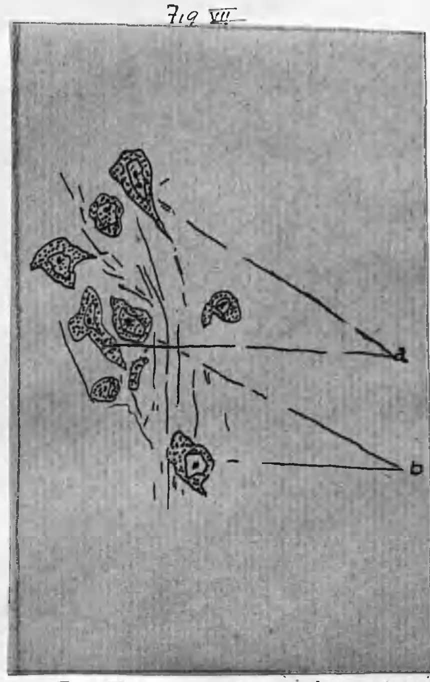
Fig. VI



(abl)

Anterior nerve root with accompanying cells
a. Cells showing outgrowths.
b - Cells with no outgrowths

Fig VII

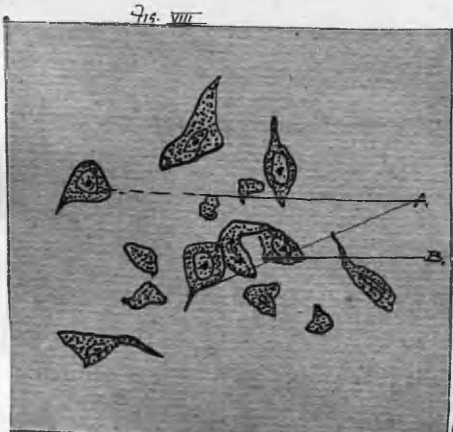


(abl)

Posterior nerve root with accompanying cells.
a - Cells with outgrowths.
b — Cells with no outgrowths

The cells accompanying the anterior root send off some of their number to join the migration from the posterior nerve to the sympathetic chain. Indications are got at earlier stages of this migration from the anterior root to the sympathetic chain but it is not until the end of the fourth day of development that definite cell chains are found joining those from the posterior nerve. The chain of cells to the sympathetic chain is composed of the two varieties of cells already referred to but the cells showing the unipolar outgrowths are comparatively more plentiful (fig.8). The outgrowths of the cells are more prominent and give a somewhat fibrous appearance to parts of this chain. The sympathetic cells of the chain are also characterised by this increase of what has hitherto been the more unusual variety (fig.9).

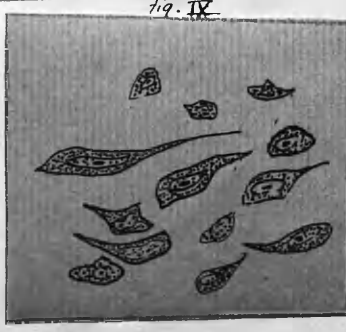
Fig. VIII



(abl)

Cells forming chain leading from the spinal nerve to the sympathetic ganglion or chain
A - Cells with outgrowths
B - Cells with no outgrowths.

Fig. IX



(abl)

Cells showing well marked outgrowths in the (sympathetic chain)

At ninety-six hours incubation therefore definite evidence is got of the migration of two varieties of cells from the spinal ganglia and the anterior nerve root to form the sympathetic chain.Further it is evident that the numerical ratios of those cells change gradually as the sympathetic chain is approached, and in the chain itself. From a consideration of the classification and description of the cells of the spinal cord given by Schaper(fig.3)the conclusion is arrived at that the two varieties of cells here described correspond with the Indifferent cells and Neuroblasts of Schaper.At the initial stages of the migration from the nerve roots it has already been pointed out that the majority of cells are roughly circular in shape,have large nuclei surrounded by granular protoplasm,and that some of them are seen in the condition of mitosis.Now these cells correspond to the Indifferent cellswhich as Schaper shows may give rise to neuroblasts,and observation shows that decrease as the number of neuroblasts increase.This explains why so many neuroblasts are found in the sympathetic chain while so few are seen passing from the spinal nerve roots.

During the latter part of the fifth day or from a hundred and eight to a hundred and twelve hours the migration of cells from the spinal nerves to the sympathetic chain is well marked.In the abdominal region there is very little accumulation of cells in the sympathetic chain since the ventral migration is so extensive.In the thoracic region on the other hand the ventral migration from the chain is either non existant or very slight so here the chain is a comparatively large structure.In the cervical region it is also a well developed structure.The upper portion of this part of the chain is closely associated with the vagal ganglion.

At a hundred and twenty to a hundred and forty-two hours the sympathetic chain is well developed in the thoracic and cervical portions of the body but in the abdominal region the ventral migration is so extensive that it effectually prevents any accumulation of the sympathetic cells in the position of the chain.At this stage also nerve fibres appear amongst the cells which migrate from the spinal nerve roots.Up to this time the sympathetic cells have taken their position some little distance from the spinal nerves as indicated in the diagrams of the earlier stages of development,but about the end of the sixth day they begin to occupy a position close to the anterior spinal nerve,the position of the secondary or permanent sympathetic chain.

At a hundred and forty-four hours incubation the secondary sympathetic chain is recognised in the thoracic region.The cells for this chain are derived partly by migration from the nerve roots but also from the primary chain.The primary chain is all along well developed and no great demands are made upon it for the formation of peripheral ganglia as is the case with the abdominal part of the chain.At this stage it seems to be a source of supply for the formation of the secondary chain.If this is not the case what becomes of those sympathetic cells which form so prominent a primary sympathetic chain in the cervical and thoracic regions and which so far as I can see are not utilised in ventral migration?They must either atrophy or be incorporated in the secondary chain.No evidence is got to suggest that do atrophy,but the rapid development of the sympathetic chain in the anterior part of the body,which is out of proportion to the cellular migration,certainly supports the suggestion that the primary chain is to a considerable extent incorporated in the secondary or permanent chain.At a hundred and sixty-eight hours the sympathetic chain in the ~~anterior~~ thoracic region is fully developed (fig.10).From the photograph its relation to the spinal nerves is clearly seen while its structure which is fibro cellular is also indicated.

Fig. X

Anterior and posterior nerve roots with the (Obl) spinal and sympathetic ganglia.

In the abdominal region the primary chain is at no time a very well developed structure the ventral migration is so marked that it is impossible to distinguish the two chains primary and secondary as in the thoracic and cervical regions. Up to a hundred and forty-four hours incubation the sympathetic cells have been passing in a continual stream from the spinal nerves to the sympathetic chain and from thence to the tissue in front of the aorta,and in many embryos the cells of the permanent chain do not appear until the latter half of the seventh day.The development of the secondary sympathetic chain seems to be associated with the completion of the ventral migration necessary for the formation of the abdominal and visceral plexuses.That is they are the last cells to migrate from the spinal cord and apparently are at their destination so soon as they emerge from the spinal nerves. In this region the secondary chain is a completely new structure and in this point forms a contrast to the secondary chain of the thoracic and cervical regions.

In the pelvic region a secondary sympathetic chain is not developed A delicate plexus is formed by this portion of the sympathetic chain from which outgrowths pass ventrally to the lowest portion of the gut.

The sympathetic chain in the cervical region has already been referred to and classed for descriptive purposes along with the thoracic portion of the chain~~but~~ but the uppermost part of the chain is a little different in its development from the other parts. The primary chain does not disappear completely but persists as a small ganglion about the level of the ganglion of the vagal trunk. A secondary ganglion is also formed in common with the secondary chain, so that the uppermost portion of the sympathetic chain terminates in two ganglia lying some little distance apart but practically at the same level. Observations made on chicks up to a hundred and ninety-two to two hundred and sixteen hours development show that those two ganglia are united by fine fibrous bands, while from them slender fibres pass upwards to the cranial region.

Up to the end of the ninth day the sympathetic chain in the abdominal region is distinctly poorer in structure than in the thoracic portion In the thorax and also in the cervical region the primary chain has quite, or all but quite, disappeared.

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Chapter 4.

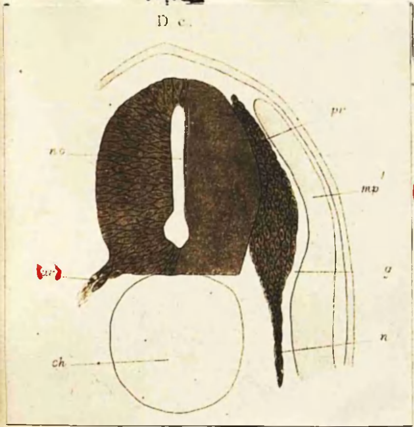
A Discussion of the results obtained in this investigation and their relation to those of other workers.

DISCUSSION

Comparing these results with those described by other workers it is evident that they agree in many points with those of His Jr.(34) whose work is described in the first section of this paper.
His recognises the primary sympathetic chain at the end of the third day as small clusters of cells, some of which are already provided with outgrowths, lying at the sides of the aorta and behind the carotids. With this description my results are practically in agreement but evidence is obtained of sympathetic cells in the mesoblastic tissue ventral to the spinal cord at an earlier date. These cells must have migrated from the spinal cord but it is the end of the third day or cell chains are seen leading from the spinal ganglia to the position of the sympathetic chain. I agree with His in tracing the sympathetic chain at this stage to a cellular migration from the spinal ganglia but at a later stage I find that cells from the anterior root join those from the spinal ganglia for the formation of the sympathetic chain. On this point our results differ as His regards the sympathetic chain as a product of the spinal ganglia. In this view His is supported by other workers among whom may be mentioned Schenk and Birdsall(29), Kolliker(17), Onodi(24), His Sen.(12), and Rabl(25.26) who all worked before His, and Lillie(21), Bryce(7), and Keibel and Mall(15) who have embodied his work in their textbooks.
Among those who regard the sympathetic chain as a product of both the spinal nerves are the following Balfour(4.5) for he describes the sympathetic ganglia as arising in swellings on the main branches of the spinal nerves, Van Wijhe(30), Kohn(16) Neumayer(25), and Kuntz(18-20). Held(11) might also be included in this second list as he finds evidence of the migration of cells along the anterior nerve roots in the chick but as this migration is comparatively scanty he concludes that the balanceof evidence is in favour of the view that the sympathetic chain is derived wholly from the spinal ganglia. Held is apparently influenced in making this conclusion by the fact that he finds no evidence of the participation of the anterior root in the formation of the sympathetic chain in amphibians. He does not appear to have quite satisfied himself that the sympathetic chain in the chick** is not to a certain extent formed by those scanty cells which he finds in the anterior nerve.
It is interesting to find corroborative evidence for the migration of nerve cells from the neural tube along the anterior nerve root in work which has been done on the central nervous system.

Balfour(3) working on Elasmobranch fishes describes the anterior root in its early stages of development as a conical prominence composed of cellswhich are derived from the spinal cord.The convergence of the cells in the cord to the point of origin of the anterior root is clearly seen(fig.1).

Fig. I

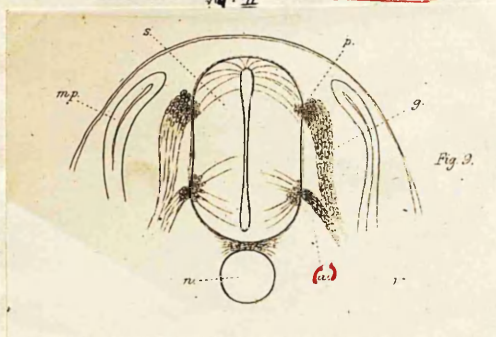


h.c. Neural Canal
(a.r.) anterior root
p.r. posterior root
m.p. muscle plate
g. ganglion
n. nerve.
ch. notochord

(Balfour)

Marshall(22) who investigated the early stages in the development of the nerves of the bird also recognises the cellular nature of the anterior nerve roots(fig.2).

Fig. II



s. spinal cord
p. posterior root
g. ganglion
(a). anterior root
m p muscle plate
n. notochord.

(Marshall)

Schäfer(27) gives a short note on the occurence of ganglion cells in the anterior root of the cats spinal nerves.These cells are generally found in that part of the which passes the ganglion of the posterior root,but they are not always situated next the ganglion.They are often found in the middle of the root or on its anterior margin.These cells although they occur in all the anterior roots are more numerous in the dorsal and lumbar regions.They resemble in type the cells of the posterior ganglia but no connection between them and those ganglia can be found.Examination of the embryos of dogs,rabbits,and mice as well as of human embryos has failed to demonstrate their presence.

Beard(6) in his investigation of the development of the peripheral nerves in vertebrates also describes the migration of cells from the spinal cord along the fibres of the anterior roots in the chick(fig.3).

Fig. III

(a) - anterior root (Beard)

Harrison(10) in his work on the development of the peripheral nervous system in the Salmo salar describes cells which migrate from the spinal cord along the course of the anterior nerve roots,some time after the fibres of the root have developed. He suggests that those cells may very probably form the motor neurones of the sympathetic system.Reference has already been made to this paper in an earlier section,but is repeated here because of the special bearing it has on the

development of the anterior nerve root.
Carpenter and Main(9) whose article is also referred to in an earlier section, also describe the migration of medullary cells into the ventral nerve root of the pig. In some sections they find cells in process of migration lying half in and half out of the spinal cord, so that there can be no dubiety as to the source of the cells which are found in the fibres of the anterior nerve up to its point of union with the posterior root.
From this summary it is evident that there is evidence of the migratio of cells along the anterior roots of the spinal nerves in fish, birds, and mammals.
As to the characteristics of those cells I find that they are exactly similar to those migrating from the spinal ganglia and consist of two types, which correspond with the Indifferent cells and Neuroblasts of Schaper(28).
His Jr.(13.14) describes two types of cells migrating from the spinal ganglia one of which shows unipolar outgrowths while the other does not. It is a little uncertain from the description whether His does not regard the latter cell as a partially developed cell that is one in which the outgrowth has not developed. Whether this is the true interpretation or not it is evident that we essentially agree in recognising a roughly circular cell with a large nucleus, and a cell possessing a unipolar outgrowth.
Kohn(16) finds that the sympathetic chain is built up of one type of cell the neurocytes of the anterior and posterior roots. The only variation being the mitotic condition which characterises almost all the cells at particular points. From his photographsthe neurocytes seem to be divisible into two classes an oval, and elongated(fig.4) No note is made in the text which would suggest any such classificatio but the appearance presented in the drawings seems to allow of no other interpretation.

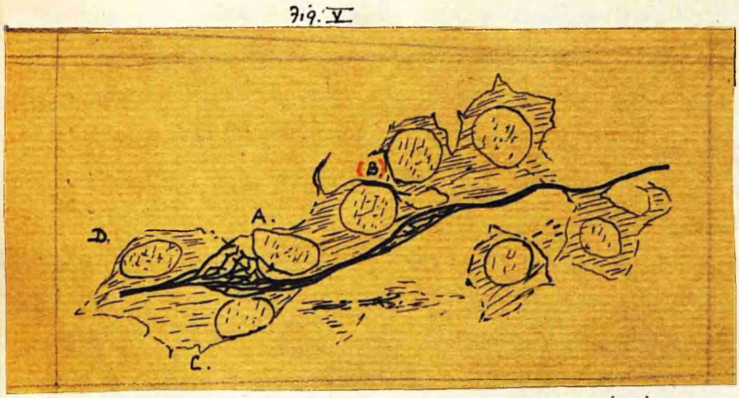
Fig. IV

(Held)

Note the elongated and roughly circular cells which form the outgrowth from the spinal nerves (For actual photograph refer Chapt. 1. page fig. 41)

Held(11) distinguishes neuroblasts and aneuroblasts in the cells which form sympathetic chain. The former are the true nerve cells while the latter probably act as supporting cells(fig.5).

Fig. V



(Held)

A. Bipolar neuroblast
C. and D. accompanying cells.
(B) — represents the temporary termination of the developing sympathetic cellular chain.

Kuntz(18-20) also recognises two types of cells in the chains migrating from the spinal nerves to form the sympathetic chain.He finds that they correspond to the Indifferent cells and Neuroblasts of Schaper.This classification he finds holds good in chicks,turtles pigs and cats.

Kuntz(18-20) is so far as I know the first to apply this wider interpretation of the work of Schaper although indications of this idea are found in the writings of Carpenter(8),and Carpenter and Main(9).

Schapers work[28] has already been referred to in the earlier section of this paper.In it he shows that the two types of cells Indifferent and Neuroblasts are the end products in the developmental evolution of the central nervous system.Histologically the Indifferent cells are characterised by a large nucleus with a delicate chromatin structure surrounded by a very little cytoplasm.The Neuroblasts are provided with large nuclei surrounded by a large cytoplasmic body which is drawn out to a point.Kuntz therefore suggests that the cells which he finds migrating along the spinal nerves and eventually passing out to form the sympathetic chain differ only from the cells which remain in connection with the spinal nerves in their final destiny and not in their structure or origin.He further suggests that some hormone may be secreted by the developing tissue in the neighbourhood of the notochord which may attract the cells for the formation of the sympathetic chain.This is however a purely speculative suggestion. In my earlier work on this subject(1) my attention ~~was~~ is directed to the development of the nerve supply in the alimentary canal of the chick and the development of the sympathetic chain is but touched on.In a subsequent paper(2) the development of the sympathetic chain is gone into in detail and I find that two types of cells migrate from both spinal nerve roots to form the sympathetic chain.From the fact that one type is more abundant than the other at the beginning of the migration while the other type is seen to gradually increase it seems evident that the two types are developmentally related

This is further supported by the fact that the more abundant type of cell is very frequently found in the condition of mitosis.At first I was inclined to regard the cells of the less frequent type that is the cells which have a unipolar outgrowth as a later stage in the development of the more frequent type the cells of which have no outgrowths.After some time it became evident that this explanation of the course of development of those cells would not clear up all the difficulties.The circular non outgrowth bearing cell which is so plentiful in the early stages of development is as already stated found very frequently in the condition of mitosis and yet as development proceeds this type of cell does not increase but decreases.It is evident therefore that they must give rise by their mitotic division to cells of another type.Parallel with the decrease of this type is the steady increase of the cells showing outgrowths.I have therefore come to the conclusion that a large proportion of ~~the~~ those cells are formed from the circular cells.When the work of Schaper was brought under my notice the description given by him of the gradual evolution of the cells of the central nervous system and the potentiality of the Indifferent cell seemed to bear out fully the theory which had been forced upon me.The types of cells which form the sympathetic chain as I find them with the Silver stain correspond~~ed~~ so closely with the Indifferent cells and neuroblasts of Schaper that I have called attention to the fact in my second paper(2) and in the preceding part of this paper.I therefore agree with Kuntz(19) who as I have already shown gives a similar account of the development of the sympathetic chain .

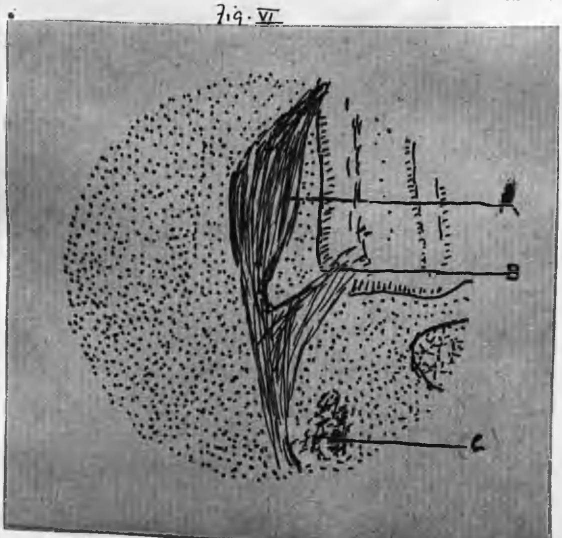
The next points which must be considered are the fate of the primary chain and the relation in which it stands to the secondary sympathetic chain.

Onodi(24) in his work on the development of the sympathetic system in the chick mentions that a secondary chain is developed but gives no particulars as to its mode of formation.

His Jr.(13.14) describes the development of the secondary sympathetic chain in the chick in great detail.He finds that the secondary chain appears at the sixth day of incubation while its development is parallel with the disappearance or degeneration of the primary chain.The cells of the primary chain are utilised to a great extent for the formation of peripheral plexuses but some of them may be incorporated in the . secondary chain although ****** His thinks that more probably they atrophy.In the abdominal region the secondary chain is more slowly

developed than in the thoracic or cervical regions,while in the pelvic area no secondary sympathetic chain is formed at all.
Kuntz(19)also describes the appearance of the secondary sympathetic chain in the chick at the sixth day of development,but he differs from His as to its mode of formation.According to Kuntz the primary chain in the anterior part of the trunk is not utilised for the building up of peripheral plexuses,and there is no evidence that the cells atrophy.He therefore concludes that as the development of the secondary chain is accompanied by the disappearance of the primary chain the latter must be incorporated in the permanent or secondary sympathetic chain.In the abdominal region the two chains can not be separated as in the anterior part of the trunk on account of the extensive migration which goes on continually from the sympathetic cells behind the aorta to the viscera.In this portion of the trunk the secondary sympathetic chain is probably formed wholly by a special migration of cells from the spinal cord.
In my first paper on the development of the sympathetic(1)I point out that my results do not agree with those of His as regards the development of the secondary sympathetic chain as I fail to obtain evidence of the definite formation of two separate sympathetic chains. In this first paper I describe the appearance of thesympathetic chain as an outgrowth of cells from the spinal ganglia which in the abdominal region pass on more or less completely to the preaortic regions.In the thoracic and cervical regions the cells form comparatively large clusters very different from the scattered and broken arrangement of cells seen in the abdominal region.At the sixth and seventh days I recognise the cell clusters in the position of the secondary sympatheti chain of His but they appear to me to be but the final stages in a hitherto continuous stream of migrating cells(fig.6).I therefore conclude that the so called secondary chain is but a stage in the development of the sympathetic chain .
In a subsecuent investigation on the development of the sympathetic system I paid special attention to the course of development of the sympathetic chain and I have adopted for the purpose of convenience the nomenclature of primary and ~~sympathet~~ secondary sympathetic chains,although I still hold my early views as to

Fig. VI



(abel)

A – Posterior ganglion (C) – Sympathetic ganglion
B — Anterior root

the development of the sympathetic chain(1).I hold that the sympathetic chain is formed by the outgrowth of cells from the anterior and posterior nerve roots and that these cells in the earliest stages of development migrate some little distance from the spinal nerves. These form the so called primary sympathetic chain.As development proceeds the cells seem to lose the power of migration or more probably the demand for cells in the ventral parts of the body has ceased at any rate the sympathetic cells accumulate just after they emerge from the fibres of the spinal nerves.This accumulation of cells forms the secondary chain.The two chains are therefore as I have already pointed out the products of one continuous process of development.

As regards the non development of the secondary sympathetic chain in the pelvic region which His Jr.(13.14) describes my results are in complete agreement.

His also describes the persistence of the primary chain in the uppermost cervical region with the result that in the fully developed chick two superior cervical ganglia are recognised the second being part of the secondary chain.

In chicks up to the tenth day of development I find a similar condition two separate clusters of cells joined by delicate fibrous bands forming the upper extremity of the sympathetic chain.

CONCLUSIONS

As a result of the foregoing descriptive and discursive sections the following conclusions are drawn up.

(1). The sympathetic chain is formed from cells which migrate from the spinal cord along the anterior and posterior nerve roots

(2). These cells correspond to the Indifferent cells and Neuroblasts of Schaper.

(3). The primary and secondary sympathetic chains are stages in one continuous developmental process.

(4). In the pelvic region the secondary sympathetic chain does not develope.

(5). In the uppermost cervical region the sympathetic chain terminates in two ganglia which are formed from the primary and secondary sympathetic chains. These ganglia are united by delicate fibrous bands.

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Chapter 5.

Historical Review of Investigations made on the Development of the Peripheral Portions of the Sympathetic System.

Remak(24) regards the peripheral portions of the sympathetic nervous system as developing in situ from the mesoblast and being joined later with the sympathetic chain. In the chick he finds that at six days incubation a circular unpaired band of nerve tissue appears in the mesentery close to the gut. This is the Intestinal nerve of Remak. At eight days nerves appear at the mesial margin of the urinary tubules. At the end of the third week of incubation the various peripheral portions of the sympathetic system are linked up with the sympathetic chain by means of a connecting nerve band, theMittelnerv of Remak

Hensen(8) although he describes no observations on the development of the peripheral portions of the sympathetic system yet suggests that they in common with all the ganglionic cells in the body are derived from the ectodermic layer.

Brunn(3) describes the development of the suprarenals in the chick and points out that a close relationship exists between the cortical or mesoblastic part and the medullary part derived from the sympathetic ganglia.

Schenk and Birdsall(28) conclude from their investigations on birds and mammals that the peripheral portions of the sympathetic system are derived from the sympathetic chain. In the chick they can trace an unbroken nervous connection between the sympathetic chain and the gut wall. In the human embryo** at 22 mm. body length a similar chain is seen extending from the ganglia of the sympathetic chain to the gut.

Braun(2) in his investigation on the development of the suprarenals in reptiles recognises the part taken by the sympathetic in the formation of the medullary portion of those organs.

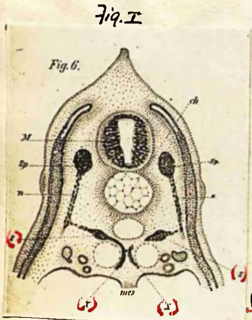
Kolliker(16) describes the coeliac plexus, and a nervous network lying in front of the aorta and between it and the suprarenals and kidneys in a human embryo of about nine weeks development. In another embryo of from three to four months a nerve plexus is seen between the muscle layers of the intestine, this plexus Kolliker names the Tunica nervosa. As to the manner in which those nerve networks are formed no suggestion is made

Balfour(1) describes the formation of the suprarenals in Elasmobranchs He finds that they develope from the fusion of a series of paired bodies derived from the sympathetic ganglia with an unpaired body developed from the mesoblast. Reference is made in this paper to some of the early work done in connection with this subject.

Foster and Balfour(6)describe the suprarenals as appearing in the rabbit at twelve to thirteen days development.This is the mesoblastic part and constitutes later the cortex of the organs.At fourteen days a mass of cells is seen lying dorsal to this portion of the suprarenal.This mass of cells is derived from the sympathetic chain with which it is at this stage directly continuous.At sixteen days these cells grow into the mesoblastic portion and form the medulla of the organ.

Onodi(21)in his investigations on the development of the sympathetic system in fish finds evidence of the migration of nerve elements from the ganglia of the sympathetic chain.These nerve elements form a chain along the lateral margins of the aorta,in front of which both chains unite,from this point they may be followed down to the root of the mesentery(fig.1).

Fig.I



(Onodi)

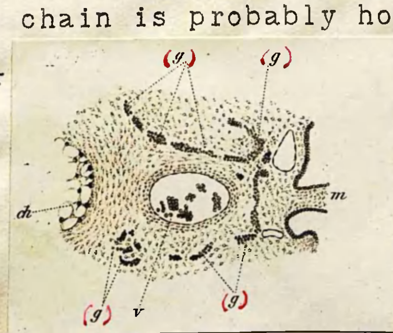
Ch - Notochord. (X) Peripheral outgrowths from the sympathetic ganglia.
M - Medullary column.
Sp. Spinal ganglion.
n - nerve trunk.
(S) - Sympathetic ganglion, Mes - Mesentery

In the bird the formation of peripheral sympathetic plexuses is clearly seen to be the result of migra~~ti~~tion of nerve cells and fibres from the sympathetic chain ganglia.In a chick of five days incubation the cells of the ganglia of the sympathetic chain are found to be arranged in a somewhat cone shaped cluster with the apex of the cone directed ventrally At this apex the cells are in active process of division while a delicate cell chain may traced from it to the dorsal wall of the aorta.This is the first stage of the ventral migration of sympathetic nerve elements.Inspection of a number of chicks at the fifth day shows that in some cases at least sympathetic nerve cells have broken off from this chain and occupy positions in front of the aorta and at the root of the mesentery.The ventral migration from the sympathetic chain is best marked in the abdominal region but it is also seen in the regions of the heart and liver.In addition to those structures a band of nerve cells is found in the neighbourhood of the rectum,it extends proximally for some distance but no connection can be demonstrated between it and the sympathetic chain.

In the duck embryo of six days development practically the same conditions are found as in a chick of five days,the ventral migration of nerve elements from the sympathetic chain is probably however a little more striking(fig.2).

In a chick of five days eighteen hours incubation the ventral migration from the sympathetic chain is well marked,the groups of cells

Fig.II



(g.g) Sympathetic ganglion zone.
V - Abdominal aorta
m - Mesentery
ch - Notochord

(Onodi)

lying in front of the aorta in the abdominal regions are the precursors of the preaortic ganglia and plexuses of the adult. The band of nerve tissue already recognised in the neighbourhood of the rectum is more prominent it is situated ·063 mm. from the intestinal epithelium and extends upwards to the level of the genital ridge, no connection can be seen between it and the sympathetic nerve cells which at this stage extend well into the mesentery.

In the duck at six days nineteen hours the same stage of development is reached. The ventral migration from the ganglia of the sympathetic chain is well marked the cells being traceable right into the mesentery. The band of nerve tissue lying in the lower part of the intestine is a prominent structure and as in the chick extends to the level of the genital ridge, but no connection can be made out between it and the sympathetic chain or its outgrowths.

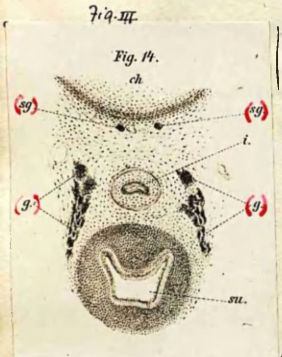
In a chick of seven days incubation the various preaortic ganglia are better formed while the chains of sympathetic cells in the mesentery are more numerous.

Onodi concludes that in the bird as in the fish sympathetic nerve cells may be traced as far as the mesentery but there is no evidence that the nerve supply in the viscera is an outgrowth from the sympathetic chain.

In the mammal observations are recorded on guinea pig, and rabbit as well as human embryos.

In a guinea pig embryo of 20mm. ganglionic cells are found to have migrated from the sympathetic chain ganglia and now form small ganglia some little distance in front of the chain (fig.3).

Fig. III



(Onodi)

Ch. — Notochord.
(Sg) — ganglia of Sympathetic Chain.
(g) — Peripheral groups of sympathetic cells.
Su — urogenital sinus
i — intestine

In the rabbit embryo at 10 mm. sympathetic cells which have migrated from the sympathetic chain form medium sized clusters in front of the abdominal aorta (fig.4).

In the human embryo of 18, 30, 32, 42, and 46 mm., the stages examined, the sympathetic chain is found fully developed, and the peripheral plexuses fully laid down.

As a result of these extensive investigations Onodi comes to certain definite conclusions on the development of the peripheral portions of the sympathetic chain

Fig. IV

(Onodi)

Y. Abdominal aorta
(g.g.) — Sympathetic cells separated from the sympathetic chain

1.The sympathetic chain is a derivative of the spinal ganglia and therefore an ectodermic structure.It forms the basis for the development of the sympathetic ganglia which lie in front of the aorta.
2.No evidence is forthcoming in fish,frogs,birds,or mammals which would support the view that the nerve plexuses and ganglia of the viscera are derived from either the sympathetic chain or the preaortic ganglia.
3.In the chick the band of nerve tissue which appears on the dorsal wall of the rectum and extends some distance up the gut is apparently quite unconnected with the preaortic ganglia.It is first recognised when ~~when~~ those ganglia are just beginning to develope.Further the structure of* this band which is generally known as the Intestinal nerve of Remak is different from that of the sympathetic ganglia, these points all indicate that it is an independently developed structure.
4.There is evidently a sharp contrast between the development of the sympathetic chain and its offshoots the preaortic plexus and the visceral plexuses the former being ectodermic the latter mesodermic.
It is but fair to Onodi to note that although he draws up those conclusions he admits the possibility of the nerves in the viscera being outgrowths from the sympathetic chain.

His sen.(9) refers to work done by Romberg and His jr.(25) on the development of the nerve plexuses in the heart and lungs.From their work it is seen that the nerve cells in those organs are derived from the sympathetic chain by the process of migration.

Paterson(22) who regards the whole sympathetic system as a mesoblastic structure describes the peripheral portion as developing in cellular buds or outgrowths from the sympathetic chain.In the mouse and rat these outgrowths appear about the eleventh or twelfth days of development.In the human embryo they are recognised about the end of the first month.These outgrowths accompany the splanchnic branches which do not join the sympathetic chain and form masses of cells along the main vessels.In older embryos some of those cells are seen to form the medullary parts of the suprarenals.

His jr.(10.11) describes the development of the cardiac nerve supply in vertebrates.In fish he finds the first evidences of the cardiac nerve plexuses at 12 mm. in trout,at 13 mm. in scyllium,and at 18 mm. in torpedo.AT these stages the heart consists of three chambers sinus auricle and ventricle.It is important to note that although the nerve supply developes after the heart has attained its adult form the

organ has been pulsating long before this stage is reached.
In fish the first nerve elements to reach the heart are the nerve cells, nerve fibres do not appear until later.
The nerve which governs the heart in fish is the vagus. This nerve has two ganglia on its course one inside the cranium and another just outside. The ganglion inside the cranium is composed wholly of large bipolar cells while the other ganglion contains two varieties of cells. One variety is large and bipolar like the cells of the upper ganglion the other is small and unipolar. These two varieties are separated by a mesoblastic layer the smaller cells forming the mesial portion of the ganglion (fig. 5). These smaller cells are exactly like the sympathetic cells in the sympathetic chain and evidently form a sympathetic segment of the vagus ganglion from which the visceral branches of the vagus develope. A branch from this segment follows the course of the upper cardinal vein to the point where the upper and lower cardinal veins meet where it sends a branch to the outer part of the sinus. The main portion of the branch from the ganglion passes down to the abdominal organs.

Fig. V

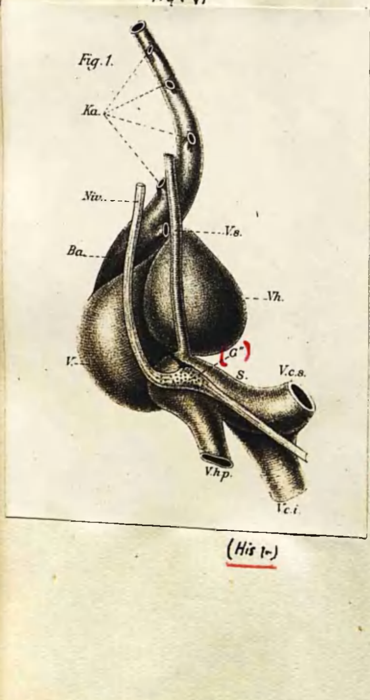
(His)

(Smaller cells) = Sympathetic Cells
Large Cells - Cells of Central Nervous System

In the Torpedo ocellata this visceral branch of the vagus is unaccompanied by cells for a considerable portion of its course, at the level of the sinus however it has a ganglion on its course from which cells pass to the sinus along the nerve supplying this portion of the heart (fig. 6).

In the Trout the sympathetic portion of the vagus ganglion is greatly elongated and accompanies the visceral branch to the point of union of upper and lower cardinal veins, where it sends off cells to the upper portion of the heart. (fig. 7).

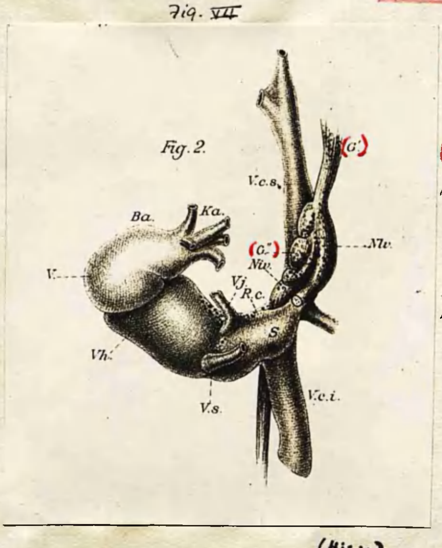
Fig. VI



(His 1-)

V - Ventricle
Vh - Auricle
S - Sinus
Ba - Bulbus arteriosus
Ka - Gill arteries
V.C.S. - Superior vena cava
V.C.I. - Inferior vena cava
V.hp. - Hepatic vein
V.S. - Subclavian vein
V.J. - Jugular vein
(G'') - lower vagal ganglion
Nio - Intestinal branch of vagus

Fig. VII



(His 1-)

(G') upper vagal ganglion
V.C.S. Superior vena cava
Nlv. Lateral vagal nerve
(G'') Lower vagal ganglion
Nio. Intestinal branch of vagus -
R.C. - Ramus cardiacus
S. - Sinus
V.C.I. - Inferior vena cava
V.J. - Jugular vein
V.S. - Subclavian vein
Vh - Auricle
Ka - Gill arteries
V - Ventricle
Ba - Bulbus arteriosus

The later stages of development are worked out in the Scyllium embryo of 25 mm. length. At this stage a branch of nerve fibres among which a few nerve cells are embedded passes from the distal end of the sympathetic portion of the vagus ganglion to the heart (fig. 8).

Fig. VIII

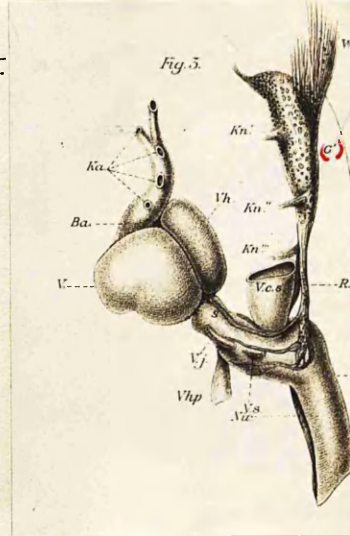
(His)

ganglionic cells.
mesoblast cells
cells of communicating ramus.

In the heart it forms a network in the sinus while branches pass down to the anterior wall of the auricle and terminate in a ganglion lying between the sinus and auricle (fig. 9).

In the larval stage of the frog at 6 to 7 mm. length the vagus is already provided with a very large ganglion which lies just outside the cranium. This ganglion is connected in front with the glossopharyngeal and behind with the sympathetic chain. The intestinal branch is as in fish derived from a portion of the ganglion which contains cells of the sympathetic type. Some of those cells accompany the cardiac branch which is an offshoot of the intestinal. The cardiac branch follows the course of the superior vena cava and forms a rich network between the vein and the sinus by its junction with the cardiac branch of the other side (fig. 10).

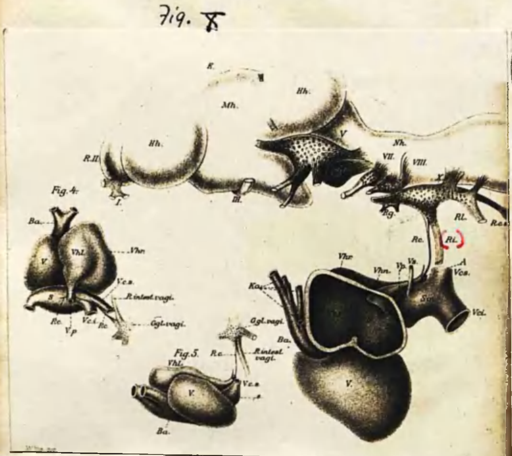
Fig IX



(His)

Rg. – Gill arteries
Ba. – Bulbus arteriosus.
V. Ventricle
S. Sinus
V.g. Jugular vein
V.s. Subclavian vein
V.hp. Hepatic vein
V.v. vagal root
(G) upper vagal ganglion
Kn". "' – Gill branches of vagus
R. Ramus cardiacus
N.i.v. Intestinal branch of vagus.

Fig. X



(His)

Figs. 4 + 5. = Frog Heart Larval length 6 m.m.
Fig. 6 – Frog Heart Larval length 13 mm.
(numbers refer to numbers in the photograph)

R.H. Nasal bulb.
H.h – Hind brain
m.h. mid brain
Hh. Cerebral hemisphere
N.h – Medulla –
I–X – nerve roots
Rg – Ramus glossopharyngeus
R.C. Ramus Cardiacus
R.L. Lateral ramus of vagus
(R.i.) Intestinal branch of vagus
A. Anastomosis of right and left Rami Cardiacus
V. ventricle
Vh. auricle
S – Sinus
B.a. Bulbus arteriosus

It is impossible to decide in the frog whether the nerve cells or nerve fibres are first to reach the heart, but it is probable that the cells precede the fibres.

In larvae of 13 mm. the nerve cells lying in the heart are found to have developed outgrowths (fig. 11).

Fig. XI

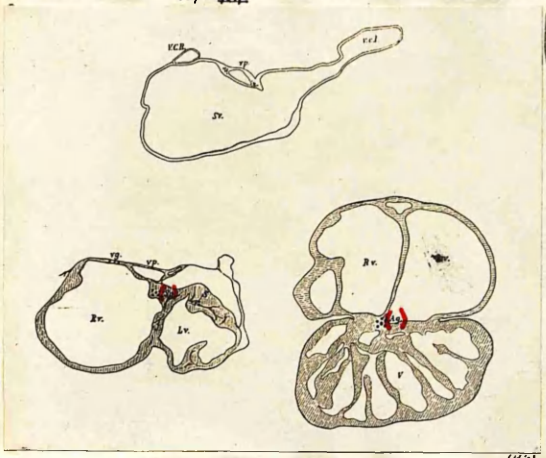
(His)

Two Nerve cells with outgrowths

The ganglia in the upper part of the heart and in the auricular septum are better developed but there are no nerve cells or fibres in the ventricle or atrioventricular area.

At 25 mm. the nerve supply is much more extensive nerve elements being found in the sinus, auricles, auricular septum, and auricular ventricular junction (fig.12). At this stage the sympathetic chain does not participate in the supply of the heart.

Fig. XII



(His)

S.V. = Venous sinus. (AS) = Atrio-ventricular ganglion
VP. = Lung veins. (RG) Remak's Ganglion
RV.-LV. = Right and left auricles. (VG) Auricular ganglion
V = Ventricles.
V.C.R., V.C.L. - Right and left superior vena cavae.
(SG) - Ganglion of septum.

In the chick the beginning of the cardiac nerve supply is found at the sixth day of incubation. At this stage the heart is fully formed and has been pulsating for several days. At this stage the cardiac nerves come wholly from the vagus which like the same nerve in the fish and frog is provided with a sympathetic segment in its ganglion. Abranch from the right vagus passes downwards under cover of the innominate artery and ends in the septum of the truncus arteriosus in a ganglionic node. From the left vagus branches also go to the septum of the **truncas** both from the main trunk and from the recurrent laryngeal (fig.13)

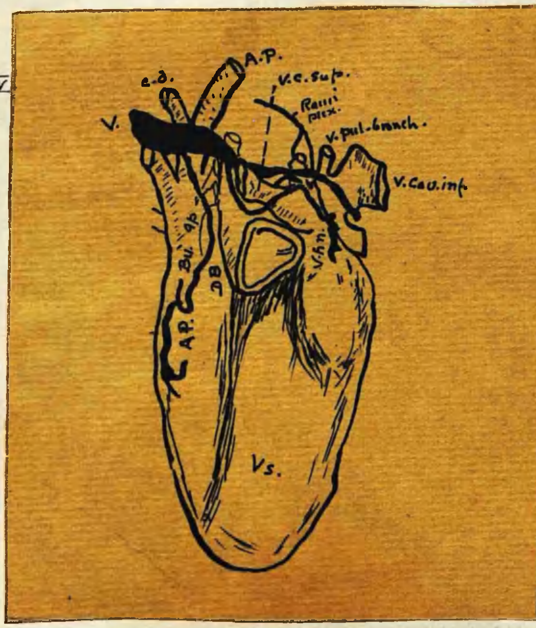
Fig. XIII

(His)

Vag. dext = Right vagus
Vag. sin = left vagus.
Nn. rec. - Recurrent laryngeal branch of right vagus.

At the eighth day there is a plexus in the the auricular wall composed partly of independent vagal branches and partly of twigs from the plexus in the bulbus arteriosus. At this stage the heart also receives a branch from the sympathetic chain which enters the auricle from the bronchial sympathetic plexus. The relationship of the nerves to the heart at this stage is shown in a reconstruction drawing (fig.14).

Fig XIV



(His)

A.P. = Pulmonary A.
c.d. = right carotid
V = vagus.
Bu = bulbar nerves.
D.B = Ductus Botalli
V.C.Sup. - Superior vena cava.
V.cau.inf. = Inferior vena cava
Vhn = auricular plexus
V.S = Left Ventricle

At ten days development the cardiac nerve supply may be classified as follows.

1. The Bulbar network.

This consists of a rich network round the aorta from which branches pass to the atrioventricular groove. From it are given off the two coronary nerves. On close examination this plexus is seen to consist of vagal branches accompanied by sympathetic nerve cells from the superior cervical ganglion, and also from the first thoracic ganglion.

2. The Auricular network.

This network surrounds the openings of the veins into the auricle and is spread over the auricular walls dipping down into the septum It is composed of one or two independent vagal branches a branch from the bulbar plexus and nerve elements from the bronchial plexus. The branch from the bulbar plexus constitutes the nervous connection between the auricle and ventricle.

The superior vena cava is accompanied by a nerve from the first thoracic ganglion. This nerve does not enter the heart but terminates proximally to the sinus.

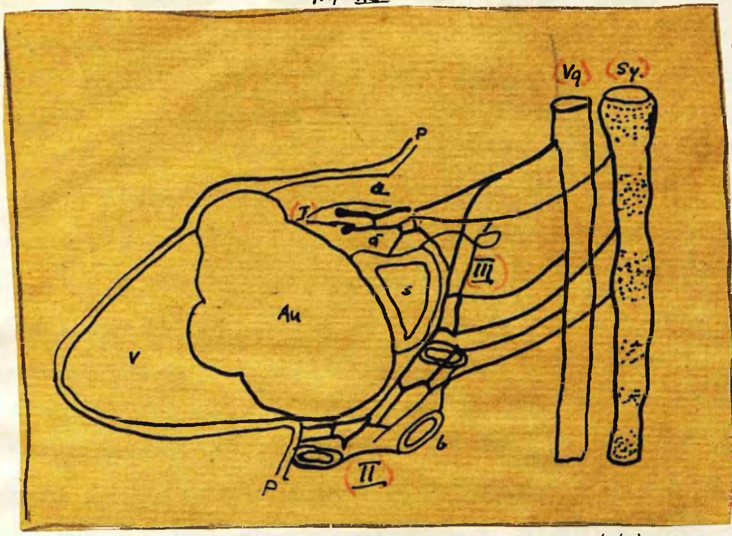
The development of the cardiac nerve supply in the human embryo is found to begin at the end of the fourth or the early part of the fifth week. The nerves come from the vagus and the sympathetic chain and cells and fibres seem to enter the heart simultaneously.

At this stage the heart consists of auricles and ventricles while the various valves and septa are in course of formation.

The right vagus at the level of the recurrent gives off a cardiac branch which is accompanied by a branch from the sympathetic chain. This branch is connected by two roots with the superior cervical ganglion which in turn is closely associated with the vagus These fibres pass down and end in the septum of the truncus arteriosus in a small ganglion. On the left side one branch goes to the heart from the trunk of the vagus and another from the recurrent laryngeal. The branch from the vagal trunk is accompanied by a sympathetic branch and they all terminate in the way described for the nerves of the right side.

From this bulbar plexus nerves pass to the venous part of the heart Independent fibres also pass to the auricles from both the sympathetic chain and the vagus (fig. 15). Examination of the vagal branches to the the heart shows that they are accompanied by sympathetic cells ~~(fig.)~~.

Fig. XII



a = Aorta
a' = Pulmonary
b = Auricle with venous openings
Au = Auricular appendage
V = Ventricle
(Vq) = vagus
(Sy) = Sympathetic
p-p = Pericardium
s = Sinus Transversus pericardii
(I) = Bulbar network or plexus
(II) = Auricular network or plexus
(III) = Connecting network or plexus.

(His)

AT seven weeks development the cardiac nerve supply consists of on the right side a branch from the superior cervical ganglion which anastomoses with the cardiac branches of the vagus and accompanies them to the origin of the Truncus anonymous(innominate artery) where they anastomose with branches from the left side, from this they pass to the bulbus.

The middle cervical ganglion does not take part in the cardiac nerve supply, but the inferior ganglion sends two strong branches which accompany the vagal fibres to the bulbus. The first thoracic ganglion also sends a branch to join this vago sympathetic cardiac supply.

At the level of the fifth thoracic vertebra the vagus gives off a strong branch which goes directly to the auricular plexus. This nerve is found to contain many sympathetic cells among its fibres.

The left vagus shows practically the same arrangement but there is in addition a branch from the recurrent laryngeal nerve.

From this network formed round the aorta and pulmonary nerves pass on to the coronary groove in the ventricle.

The auricular network is composed of branches from the vagus and the sympathetic which reach it in the manner already described

The heart is at this stage distinguished from the condition found in the adult by the absence of the coronary nerves and the incompleteness of the auricular plexus.

As a result of these investigations His draws up certain conclusions and tabulates his observations as follows.

(1). The cardiac ganglia in vertebrates is formed by the migration of cells from the sympathetic ganglia.

(2) These cells follow the route taken by the veins in fish and frogs while in birds and mammals they follow the course of the arteries.

(3).The ganglion of the vagus and possibly of the glossopharyngeal contribute sympathetic cells for the supply of the heart.

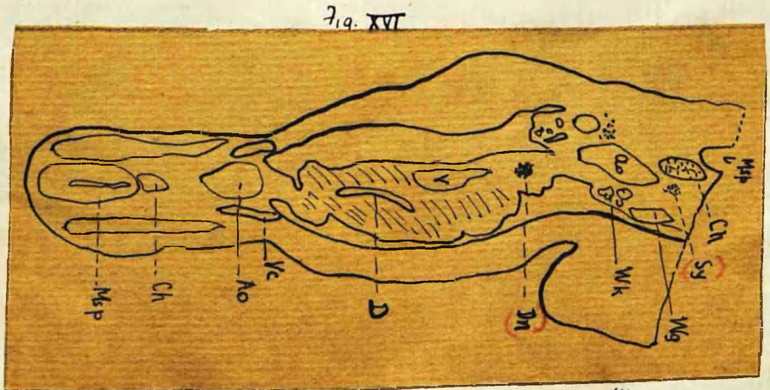
(4).In the higher vertebrates the sympathetic portions of the vagus and glossopharyngeal ganglia do not persist as independent structures but it is probable that the sympathetic cells from those ganglia pass over to the first cervical ganglion.This is what happens in the chick.When the primary sympathetic is fully formed in the chick there is a double sympathetic supply in the neck.This is derived from the vagus ganglion and the first cervical ganglion of the spinal cord. When the secondary chain appears a large sympathetic ganglion is found closely associated with the vagus and occupying the position of the first cervical sympathetic ganglion in the mammal.This ganglion is formed from the cells which formed the double sympathetic supply in the neck earlier in development.Besides this ganglion there is a second first cervical sympathetic ganglion which is formed in connection with the first cervical spinal root.There is therefore a permanent double sympathetic supply in the neck of the chick.

5.The ganglia and plexuses found in the heart are formed by the migration of sympathetic ganglia from the sympathetic segments of certain cranial nerves as well as from the cells of the ganglia of the sympathetic chain.There is no evidence to show that any part of the cardiac nerve supply is formed in situ.

Some four years later His Jr.(11) published a second paper dealing with the development of the abdominal sympathetic.In this as in his earlier work he uses the Haematoxylin Eosin stain and recognises the nerve cells by their deeper colouration as well as by their shape and size.

In the chick at the end of the third day of incubation the intestinal nerve of Remak appears.At this stage it is represented by a cluster of cells sympathetic in type lying in the mesentery in the lower part of the gut.At this stage no cells can be seen connecting the sympathetic chain with this group of nerve cells but it is possible that such a connection does exist(fig.16).

Fig. XVI



M.sp = Spinal cord.
Ch = Notochord.
Ao = Aorta
Vc = Cardinal vein
D = Intestine
(Dn) = Intestinal Nerve of Remak
Wk = Urinary tubule
Wg = Wolffian tubule
(Sy) = Sympathetic chain
Ao = Aorta
Msp = Spinal cord.

(His)

At the end of the fourth day a swarm of cells passes from the sympathetic chain a little above the level of the heart migrating to the ventral surface of the aorta where they form a loose plexus in the connective tissue. This plexus extends down to the root of the lung. In the region of the stomach and from below the level of the omphalomesenteric artery there are comparatively large clusters of cells lying in front of the aorta which have migrated from the sympathetic chain. The development of the sympathetic system is shown in a diagram made from a reconstruction of a chick at this age (fig. 17)

Fig. XVII

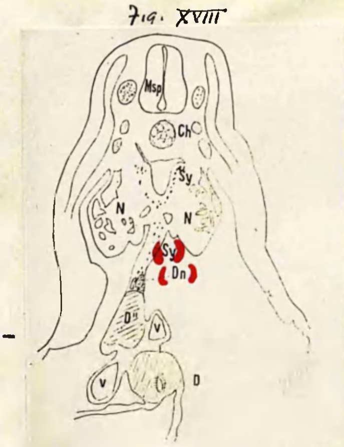
(His)

R.M = Spinal cord, Ch = Notochord.
1) Primary cervical & thoracic sympathetic chain, P = larynx.
T = Trachea, L = Lung,
M = stomach, PG. LG. Pancreas and liver diverticulae (4) Abdl. plexus
(6) = Remak's nerve, (5) Pelvic plexus
(2) Pelvic part of chain.

At the fifth day nerve cells are seen for the first time joining the sympathetic chain to the Intestinal nerve of Remak (fig. 18)

In the stomach wall nerve cells appear. They are derived from a cluster of sympathetic cells lying at the root of the omphalomesenteric artery. They enter the stomach along with the vagal branches and are dispersed at different levels in the wall of the stomach (fig. 19). In the intestine there are as yet no nervous structures with the exception of the Intestinal nerve of Remak, already referred to. In the thoracic region the outgrowth of cells towards the root of the lung is better marked (fig. 20).

Fig. XVIII



Msp. Spinal cord - (His)
(Sy) = Sympathetic cells -
(Dn) = Intestinal nerve of Remak
D = Intestine
N = kidneys -

Fig. XIX

(His)

Pyloric end of stomach showing sympathetic nerve cells

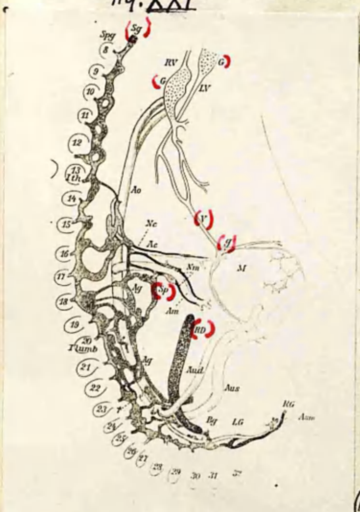
Fig. XX

Msp: Spinal cord
(X') Vagus root
(X) upper vagal ganglion
V = Vein
(Sy) Sympathetic chain (cranial portion)
C = Carotid
M = Mouth
Ch = Notochord

(His)

At the sixth day the secondary or permanent sympathetic chain appears The primary chain has vanished almost wholly from the upper portion of the trunk but is fairly well represented in the abdominal region while in the pelvic region it is complete.No secondary sympathetic chain is formed in the pelvic area.The preaortic plexus referred to at earlier stages of development has completely disappeared in the cervical portion it is probable that this plexus has all been utilised in forming the cardiac and pulmonary plexuses.In the abdominal region on the other hand the preaortic plexus is very extensive and in connection with it the splanchnics now begin to develope From the preaortic abdominal plexus go three nerves one to the stomach liver and duodenum while the other two accompany the omphalomesenteric artery and supply the three loops of small intestine which are developed.In the intestinal wall nerve cells now appear but they decrease in number the further the portion of gut is from the stomach.In the large intetine there are no nerve cells with the exception of those forming the Intestinal nerve of Remak and a few in the rectal portion which have migrated from the pelvic segment of the sympathetic chain. The general arrangement of the sympathetic system at this time is best seen in a reconstruction diagram this has been prepared(fig.21)

Fig. XXI



(His)

R.V. L.V. Right & Left vagi. N.c. Coeliacus nerve
(G.G) = Lower or cervical vagal ganglia
(V) = Gastric branch fr. both vagi
(g) = Ganglion of lesser curvature of stomach
(R.D) - Remak's nerve (S.S) Secondary Sympathetic chain, (Sp) Splanchnic plexus

At the tenth day the whole of the general plan of the sympathetic system is laid down.The primary chain has vanished wholly in the cervical region with the exception of the superior sympathetic cervical ganglion whose mode of origin has already been discussed.In the abdominal area the only trace of the primary chain is a longitudinal strand running between the seventeenth and nineteenth segments. The preaortic plexus described as being so well marked at six days is drawn in at the upper portion to the coeliac plexus.From the nineteenth segment downwards it forms a band containing many ganglionic cells which however decrease in number from above downwards The splanchnic plexus or the early stage of the splanchnic nerves is now clearly differentiated into nerve fibre and ganglia. The mesenteric plexus is formed about this stage.It consists of a long band of ganglionic cells which branch off from the preaortic plexus about the level of the sixteenth segment.From this ganglion nerves pass for the supply of portions of both the large and small intestine. Another plexus lies near the level of the sixteenth intervertebral ganglion in front of the aorta and to the right of the origin of the coeliac axis. This plexus receives branches from the right vagus and the uppermost part of the aortic plexus. From this plexus nerve fibres unaccompanied by ganglion cells pass to the liver, stomach, pancreas, and small intestine. The two vagi anastomose above the level of the stomach and enter the stomach by several branches between which are numerous ganglionic cells. The vagal fibres are accompanied in their course through the gut wall by many ganglionic cells. The Intestinal nerve of Remak now forms a compact band of nerve cells in the descending colon, in the transverse colon it is thin and somewhat broken; at higher levels in the gut it is still more broken and slender in structure but it may be traced up to the junction of the second and third loops of the small intestine. It is possible that at its upper limit an anastomosis takes place between the Intestinal nerve and the mesenteric nerves. (fig. 22) At this age also the two layers of nervous tissue develope in the gut wall. The outer which is wide meshed lies under the peritoneal covering while the inner plexus which is closer in arrangement lies between the circular muscle layer and the mucous layer.

The whole process of the development of the peripheral portion of the sympathetic system may be summarised as follows

The sympathetic chain is first developed and from it developes the preaortic plexus which in turn gives rise to splanchnic nerves and the plexuses of the hollow viscera (fig. 23)

The only exceptions are the Intestinal nerve and the secondary sympathetic chain whose mode of origin has already been shown to be peculiar

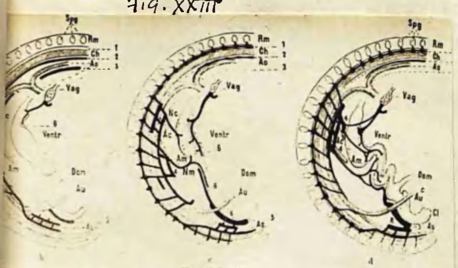
In the adult or fully developed chick the only remnants of the primary sympathetic chain are the superior cervical sympathetic ganglion, a thin chain connecting the roots of the splanchnic nerves, a thin chain from the superior cervical sympathetic ganglion to the heart, and the pelvic portion of the sympathetic chain.

Fig. XXII

(His)

(1) Aortic plexus, (2) Coeliac ganglion, (3) Ganglion with mesenteric nerves, (4) Remak's nerve
R.V. L.V. Right & left vagi. Nr. Right recurrent.
An = anastomosis of both vagi, Vm. gastric branch of vagi. Gm - Ganglion of the vagus in small curvature of stomach.

Fig. XXIII

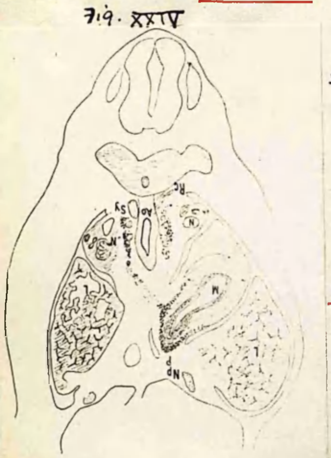


spinal cord, sympathetic chain, and outgrowths chick of 4. 6, and 10 days incubation.
(His)

His also considers the formation of the abdominal sympathetic system in man.

In a human embryo 10·2 mm. long the plan of the sympathetic system as it appears in the adult is already laid down. At this stage the sympathetic chain is unsegmented while on both sides sympathetic cells have migrated round the aorta and form ganglia above and below the omphalo mesenteric artery. From these ganglia nerve fibres pass to the kidneys and gut. A branch also goes from the upper ganglion to the stomach. The two nerve bands which join this upper ganglion with the sympathetic chain are the first stages in the development of the splanchnic nerves. About the level of the umbilical artery large ganglia are formed the sympathetic chain they converge and partly unite in front of the aorta. These ganglia form the basis for the development of the mesenteric pelvic and lower abdominal ganglia and plexuses. The vagal branches as they enter the stomach wall are accompanied by sympathetic cells which are dispersed in the walls of the organ. Sympathetic cells may also be seen at earlier stages of development entering the stomach directly from the sympathetic chain (fig.24) From a reconstruction of an embryo of 10·2 mm. length the relationship of the various portions of the sympathetic system is easily seen (fig.25).

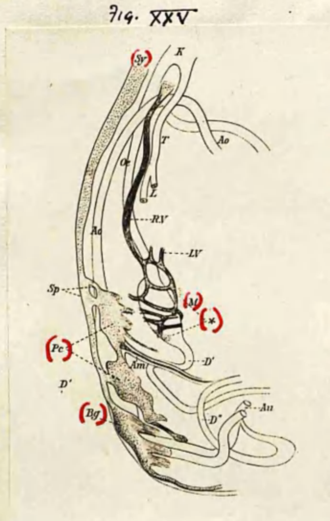
Fig. XXIV



Showing outgrowth of sympathetic cells to the stomach in

(His)

Fig. XXV

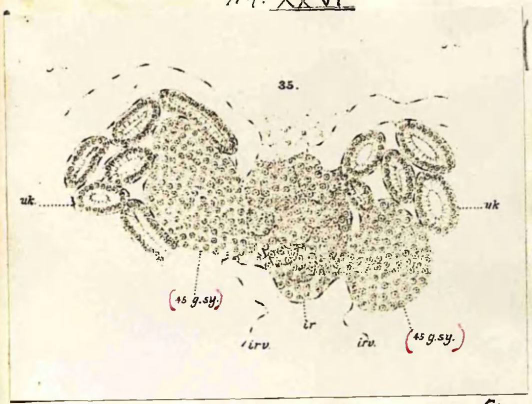


(Sy) = Sympathetic chain
Sp - splanchnic nerves
(Pc) = Coeliac plexus
(Bg) = Pelvic plexus
(*) = Ganglion cells in stomach wall.
K = Larynx
T = Trachea
L = Lung
Oe = Oesophagus
(M) = stomach c̄ vagal fibres
D' " = intestine small & large
Ao = Aorta
Am = Omphalomesenteric A.
Au = Umbilical Artery

(His)

Rabl(23,24) and Hoffmann(12,13) in their investigations on the development of sympathetic system limit their observations to the development of suprarenal. They both describe the formation of a series of paired bodies derived from the sympathetic chain. The close relationship existing between these bodies and an unpaired body derived from the mesoblast is described by Hoffmann in the embryo of Acanthias vulgaris 40 mm. long (fig.26). Later in development the portion developed from the sympathetic chain forms the medullary part of the organ the

Fig. XXVI



(45 g. sy) = origin of the sympathetic ganglion (Hoffmann)
ir = interrenal organ   uk = urinary canal.
irv = interrenal vein   (Hoffmann)

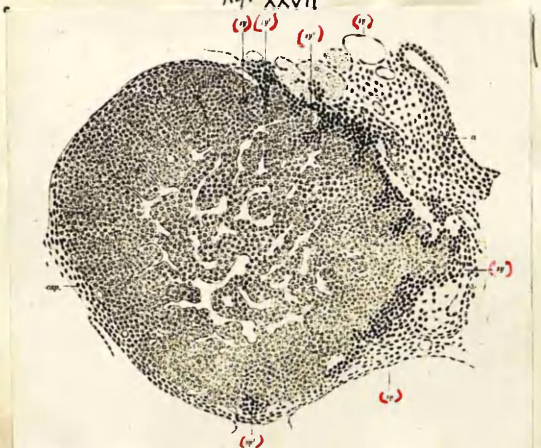
cortical part is formed from the mesoblastic unpaired body.

Kohn(15) describes a well marked migration from the sympathetic chain to the ventral surface of the aorta in a rabbit embryo of thirteen days development. In the region of the suprarenals there are comparatively large masses of cells. Among these are some which are distinguished from the other nerve cells by their granular appearance they are regarded as the forerunners of the chromaffine cells. Kohn suggests that all the nerve cells seen in front of the aorta are not derived from the sympathetic chain but that some are developed directly from the cells accompanying the spinal nerves.

Lillie(20) gives a short resume of the result got by some workers principally His Jr. but adds nothing new .

Bryce(4) also gives a short extract of the more important work. In connection with the development of the suprarenal bodies he gives a drawing showing the relationship of the abdominal sympathetic to the cortical portion of these organs(fig.27).

Fig. XXVII



(sy) - abdominal sympathetic   (Bryce)
(sy' sy') = Groups of cells from the sympathetic stretching from the sympathetic into the suprarenals.
Cap = Capsule of gland -
a - aorta

Cajal(5) describes sympathetic cells lying in front of the aorta in chicks incubated for fifty-two hours. These cells migrate down the mesentery and form the preaortic and intestinal plexuses.

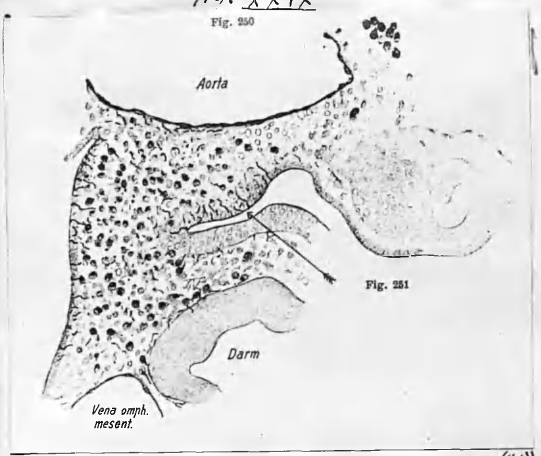
Held(7) demonstrates the ventral migration from the sympathetic chain to form the sympathetic supply in the intestine in reptiles(fig.28) and birds(fig.29).

Fig. XXVIII

(outgrowth of sympathetic cells from the sym-pathetic chain past the aorta between it and the kidney.)

(Held)

Fig. XXIX



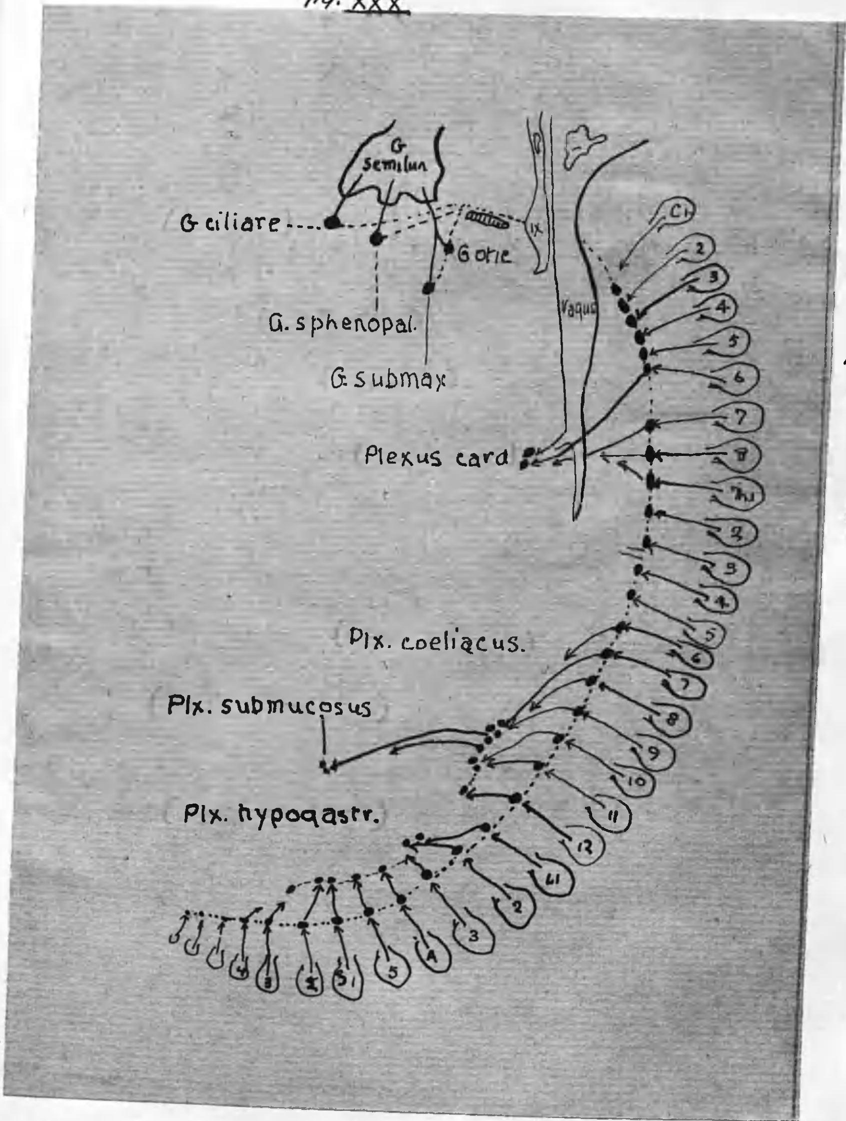
(Held)

(Sympathetic cells migrating from the sympathetic chain towards the intestine (Darm) and omphalomesenteric vein. Sixty hours incubation)

Kuntz(17-19) discusses the role played by the vagi in the development of the peripheral nervous system.
In the pig embryo of 6 to 7 mm. transverse sections show the vagal trunks in the region of the oesophagus accompanied by numerous ganglionic cells. These cells leave the vagal trunks and migrate into the tissues. They wander into the oesophageal wall and form the basis of the oesophageal plexus which is recognised at 12 mm. The intestine also receives cells from the same source. They precede the vagal fibres and lay the foundation of both submucous and myenteric plexuses. These plexuses are not connected with the sympathetic chain until later in development. The pulmonary plexus is also begun by these vagal cells which branch off to the lungs at the bifurcation of the trachea. The cardiac plexus which is first recognised at 12 mm. body length is at this stage wholly formed by the vagal cells. Cells from the sympathetic chain take part in the formation of the plexus only when the embryo is some 16 mm. in length. In the stomach and intestine the bases of the plexuses are also connected with the sympathetic chain at this time.
These ganglionic cells which accompany the vagal fibres are sympathetic in character and come from the hind brain. In embryos of 10 mm. they may be seen migrating along the roots of the vagus and spinal accessory. In form they vary the majority have large round or elongated nuclei with delicate chromatin structure and very little cytoplasm and correspond to the indifferent cells of Schaper(27). The others have large nuclei with distinct nucleolei while the cytoplasm is abundant and is drawn out to a point. These correspond to the neuroblasts of Schaper(27). The hind brain must therefore be looked on as a source of supply for the cells forming the early stages of the peripheral plexuses.
In a second paper on the development of the sympathetic system in mammals Kuntz(18) describes the formation of the prevertebral plexuses These plexuses are formed by the migration of cells from the sympathetic chain and appear in the pig embryo of 10 mm. length, the connection between them and the plexuses in the hollow viscera is established later. The greater portion of the plexuses in all the viscera is supplied by the cells which accompany the vagal fibres from the

hind brain,the sympathetic chain contributes only a small proportion In the chick~~##~~ practically the same conditions are found.The plexuses in the heart and lungs are laid down by the sympathetic cells accompanying the vagus.The cells for the pulmonary plexus branch off from the vagal trunks in the same way as is described in mammals. The cardiac plexus is begun by cells from the pulmonary plexus which enter the heart by the atrial septum.In the gut the vagal sympathetic cells form the basis of the greater portion of the intestinal plexuses but it is probable that cells from the sympathetic chain participate in the formation of the plexuses at a comparatively early date.
The Intestinal nerve of Remak is recognised about the fourth day and is found to be connected with the sympathetic chain
Kuntz(19) also investigates the development of the sympathetic chain in turtle.The same developmental relationship is shown to exist between visceral plexuses and the sympathetic cells accompanying the vagus. The connection between the sympathetic chain and those viscera is formed after the plexuses are well established.
Keibel and Mall(14) give an account of the development of the peripheral portions of the sympathetic system in the human embryo.
In the cranial region the sympathetic system is represented by the four ganglia the ciliary,otic,sphenopalatine,and submaxillary.These ganglia are derived from the semilunar ganglion mass,the cells migrating early in the course of development.
The cardiac ganglia are recognised in embryos 16 mm. long while the main features of the plexus are laid down at 19 mm. neck-rump length. The coeliac and hypogastric plexuses together with the splanchnic nerves are all recognisable in an embryo of 16 mm..Continuous with the coeliac plexus is a group of cells which extends into the substance of the cortical portion of the suprarenal gland and constitutes its nerve supply.A number of the sympathetic cells in this region undergo special modifications in development and because of their affinity for the chrome salts are known as chromaffine cells.These chromaffine cells are of special importance in the structure of the suprarenals as they form the medullary portion of these organs.The immigration of those cells into the cortical or mesoblastic portion of the suprarenals begins about the time when the embryo is 19 mm. long.
The general plan of the sympathetic system as seen in the human embryo is represented in a diagram here reproduced(fig.30).

Fig. XXX



(Keibel and Mall)

Diagram showing the migration paths of the sympathetic cells.

Dotted lines indicate secondary subsequent communications which link the ganglia together and form a longitudinal chain continuous throughout head and trunk. Secondary and tertiary migrations result in the formation of prevertebral and visceral plexuses.

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Chapter 6.

The mode of development of the peripheral portions of the Sympathetic System as shown in the present investigation.

The Development of the Peripheral Portions of the Sympathetic System.

1.The Development of the Sympathetic Supply accompanying the Vagus. In chicks of over four days incubation the vagus is a very prominent structure and is found entering into relationship with the various organs which it supplies either wholly or partly in the adult. During the process of development the vagal fibres are found to be accompanied by nerve cells which come from vagal ganglia.

The developmental course of these cells is found to be as follows. The examination of the root of the vagus at four days or ninety-six hours development shows that the ganglion of the root is composed of two types of cells a large and small.The large cells which are by far the more numerous,are bipolar and closely resemble in size and general appearance the cells of the spinal ganglia.The small cells are mostly circular in shape with prominent nuclei,but a few of them have a unipolar outgrowth.In appearance and size they correspond with the cells of the sympathetic chain,while the same ratio is seen between the numbers of the cells with and without outgrowths as has already been described in the early developmental stage of the chain. I therefore regard them as a sympathetic section of the vagal ganglion which is developed from an outgrowth of sympathetic cells from the hind brain.Some of the sympathetic cells can be traced directly from the cortex to the sympathetic portion of the ganglion,but a number are found migrating from the other portion of the vagal ganglion while some seem to migrate from the adjacent ganglion of the glosso-pharyngeal.The cells from the vagal and glossopharyngeal ganglia do not in all cases join the sympathetic group in the vagal root ganglion but pass downwards to the ganglion of the trunk,where they are joined by the sympathetic cells migrating from the root ganglion and together they form a segment of this ganglion also.From this point they pass downwards along with the vagal fibres to the different organs. Although the sympathetic portion of the vagal ganglia is situated in the immediate vicinity of the superior cervical sympathetic ganglion I am not aware of any intercommunication between the ganglia, at least in the earlier stages of development.

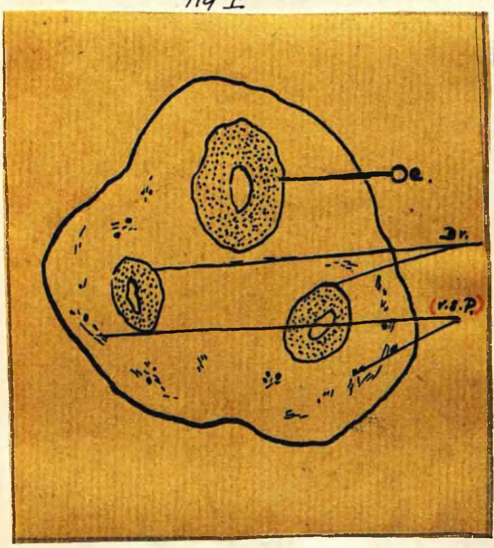
2. The Development of the Pulmonary Plexuses.

In an embryo of a hundred and thirty hours incubation delicate branches pass from the vagi towards the bronchi. These fibres are accompanied by the sympathetic nerve cells which form the special sympathetic supply for the vagus and whose development has already been described. These nerve cells and fibres form the basis of the bronchial plexuses.

At a hundred and forty hours a delicate plexiform arrangement is found round each bronchus(fig.1)This plexus is formed solely from the vagus and its accompanying sympathetic cells.

At a hundred and forty-four hours the plexus is better marked the vagal fibres being especially more numerous (fig.2).

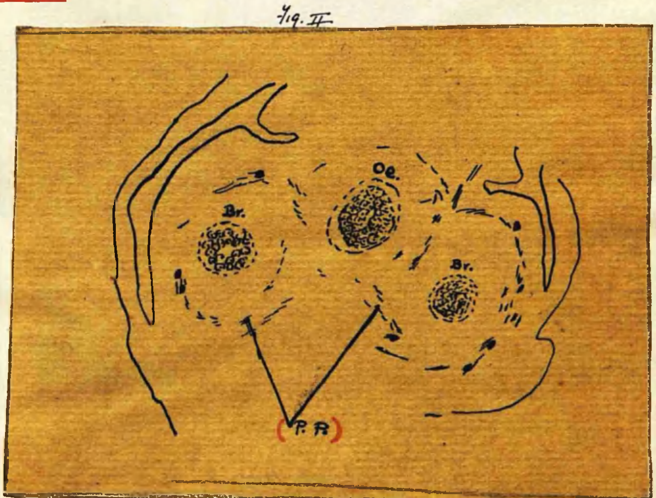
Fig I



(Abel)

Oe – Oesophagus
Br – Bronchi
(V.S.P.) – Vagal sympathetic plexus

Fig. II



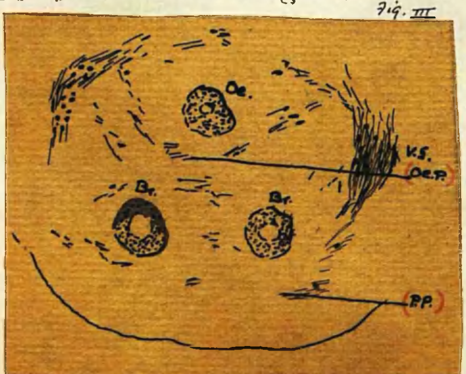
(Abel)

Oe – Oesophagus
Br – Bronchi
(P.P.) – Pulmonary plexus.

At a hundred and sixty-eight hours the bronchi are surrounded by a very well developed plexus(fig.3).The comparatively rapid development of the plexus on the seventh day is seen by comparing figures and .

It is evident therefore that a rich pulmonary plexus exists before any outgrowths from the sympathetic chain take part in the nerve supply of this region.

Fig. III



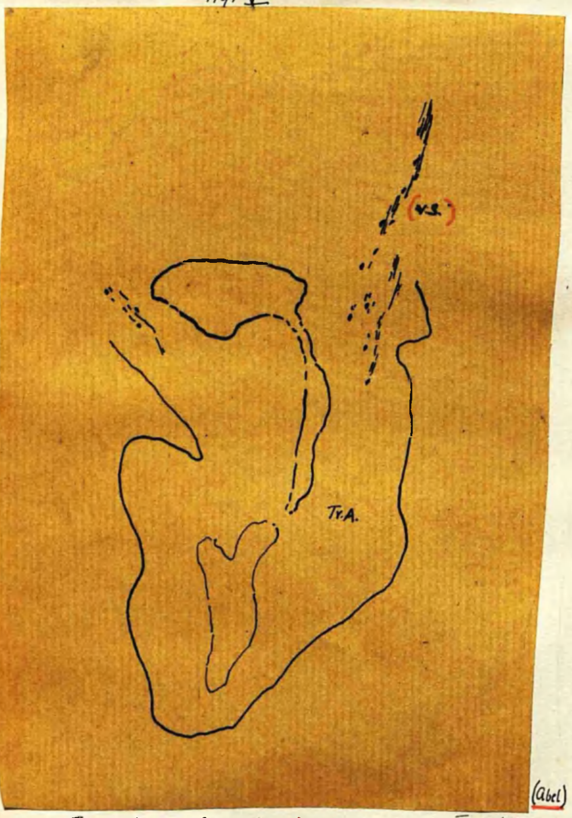
Oe – Oesophagus
(Oe. P.) – Oesophageal plexus
Br. – Bronchi
(P.P.) – Pulmonary Plexus
V.G. – Vagal ganglion

(Abel)

3. The Development of the Cardiac Nerve Supply.

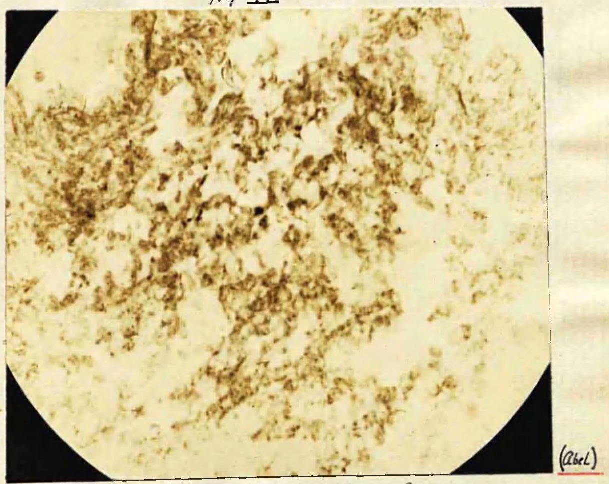
At a hundred and eight to a hundred and twelve hours incubation nerve cells and fibres are found accompanying the arterial arches to the truncus arteriosus. The nerve fibres are branches from the vagi while the nerve cells are part of the sympathetic supply which accompanies the vagi and their various branches. The vagal trunks are found at this stage studded over with cells which lie between and on the nerve fibres, and where branches are given off the nerve cells not only accompany the nerve branches but in many cases seem to precede them. This is seen in the case of the cardiac branches where the nerve cells are recognised in the truncus arteriosus at a lower level than the vagal fibres (figs. 4.5).

Fig. V



Tr.A. Truncus Arteriosus: (V.S.) Vagal sympathetic fibres & cells.

Fig IV



(Sympathetic nerve cells) in Truncus Arteriosus
sympathetic cells are stained a darker tint than the mesoblastic cells.

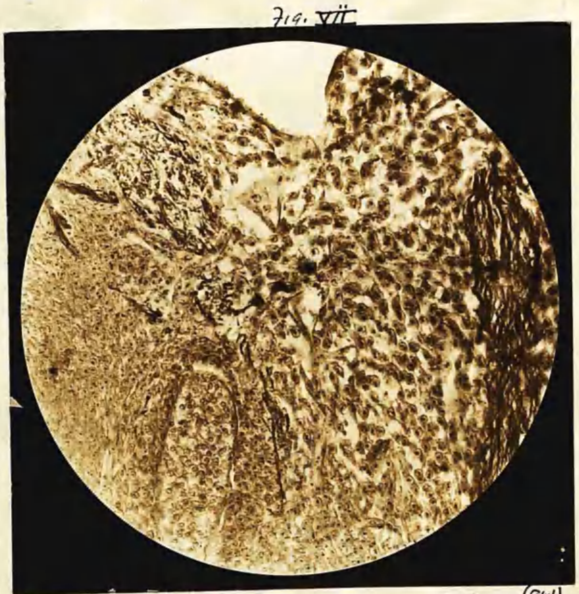
At a hundred and twenty to a hundred and forty hours incubation the migration of sympathetic cells to the truncus arteriosus is greater while the vagal fibres may be traced right down to the septum of the truncus (arteriosus). In the dorsal mesocardium nerve cells and fibres also appear. They are somewhat scanty and sparse in their distribution but they are found to be outgrowths from the peribronchial or pulmonary plexuses already described (fig. 6). As these plexuses are formed by the vagus and its sympathetic supply the mesocardial plexus must also be regarded as an offshoot of this system.

At a hundred and forty-four hours the carotid aortic and pulmonic arches are seen to be accompanied by a rich plexiform network of nerve cells and fibres(fig.7)

Fig. VI

Oe. Oesophagus
Br. Bronchi
D.Mes. Dorsal Mesocardium
(V.S.C.) Vagal fibres with sympathetic cells.
L.Mes. Lateral mesocardium
S.V. Sinus Venosus
A - Auricle

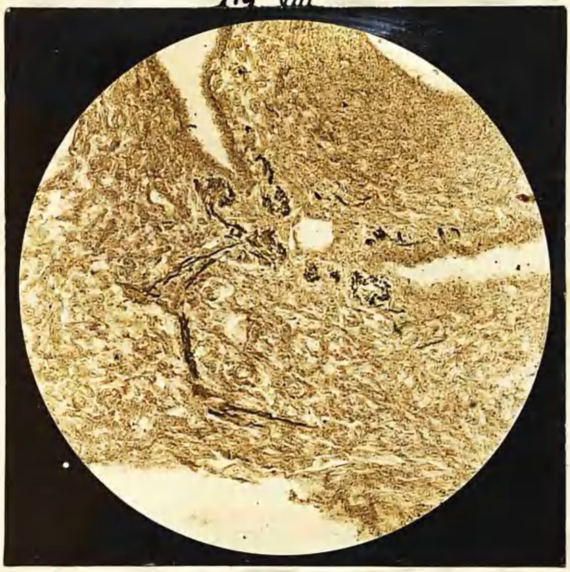
Fig. VII



(Nerve cells & fibres) following the course of the pulmonic artery to the Truncus Arteriosus

The nerve fibres are derived from the two vagal nerves, while a branch also comes from the recurrent laryngeal of the left side. In their arrangement along the arterial arches the nerves are subject to a good deal of variation but as a general rule the branch accompanying the carotid arch passes from its outer to its mesial side. The pulmonic arch is also encircled by a nerve trunk which is provided on the left side with a small ganglion. The aortic arch has as a general rule to have nerves passing down both sides. At this age the septum of the truncus arteriosus extends into the proximal part of the bulbus and in this septum a delicate plexiform network is formed. This plexus is directly connected with the nerve supply accompanying the arterial arches ~~(fig.8)~~.
In the dorsal mesocardium the nerve cells and fibres already referred to now form a definite plexus round the openings of the veins into the auricle, but it is uncertain whether any nerve elements actually enter the auricular wall(fig.8). The increase of nerve elements both here and in the bulbar part of the heart since the previous stage described is very striking.

Fig VIII



(abel)

(Nerve cells and fibres) in dorsal mesocardium

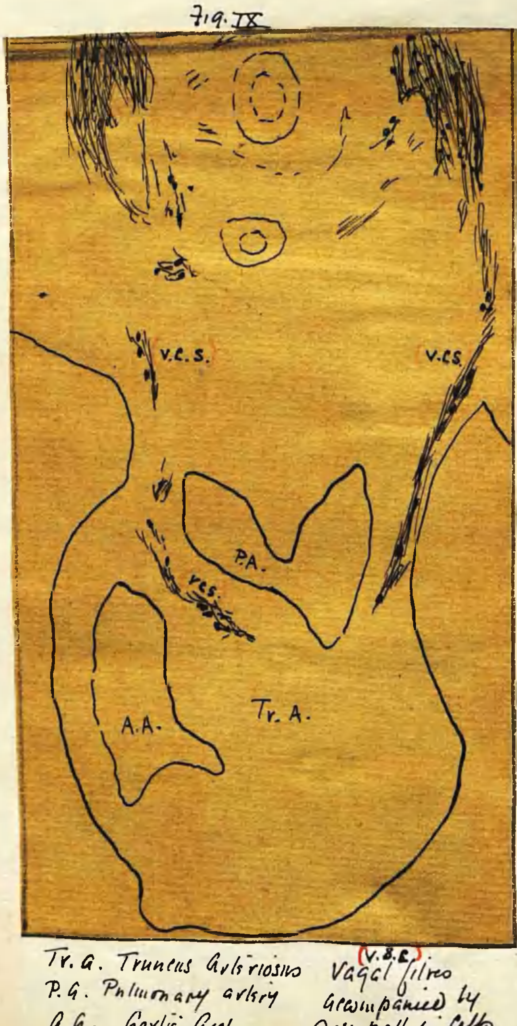
At a hundred and sixty-eight hours it is seen that development is proceeding along the lines already described.

The plexus in the septum trunci et bulbi is much better developed, while indications exist of a plexus at the junction of the arteries with the ventricular wall (fig. 9). This is evidently the beginning of the "Bulbusnerven" of His (fig. 10).

Careful examination of the ventricular wall and the auricular ventricular groove shows no nervous tissue, but in the visceral layer of the pericardium opposite the posterior inteventricular groove are well marked nerve fibres. These fibres may be traced upwards to the plexus lying round the venous openings in the auricular wall.

This plexus in the auricular wall is the later development of the plexus recognised at an earlier stage in the dorsal mesocardium.

Fig. IX

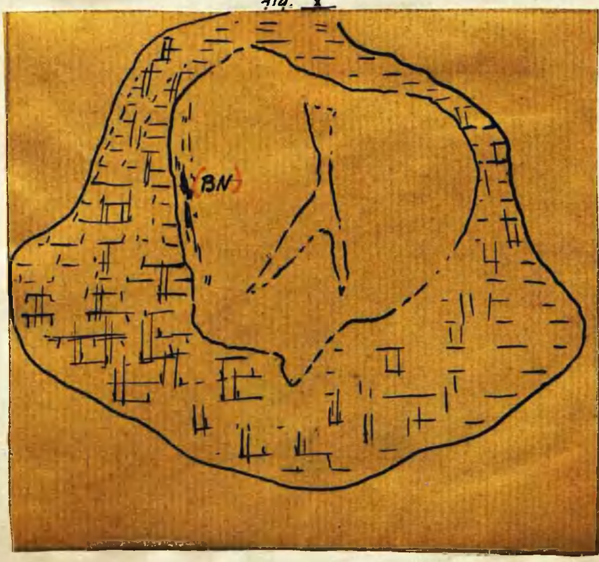


(abel)

Tr. A. Truncus Arteriosus
P.A. Pulmonary artery
A.A. Aortic Arch

(V.S.E.) Vagal fibres accompanied by Sympathetic Cells

Fig. X

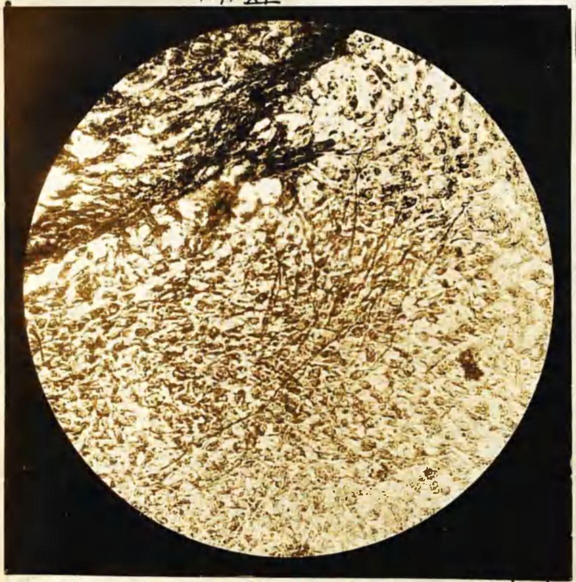


(B.N.) Nerve cells and fibres at junction of Aorta with Ventricle

(abel)

At a hundred and ninety-two hours incubation the cardiac nerve mechanism shows increase both in the number and distribution of the constituents. The plexus indicated at a hundred and sixty-eight hours is now represented by a rich network of nerve cells and fibres (fig. 11). From this plexus nerve cells and fibres pass upwards towards the auricular ventricular groove but no plexus appears as yet in this area. In the auricles the nervous plexus is better developed and now a delicate network of nervous tissue is found over the greater part of the auricular wall. The posterior inter-ventricular branch described at the seventh day does not seem to have altered appreciably from that stage (fig. 12).

Fig. XI



(Nerve cells and fibres) in aortic area of Ventricle (abl)

At two hundred and sixteen hours the connections between the heart and the vagus with its accompanying sympathetic supply may be followed out with no difficulty. The nerve plexus at the junction of the arteries with the ventricle is extremely rich. At the auricular ventricular junction nerve cells and fibres are recognised. A strong band of nerve fibres lies in the visceral layer of the pericardium at the level of the auricular ventricular groove. This nerve is directly connected with the branch which passes down the posterior interventricular groove, and like it is derived from the auricular plexus. The nerve in the posterior interventricular groove sends offshoots to the ventricular wall in the upper third. In the auricular wall the plexus is very well marked and extends downwards to the auricular ventricular groove where it meets the branches from the aortic plexus. The nerve supply of the heart is

Fig. XII

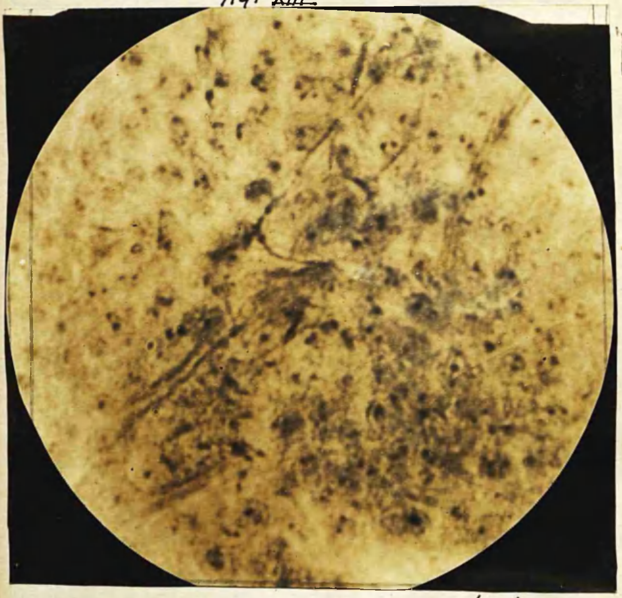
V. Ventricle
(N.) Nerve fibres.

(abl)

therefore well developed at this age.The auricular ventricular groove is however poorly supplied with nerves compared with the auricles and the arterial area of the ventricle.

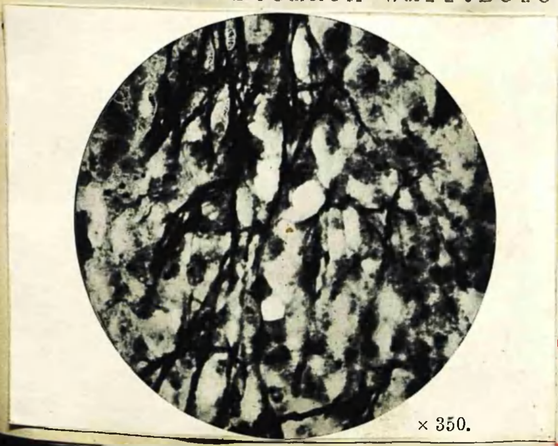
4.The Development of the Sympathetic nerve supply for the alimentary canal. During the fourth day the migration of cells from the abdominal portion of the sympathetic chain is seen.
At a hundred and eight to a hundred and twelve hours incubation vagal fibres accompanied by sympathetic nerve cells are found entering the stomach wall in which a delicate plexiform network is seen (fig.13).This plexus is formed solely by the sympathetic cells which

Fig. XIII



(Plexus in stomach wall) (Abel)

accompany the vagus,no cells from the sympathetic chain can as yet be traced to the gut wall at this level.In the lower part of the gut no nerve cells are recognised except the cells of the Intestinal nerve of Remak.This nerve is represented by a band of nerve tissue lying along the posterior margin of the gut.A very delicate band of nerve cells connects it with the sympathetic chain.
In embryos of a hundred and twenty to a hundred and forty-two hours development the number of vagal fibres and sympathetic cells has increased considerably.A very close relationship is seen in many parts of the stomach wall between the sympathetic cells and the vagal fibres(fig.14).At this age it is comparatively easy to distinguish the sympathetic cells along the course of the vagus but no evidence is got of the migration of sympathetic nerve cells from chain to the stomach wall.Below the stomach nerve cells are found in



× 350.

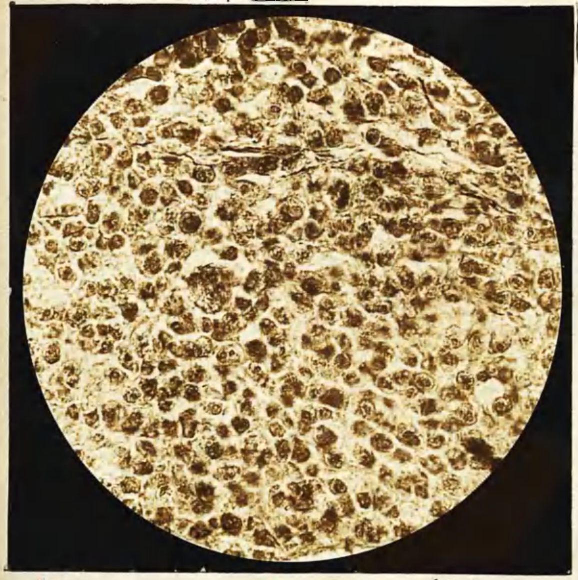
Fig XIV

(Vagal fibres intimately mixed with sympathetic cells.)

(Abel)

fair numbers in the intestinal wall where a delicate plexus is seen (fig.15).In the mesentery delicate chains of nerve cells are found extending from the sympathetic chain to the gut wall.They do not appear to penetrate into the gut wall at least

Fig. XV



(Plexus in gut wall) (abd)

to any depth but form small clusters at the junction of gut and mesentery. The Intestinal nerve of Remak is a prominent structure in the lower gut. It is longer and its connections with the sympathetic chain more easily seen. In the hind gut also nerve cells are found which come from the pelvic plexus along the mesorectum, these form the basis of an intestinal plexus independent of the Intestinal nerve of Remak. At a hundred and forty-four hours incubation the upper portion of the fore gut or the oesophagus is provided with a plexiform arrangement of nerve cells and fibres. These cells and fibres may be traced from the vagus for as in the stomach wall the basis of the oesophageal plexus is formed from the vagus and its accompanying sympathetic supply. In the upper gut that is in the stomach and first part of the small intestine vagal fibres are found widely scattered while the plexus in the walls is extremely well developed (fig.16). In the mesentery there well marked bands of nerve cells which pass ventrally from a plexiform arrangement of sympathetic cells lying in front of the aorta. (fig.17).

Fig. XVI

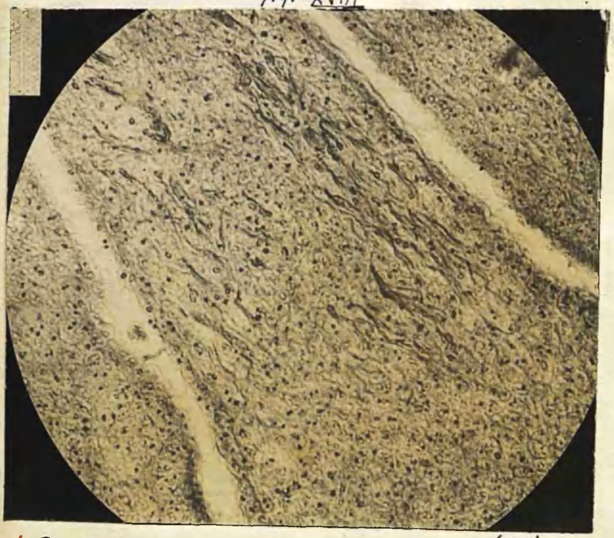
(Plexus in gut wall) (abd)

Fig. XVII

(Sympathetic nerve cells and fibres in front of the aorta.) (abd)

In the mesentery the outgrowth of nerve cells is exceedingly well seen at certain points(fig.18),and at the junction with the gut these cells pass into the wall and form a plexiform network.In the gut wall

Fig. XVIII

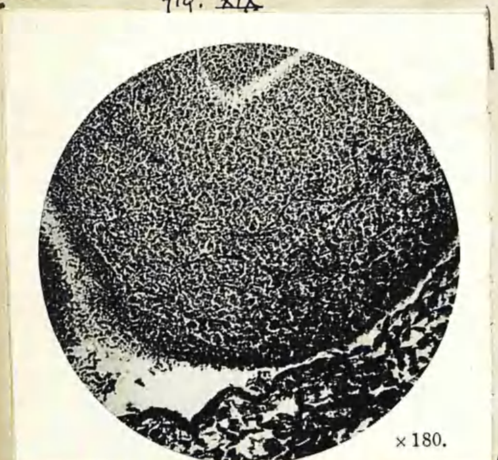


(Sympathetic nerve cells in Mesentery) (abel)

at this period of development a differentiation of the plexiform nerve network into a peripheral and deep portion has begun(fig.19).In the lower portions of the hind gut this plexus is poorly developed the Intestinal nerve of Remak and its connections with the sympathetic chain forming the outstanding nervous structures in this region.

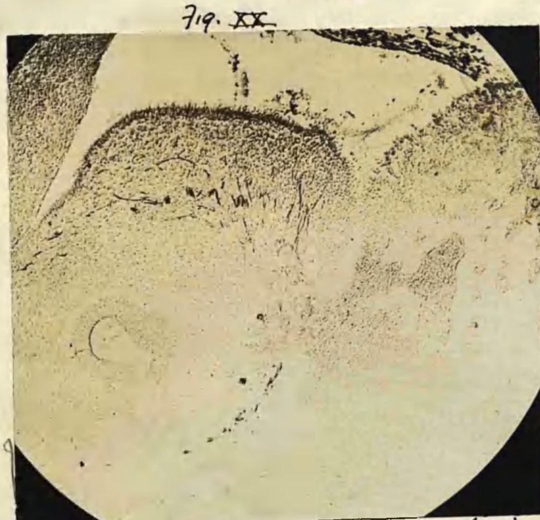
At a hundred and sixty-eight hours the oesophageal plexus is now represented by a complete ring of nerve plexus.In the stomach and upper parts of the small intestine the nerve plexus is extremely rich,while its arrangement in two zones is better marked.The distribution of the vagal fibres in this portion of the gut is very extensive(fig.20).

Fig. XIX



(Plexus in gut wall differentiated into a peripheral and deep zone.) (abel)

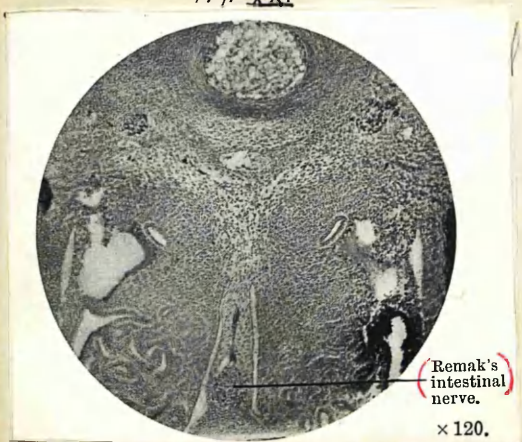
Fig. XX



(Vagal fibres in stomach wall) (abel)

In the mesentery the chains of sympathetic cells are replaced by bands of nerve fibre in many places but clusters of nerve cells are still found along the course of the mesentery.The Intestinal nerve of Remak is now connected to the sympathetic chain by well marked nerve fibres(fig.21),which may be traced from the lowest part of the sympathetic chain to the nerve.

Fig. XXI



(Part of the fibrous connection between the (abel) sympathetic chain and Remak's intestinal nerve is seen.)

At theend of the eighth day therefore the plexuses in the alimentary canal are laid down, while the connections between them and the sympathetic chain are well developed.

5. The Development of the Nerve Supply of the Liver.

The liver at a hundred and forty-four hours incubation is a well developed organ, but its nerve supply is just beginning to develope. from the plexus in the duodenal wall nerve cells and fibres pass along the bile ducts into the liver where they form a delicate plexus at their point of entrance (fig. 22) The exact origin of those cells is a little doubtful

Fig. XXII

L - Liver - S. Gut - B.D. Bile duct - (abel)
(S.C.) Sympathetic cells and nerve fibres

for at this stage cells enter the gut from the sympathetic chain as well as those which accompany the vagus. It is possible that both sources contribute towards the hepatic supply but it seems highly probable that the majority at least of the cells come from the vagal sympathetic supply. Round the venous channel in the liver just before it emerges as the meatus venosus a few very delicate nerve fibrils are seen. These are apparently derived from the dorsal mesocardium, the origin of whose nerve supply at this stage has already been discussed. At a hundred and sixty-eight hours incubation the nerve supply to the liver may be traced some little distance into the the liver substance (fig. 23). A fine plexus is seen round the gall bladder.

Fig. XXIII

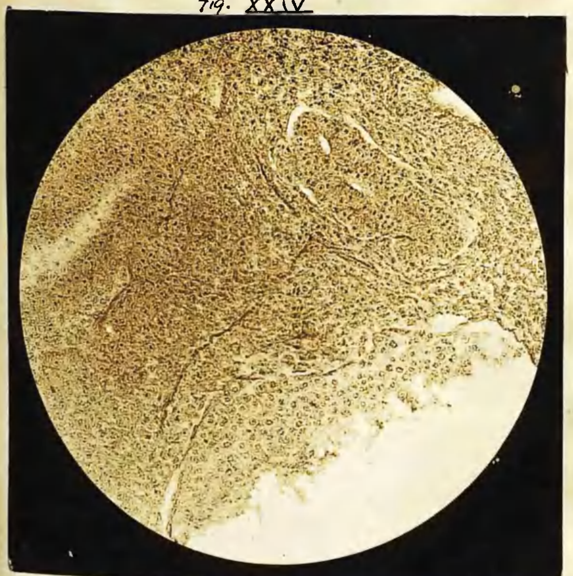
(Nerve Cells and fibres passing along Bile Duct to Liver) (Abel)

Observations made up to two hundred and sixteen hours of incubation show that nerve fibres ramify to some considerable extent amongst the trabeculae,but the density of the tissue makes the task of following out the nerve distribution in the liver extremely difficult.

6. The Development of the Nerve Supply of the Pancreas.

At a hundred and forty-four hours incubation the pancreas is well developed both as regards its dorsal and ventral diverticula.From the duodenum numerous nerve cells and fibres pass towards the diverticula round which they form a rich network,branches of which penetrate between the columns of glandular cells.As the pancreas is developed in connection with the fore gut which receives its nerve supply largely if not wholly from the vagus and the sympathetic cells which accompany the vagus it is probable that the majority at least of the nerve elements to the pancreas are derived from the same source (fig.24).At a hundred and sixty-eight hours incubation the pancreatic plexus is better marked.The ramifications of the fine nerve fibrils between the cells of the glandular clusters are especially noticeable.

Fig. XXIV

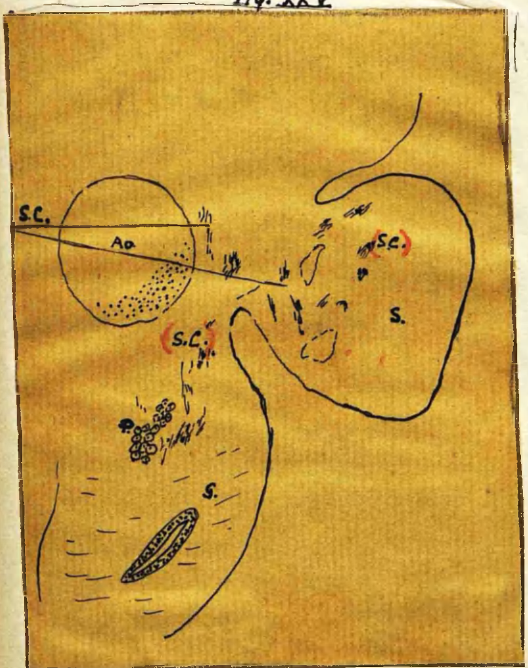


(Nerve cells and fibres passing to Pancreas.) (Abel)

7. The Development of the Nerve Supply of the Spleen.

At a hundred and forty-four hours incubation the spleen is readily recognised and is quite a well developed structure,but repeated examinations fail to demonstrate any nerve tissue in its structure. At a hundred and sixty-eight hours incubation both nerve cells and fibres may be recognised in the organ.These nerve elements enter the spleen as outgrowths from the sympathetic chain. A chain of nerve cells and fibres is seen extending between the nerve supply for the spleen and the loop of gut immediately adjacent, thus giving the impression that the splenic supply is an offshoot from the sympathetic supply for the gut. In the spleen there is a delicate plexiform arrangement of the sympathetic cells and outgrowths (fig. 25).

Fig. XXV



S. spleen. P. Pancreas. G. Gut. (Abel)
Ao - Aorta (S.C.) Sympathetic nerve cells.

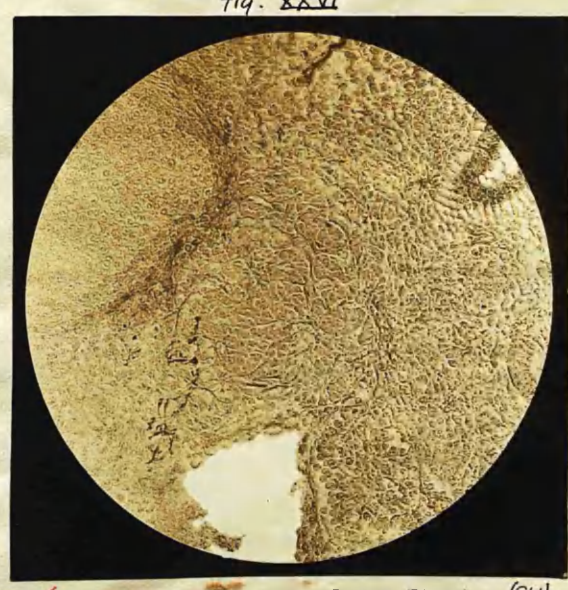
At a hundred and ninety-two and two hundred and sixteen hours incubation there is comparative little change seen in the arrangement and distribution of the nerve supply of this organ.

8. The Development of the Nerve Supply of the Suprarenals.

At a hundred and sixty-eight hours incubation groups of circularly arranged cells, the basis of the cortical portion of the suprarenals is recognised. A ~~distin~~ distinct group of sympathetic nerve cells andfibres is seen in close relationship to the cortical portion, while at one point delicate outgrowths from this group pass in between the groups of cells (fig. 26).

At a hundred and ninety-two hours the sympathetic elements are more numerous and are in still closer relationship with the cortical cellular mass (fig. 27).

Fig. XXVI



(Nerve cells from the Sympathetic chain passing to the cortical portion of the supra renal.) (Abel)

Fig. XXVII

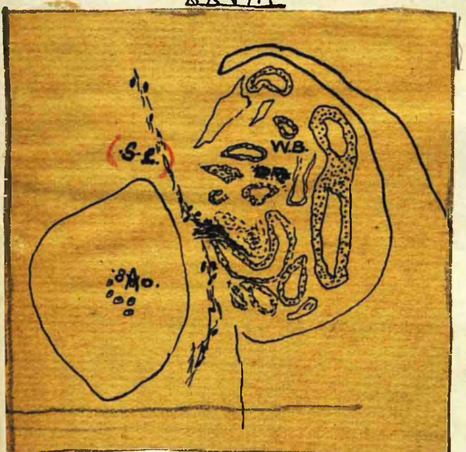
S.R. Supra renal tissue
(S.C.) Sympathetic cells.

(Abel)

9. The Development of the Nerve Supply of the Wolffian Body.

At a hundred and forty-four hours incubation the Wolffian Body is a very prominent structure in the chick. Along its mesial surface at various levels sweep strong well marked bands of nerve cells and fibres passing from the sympathetic chain to the mesentery. Small ganglia are dotted along the mesial aspect of the Wolffian body but only at one point are nerve elements directly traceable into the organ(fig.28).

XXVIII



Ao - Aorta. (S.C.) Sympathetic Cells (abl)
W.B. Wolffian Body

At a hundred and sixty-eight hours several offshoots pass into the Wolffian body from the sympathetic chain. These nerves lie mostly on the postero mesial aspect of the organ and do not ramify to any extent among the ~~tubul~~ tubules.

Up to the two hundred~~th~~ and sixteenth hour of incubation comparatively little change is seen in the distribution of the nerve elements in this organ.

10. The Development of the Nerve Supply of the Gonad.

At a hundred and forty-four hours incubation the gonad is well developed. At the angle between the germinal ridge and the body wall is a small ganglion composed of sympathetic cells and directly connected with the sympathetic chain, from this ganglion delicate outgrowths pass towards but do not actually enter the gonad(fig.29)

At a hundred and sixty-eight hours sympathetic nerve elements enter the gonad and form a delicate plexiform network a little posterior to the germinal ridge(fig.30).

Fig. XXIX

W.B. Wolffian Body
(Sym.C.) Sympathetic Cells -
Ao. Aorta
G - Gonad -
Mss - Mesentery -

(abl)

Fig. XXX

(Nerve fibres passing down to (abl) gonad.)
(The course of the nerve fibres is made more plain by outlining with ink.)

From the results just described it is evident that two sources are recognised for the sympathetic supply of the viscera, the sympathetic chain and the sympathetic supply accompanying the vagus. In some cases the basis of the nervous supply is laid down wholly from the vagal sympathetic supply, in othercases the sympathetic chain supplies all the nerve elements ,while in a few cases both the sympathetic chain and the vagal sympathetic supply participate in the formation of the nerve supply at the earliest stages.

Chapter 7.

A discussion of the results of this investigation on the mode of development of the peripheral portions of the sympathetic system contrasted with the results described by other workers.

circular cells from the hind brain into the vagal root.These cells form a segment of the upper ganglion which is distinguished from the rest of the ganglion chiefly by the small size of the cells. From the ganglion cells pass down the fibres of the vagusand are joined by similar cells from the glossopharyngeal ganglion and from the distal part of the vagus ganglion.In the second vagal ganglion they form a well marked group,while below this level they accompany the various branches of the vagus to the visceral organs.In some cases they actually precede the vagal fibres in their entrance into the organs.It appears to me that the peripheral migration of the sympathetic cells from the vagal ganglia is so extensive that the number of sympathetic cells remaining in the ganglia must necessarily be small,and further I fail to get evidence for the separation off of a large sympathetic ganglion such as His describes as originating from the vagal ganglia.The two sympathetic ganglia which lie at the uppermost part of the secondary chain seem to be derived from the primary and secondary chains respectively as described in the third and fourth chapters.

Passing to the consideration of the development of the pulmonary plexuses I agree with Kuntz in describing them as formed from the sympathetic cells which accompany the vagus,and not from cells which have migrated from the sympathetic chain.

For the cardiac supply His describes the development of a vagal supply to the heart which follows the course of the arteries to the Truncus Arteriosus.These fibres which reach the heart at the sixth day are accompanied by nerve cells which apparently come from the sympathetic part of the vagal ganglion.At this stage no nerve cells pass to the heart from the sympathetic chain.Kuntz also describes the cardiac nerve supply about the same stage of development and gives an account of the outgrowth of vagal fibres accompanied by sympathetic nerve cells which enter the heart at the atrial septum.From my own results it is evident that I agree with the description of His so far as the outgrowth of vagal fibres and nerve cells to the heart is concerned but I have been able to recognise cells of a sympathetic character in the Truncus Arteriosus as early as the hundred and twelfth hour of incubation.Further I find no evidence to support the view taken by Kuntz that the nerves enter the heart first through the atrial septum.At the end of the seventh day I find the auricular plexus which is formed by the outgrowth of cells from the peri-bronchial or pulmonary plexuses along the dorsal mesocardium.This practically is in agreement with the description given by His at the eighth day .As regards the later development up to the end of the ninth day of incubation my results are practically in agreement with those of His.As we differ however in the matter of the development of the peribronchial or pulmonary plexuses,His regarding them as developing from the sympathetic chain,it is obvious that he dates the participation of the sympathetic chain in the cardiac nerve supply considerably earlier than I do.

For the nerve supply of the intestine or the alimentary tract my description agrees to a certain extent with the results of both workers. At a hundred and eight to a hundred and twelve hours incubation I find that the vagal fibres reach the stomach and the sympathetic cells which accompany them form a delicate plexus.I agree with Kuntz that this plexus is formed from the vagal sympathetic supply and I find no evidence for the ventral migration of cells from the primary chain to the stomach such as His describes at the end of the fourth day.In the lower parts of the gut there is however abundant evidence of cellular migration from the sympathetic chain which takes part in the formation of the plexuses in the gut wall.Kuntz although he admits that cells may come from the sympathetic chain to the gut yet apparently regards it as more probable that the intestinal plexuses are laid down by the vagal sympathetic cells.The formation of intestinal nerve of Remak is also a matter for discussion.His recognises it at the end of the third day but is unable to establish a connection between it and the sympathetic chain until the fifth day.He admits however that such a connection is in all probability present at an earlier stage.Kuntz on the other hand recognises the intestinal nerve and its connection with the sympathetic chain at the fourth day.From my own investigations I fail to demonstrate a definite connection between the two structures until a little later,from the appearance of the intestinal nerve at this stage it appears highly probable that an earlier connection exists between it and the sympathetic chain but repeated attempts fail to demonstrate it.Even at this stage the cellular chain is very slight and it is possible that the earlier connection if such exist is extremely fragile and disconnected.

In connection with this question of the development of the nerve supply to the gut it is interesting to note that while I recognise the ventral migration of sympathetic cells to the tissue in front of the abdominal aorta at the fourth day Cajal(1)and Held (2)both describe sympathetic cells lying in front of the aorta as early as fifty-second and sixtieth hours of incubation.Although I recognise a migration of the sympathetic cells to the ventral surface of the aorta at the fourth day,I can however get no evidence of such a migration at an earlier period.

As regards the development of the nerve supply in the other abdominal organs there is not so far as I am aware any detailed account but from the general consideration of the work of His it appears probable that he regards their nerve supply as the result of a cellular migration from the sympathetic chain.From my investigations on this subject I find evidence to show that the nerve supply for both the pancreas and liver is derived at first from the migration of cells in the gut.These cells are in turn derived from the vagal sympathetic supply,and probably also from the sympathetic chain.For the Wolffian body,suprarenals,gonads,and spleen direct evidence is got of the migration of cells from the sympathetic chain which form the basis of their nerve supply.

Conclusions.

As a result of the present investigation the following conclusions are drawn up:

(1). The vagus nerve is provided with a special sympathetic supply which accompanies the branches of this nerve in their distribution in the different visceral organs.

(2). The pulmonary plexus is laid down from the sympathetic cells which accompany the vagal fibres and not from acellular migration from the sympathetic chain.

(3). In the heart the vagus and its accompanying sympathetic cells form the entire basis of the cardiac nerve supply, the connection with the sympathetic chain being secondary.

(4). The alimentary tract obtains its nerve supply partly from the sympathetic supply of the vagus and partly from the sympathetic chain.

(5). In the liver and pancreas the nerve supply is at first derived from cells which migrate from the gut. ~~which~~ It is possible that some of them are derived from the sympathetic chain but the majority come the vagal sympathetic supply .

(6). In the spleen, Wolffian body, suprarenals, and gonads the nerve elements are derived directly from the sympathetic chain.

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Chapter 8.

The minute Anatomy of the Sympathetic cells and ganglia in various Vertebrates.

Wagner(40) is ~~one~~ one of the earliest investigators on the histology of the sympathetic system. He points out that the sympathetic cells are smaller than those of the central nervous system, while their outgrowths are slighter and only provided with a myelin sheath for a part of their course. In both varieties of cells outgrowths from the opposite poles serve to link the cells together.

Bidder(10) who describes the sympathetic system in the frog disagrees with Wagner as to the distribution of the outgrowths from the sympathetic cells and describes them as passing in the same direction.

Volkmann(38) also agrees with Bidder and states that it is extremely rare to find a cell with outgrowths passing from its opposite poles in the sympathetic system.

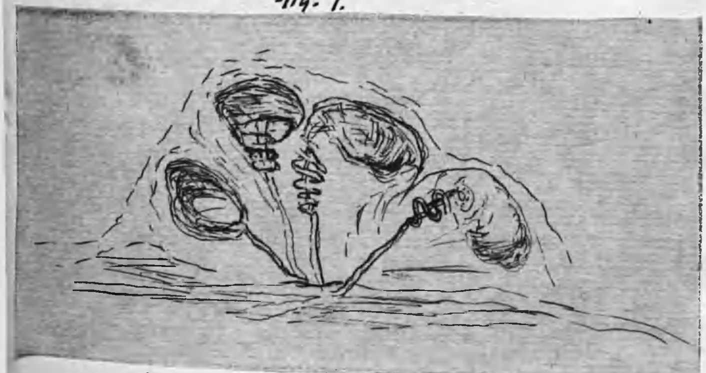
In an ~~later~~ article on the nerve cells in the frogs heart Wagner(41) describes unipolar sympathetic cells, and therefore agrees with Ludwig(30) who described them some three years earlier

Lieberkuhn(29) recognises two varieties of sympathetic cells, a unipolar and a bipolar, thus reconciling the results of the earlier workers.

For some years the histology of the sympathetic system was a matter of controversy but it is not until the work of Arnold(3-5) and Beale(9) appears that any new information is brought to bear on the subject.

Arnold(3) first of all describes cells which he finds in connection with the nerve supply of the lungs and points out that those cells have a straight and spiral outgrowth (fig. 1). These cells he at first regards as peculiar to the nerves of the lungs but in later works(4.5) he describes similar cells in the heart and sympathetic chain. He is also able to trace the straight fibre through the protoplasm of the cell to the nucleolus. The spiral fibre he finds originates in a network which lies on the surface of the cell and which is connected by branches with the nucleolus (fig. 2).

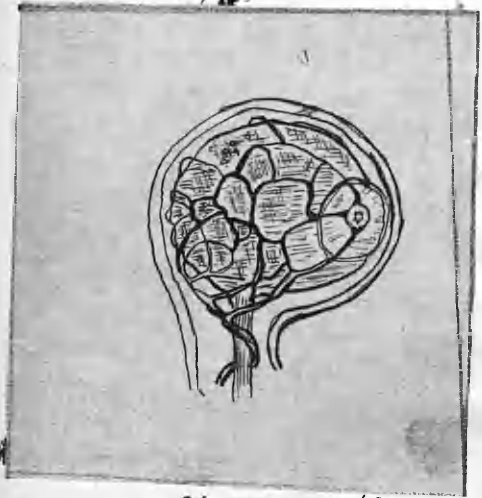
Fig. 1.



Note straight and spiral fibres. (Arnold)

Beale(9) whose paper appears at the same time as Arnolds first paper also describes pear-shaped cells which have two outgrowths a straight and a spiral. The straight fibre, he finds, is continuous with the central part or body of the cell, while the spiral fibre is continu- with the circumference of the cell and is coiled round the straight fibre (fig. 3). Further he finds that in very young ganglion cells the spiral fibre is represented by an almost straight fibre, the

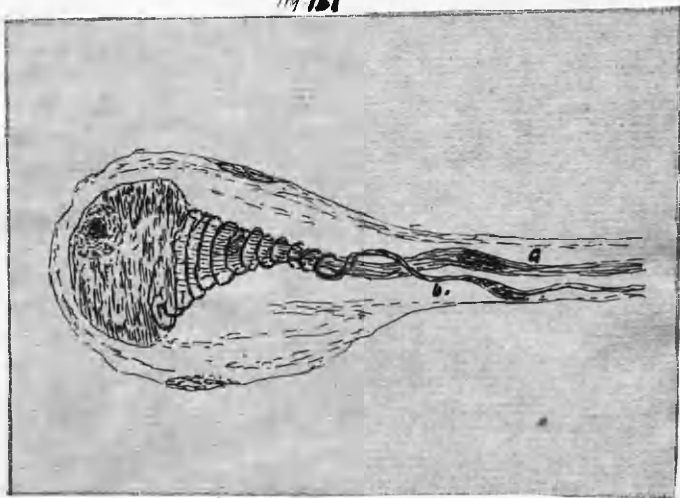
Fig. II



(Arnold)

spiral formation developing as the age of the cell increases(fig.4).

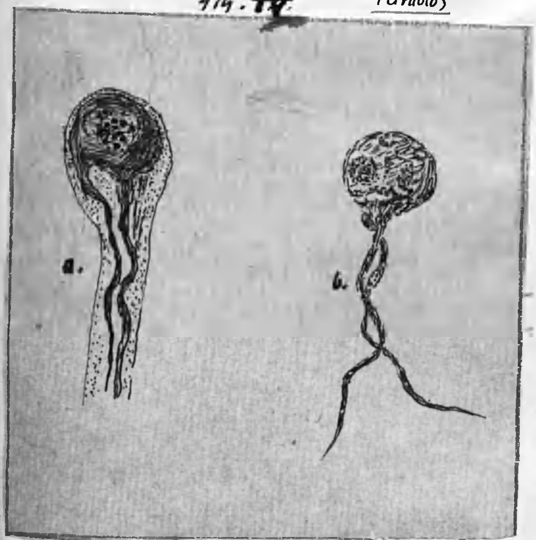
Fig. III



(Beale)

a - straight fibril
b - spiral fibril.

Fig. IV

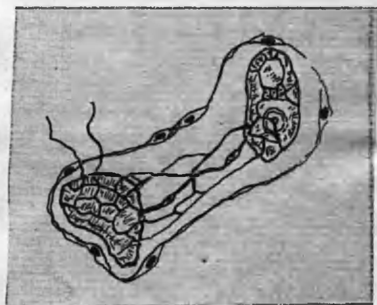


(Beale)

a - Cell early in development.
b. Cell later in development showing spiral fibril

— Courvoisier(13.14) describes the sympathetic cells in much the same way as Arnold. The straight fibre of a ganglion cell is seen to pass into the body of the cell and to terminate in the nucleus. The spiral fibre is connected by a network with the nucleolus. From this network fibres also pass off to unite with the cellular network in other cells(fig.5)

Fig. V



(Courvoisier)

It is important to note that Courvoisier describes the straight fibres as terminating in the nucleus of the sympathetic cell. These straight fibres he regards as cerebrospinal fibres which originate in cells in the brain or spinal cord, the spiral fibres are recognised as the true sympathetic fibres. The suggestion is made that the cells of the sympathetic chain are either nutrition centres for the fibres of the central nervous system or they may serve as inhibitory centres and modify impulses passing from the central nervous system. In a second paper on the spinal ganglionic and sympathetic cells in the frog Courvoisier(14) tabulates the points of contrast between those cells as follows. The sympathetic cells have two outgrowths while the spinal cells have but one, this is probably the most striking distinction. The pericellular intrinsic network already described in the sympathetic cells is wanting in the spinal cells, while the shape of the cells is different the sympathetic cells being balloon-shaped, the spinal cells pear-shaped. If the outgrowths of the cells be examined it is found that these belonging to the spinal cells are myelinated while the sympathetic outgrowths are non-myelinated.

About this time several articles appear by workers who criticise the work of Beale, Arnold, Courvoisier and others on the minute structure of the sympathetic cells. Reference is here made to two of the more important of those articles.

Krause(26) regards the so-called spiral outgrowth of the sympathetic cell as formed either by elastic tissue or a fold in the neuilemma, and not as an outgrowth from the sympathetic cells.

Sander(34) describes the changes which occur in the capsule of the sympathetic cells under the influence of a weak acid such as would be used in fixation, and points out that the puckering which results simulates a network on the cell wall. This is what Beale, Arnold and others mistake for an actual network. He supports his theory by a few very unconvincing diagrams which are subjected to much criticism by later workers.

Kollman and Arnstein(27) who describe the sympathetic cells in the frog substantiate the work of Courvoisier in every detail and need not be quoted more fully here.

Schwalbe(35) describes an extensive investigation made by him on the sympathetic cells in mammals, birds, and frogs. In the mammals he finds that the sympathetic cells are distinguished from the cells of the central nervous system by multipolarity. The suggestion is made that all the outgrowths with the exception of one correspond to the Deiter outgrowths from the cells of the central nervous system. This suggestion is supported by the condition found in the sympathetic cells of the cat where all the outgrowths of a cell contain fine granules with the exception of one branch which is supposed to correspond with the axis cylinder of the cell. In the frog two varieties of sympathetic cells are recognised. In one variety the cells have two outgrowths a straight and spiral. The spiral outgrowth originates in the cell body and makes one or two turns round the straight fibre. In the second variety which is the more numerous the cells are unipolar the spiral fibre being absent.

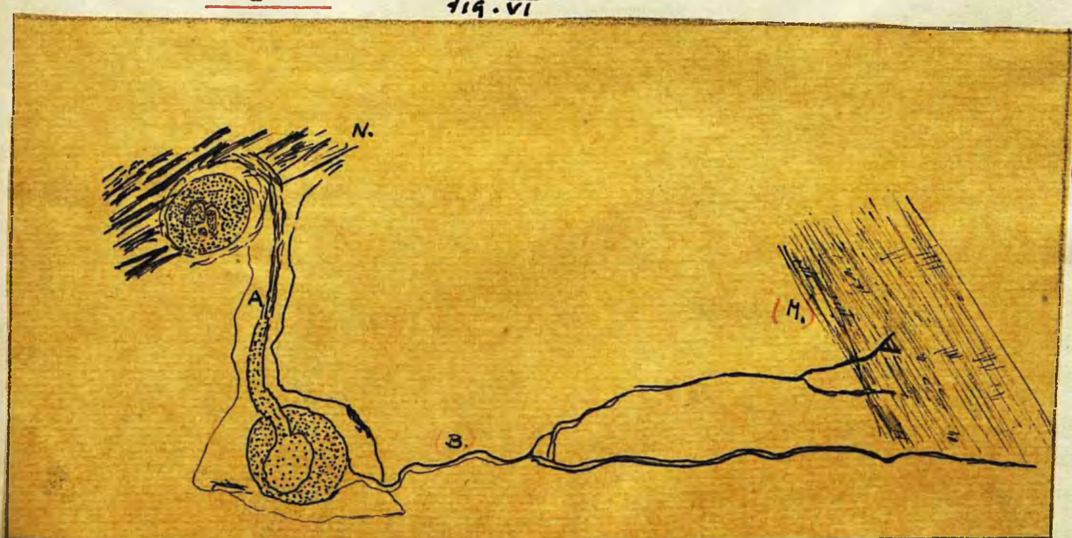
Arndt(2) also investigates the formation of the sympathetic cells in mammals, birds, and fish, and frogs. He finds that bipolar cells are the most usual type in birds, fish, and frogs but it is seen in all classes of vertebrates examined. Multipolar cells are also numerous while it is suggested that the unipolar cells are derivatives of the multipolar and bipolar cells. As regards the shape of the cells they vary and in the same animal circular, angular, and poygonal types exist side by side. They are pearl grey in colour and extremely elastic in texture while the degree of granularity varies. As regards the spiral outgrowth of the sympathetic cells in the frog Arndt suggests that the fibrillar arrangement of the cell capsule may at times simulate a spiral fibre. At the same time no decisive opinion is given as to the non-nervous or nervous nature of the spiral fibres.

The work of Axel, Key, and Retzius(8) is important since they are the first to demonstrate the presence of a medullary sheath on the spiral fibre and so to demonstrate conclusively its nervous nature.

Ehrlich(19) describes the course of the spiral fibres very completely. From the fact that it is medulated he concludes that it is a cerebro-spinal fibre which after splitting up into numerous fibrils ends in small swellings on the sympathetic cell walls. He suggests that those fibres carry impulses from the central nervous system to the sympathetic cells.

Arnstein(6) describes the sympathetic cells in the frog and is able to trace the spiral fibre to the periphery in the pharynx. In a second paper with Nikita Lawdowsky(7) he describes a similar arrangement in the nerve cells forming the ganglia of the heart. He demonstrates the presence of two outgrowths from the cells a broad and fibrillar one corresponding to the straight fibre and a delicate somewhat convoluted fibre which passes to the muscle and corresponds to the spiral fibre (fig. 6).

Fig. VI



A. nerve outgrowth to join N. nerve trunk

(B.) nerve outgrowth going to muscle. (M.)

(Arnstein, Nikita Lawdowsky)

Retzius(32) like Courvoisier regards the straight fibres found in connection with the sympathetic cells in the frog as cerebro-spinal fibres which pass into the sympathetic cells and so establish a means of communication between them and the central nervous system. In later work on the sympathetic cells of higher vertebrates( ) he describes the sympathetic cells as multipolar structures with one axis cylinder.

Kolliker(23-25) whose investigations extend over a number of years also describes the sympathetic cells in the mammal as a multipolar structure with one axis cylinder. The axis cylinder goes either directly to involuntary muscle or after breaking up into numerous small branches terminates in a neighbouring ganglion. By this means a motor impulse in one ganglion is conveyed to the cells of another ganglion.

Ramon y Cajal(11) who also describes the sympathetic cells in the mammal as multipolar with one axis cylinder, gives an interesting explanation of the function of the other outgrowths from the sympathetic cells. These outgrowths he states form a fibrous network round the individual cells of a ganglion and so establish a means of communication between the cell (fig. 7). He also describes the sympathetic plexus in the gut wall which he finds is built up of star-shaped, spindle-shaped, and angular cells with the usual leash of dendritic outgrowths and one axis cylinder.

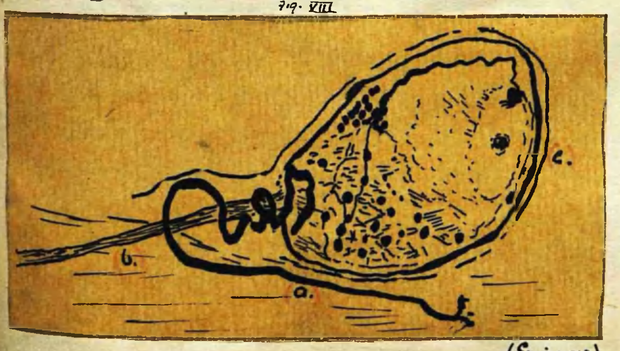
Fig. VII

(Cajal)

(a) - axis cylinder.
(b) - dendritic outgrowths
(c) - sympathetic cells.

Smirnow(34) in his article on the structure of the sympathetic cells in the frog agrees with Courvoisier as to the presence of a commissural network which joins the intrinsic network of the different cells. This cellular network which lies on the superficial aspect of the cell is directly connected with the spiral fibre which on emerging from the cell is seen to take an opposite direction from the straight fibre (fig. 8). He is also inclined to agree with Arnstein that the spiral fibre goes towards the periphery while the straight fibre is directed towards the central region.

Fig. VIII



(Smirnow)

(a). spiral fibre
(b). straight fibre
(c) - sympathetic cell.

Feist[20] who uses the methylene blue stain describes the course of the spiral nerve fibre which constitutes an outgrowth of the sympathetic cell in the frog. He finds that outside the cell the spiral fibre is very darkly stained while it shows several varicosities along its course. Where it enters the cell it can be traced through the very granular zone which marks its point of entrance to a fine network in the cell wall. The relation of the spiral fibre to this network is easily seen in the drawing (fig. 9). The straight fibre which is also shown is much broader and is studded by numerous granules. Feist seems to regard the spiral fibre as the axis cylinder and the straight fibre as a prolongation of the cell substance.

Fig. IX

(a) - spiral fibre
(b) - straight fibre (c) sympathetic cell (Feist)

A. van Gehuchten[38] describes the sympathetic cells in man as multipolar ~~which have~~ with one axis cylinder and numerous dendritic outgrowths which terminate between the cells of the ganglion

Sala[33] practically agrees with van Gehuchten in his description of the construction of the sympathetic cells and is therefore not quoted more fully here.

Lenhossek[28] in his writings on the minute structure of the sympathetic cells differs in no essential point from the opinions already referred to under Retzius, Kolliker, Sala, and van Gehuchten it therefore seems unnecessary to do more than refer to his work.

At this stage Dogiel[15] contributes an extremely important article on the minute structure of the sympathetic cells and ganglia in mammals. In this paper he passes under review the chief work already done on the subject and then proceeds to give an account of the sympathetic ganglia. Since this is a paper which forms an epoch in the knowledge of the minute structure of the sympathetic ganglia I have considered it advisable to give a detailed account of the results described in it. Dogiel considers first of all the structure of the ganglia in the mammalian gall bladder. The cells are found to be irregularly circular in shape with numerous granules which stain a deeper tint than the groundwork of the cell, while the nucleus is prominent on account of the pale colour it assumes with the methylene blue stain. From the cell go many outgrowths one of which is the axis cylinder of the cell while the others correspond to the dendrites of the cells of the central nervous system (fig. 10).

Fig. X

(Dogiel.)

(a) - axis cylinder derived from an outgrowth.
(b) - dendritic outgrowths.

Protoplasmic outgrowths or dendrites arise from all portions of the cell wall where the cell lies in the middle of a ganglion. If the cell be situated at the periphery of a ganglion the outgrowths either come from the poles of the cell or from the cell wall which lies nearest the centre of the ganglion. These outgrowth which vary to a great extent in thickness subdivide into numerous smaller branches and terminate finally as extremely fine fibrils. The number of outgrowths given off by one cell is frequently about five but it varies from two to twelve. These protoplasmic outgrowths form a rich network round the cells of a ganglion and form a basis of association for all the cells of a ganglion. This association is not the physiological communication which Ramon y Cajal describes as established between the cells through their dendritic outgrowths. The axis cylinder of the cell is derived either from the body of the cell or from a dendritic outgrowth (fig 10). At the first part of the axis cylinder there is usually a cone-shaped thickening but after this the fibre is seen to decrease gradually in calibre terminating finally as a very minute fibril. The axis cylinder is seen to give off numerous branches both from the first portion or conus shaped thickening as well as from the fibrous part of its course. Up to this time the structure of the axis cylinder had been a matter of controversy some of the workers describing it as giving off branches while others fail to recognise any collaterals, Dogiel is therefore able to give definite and conclusive evidence on the subject.

To the various ganglia pass sympathetic and cerebro spinal nerve fibres. The sympathetic fibres end in the ~~peri~~intercellular network between the cells while the cerebro spinal fibres terminate in the peri ~~gangli~~-

cellular network.The sympathetic fibres terminate in very fine varicose swellings between the cells which are in close ontact with the dendrites of the cells.The cerebro-spinal fibres on the other hand are thick fibres which are studded with comparatively coarse varicose swellings while the fine terminal fibres penetrate the capsule of the ganglionic cells It is interesting to note that so far no evidence is got of the penetration of the cell capsule by sympathetic fibres.
If the network of a ganglion be examined as a whole it is found that by far the greater number of the fibres in it are non-medullated.They are known as Remaks fibres.The various fibres lying in the ganglia of the mammalian ****** gall bladder are derived from the cerebro-spinal system,the sympathetic chain,the solar plexus,and the ganglionic cells in the organ itself.

In a second paper Dogiel(16)discusses the formation of the intestinal plexuses as shown by his own investigations and those of Ramon y Cajal ( ).Dogiel finds in the ganglia of the Auerbach and Meissner plexuses cells which are oval,angular,and circular in shape.From these cells go numerous outgrowths which are all of a dendritic character except one which is the axis cylinder. he nuclei of the cells are either oval or round and are relatively large in size.The dendrites vary in number from one to eight and come from different parts of the cell wall,or in some cases from the two poles.They course between the various cells of the ganglion and give off many lateral branches which form a network at the periphery of the ganglia(fig. 11).

Fig XI a.

(Dogiel)

(a.)
(a)- axis cylinder.
(b)- Dendrites
(c)- sympathetic cells stained to show granules only

(b.)
Portion of ganglion showing cells similar in structure to
(a.)
Note arrangement of axis cylinder and dendrites -

Fig. XI - b.

(Dogiel)

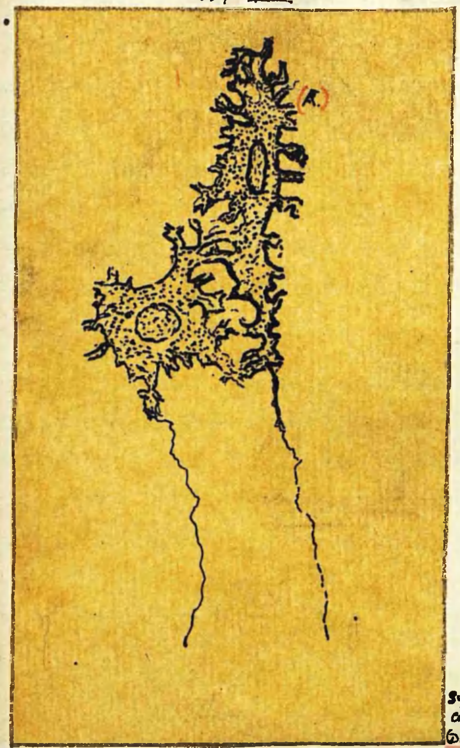
Besides the dendritic outgrowths and the axis cylinders of the cells in the ganglion axis cylinders from the cells in neighbouring ganglia extend into and assist in forming the fibrous network of a ganglion. In addition to those fibres there are numerous fine varicose fibrils which subdivide and form a pericellular network round the cells of the ganglion.It is probable that these fine varicose fibrils are derived from the cerebro spinal system.
There are other cells in the intestinal nerve mechanism besides those which have just been described.They are spindle-shaped or in some cases star-shaped with flattened oval nuclei,and give off from their angles or poles three to five outgrowths.They are found along the course of the fine arteries and veins,and along the capillaries, as well as on the superficial aspects of nerve fibres and ganglia (figs. 12).These cells correspond with the "ganglions interstitiels" of Ramon y Cajal,and they are not the cells of the Auerbach or Meissner plexuses although Ramon y Cajal describes them as such.

Fig. XII

(Dogiel)

In later work on the sympathetic cells Dogiel(17) describes two types of cells in the stellate ganglion,the thoracic portion of the sympathetic,the coeliac ganglion,and the ganglia of the plexuses of Auerbach and Meissner.The cells of the first type vary in size and are round,oval,spindle or star-shaped.From each cell go dendrites and one axis cylinder.The dendrites are short and relatively thick and vary in number from five to twenty.They display numerous varicosities on their course and branch and subdivide so as to form a thick network.The axis cylinder either starts from the cell or from a dendrite in a cone-shaped thickening after which it forms a comparatively fine fibre(fig.13).The second type ~~of~~ The cells ~~are~~ are also unequal size and multipolar but in shape they are either circular or oval

Fig. XIII



(A.) Sympathetic Cells. Type 1. (Dogiel)

They have one to sixteen dendritic outgrowths and one axis cylinder.The dendrites are all thick at the point where they leave the cell but at varying distances they subdivide up into long thin branches.All these branches are either smooth or show round or oval swellings.In their whole course they are finer than the outgrowths of the first type of cell.The axis cylinder of the cell comes either directly from the cell or from an outgrowth.Where the cell lies in one of the large ganglia the outgrowth is comparatively thick but in the gut wall it is a very fine structure,in both situations the axis cylinder may be quite smooth or it may show varicose swellings(fig.14).

The cells of the second type are usually not so abundant as those of the first type and in some of the very small ganglia they are wanting.

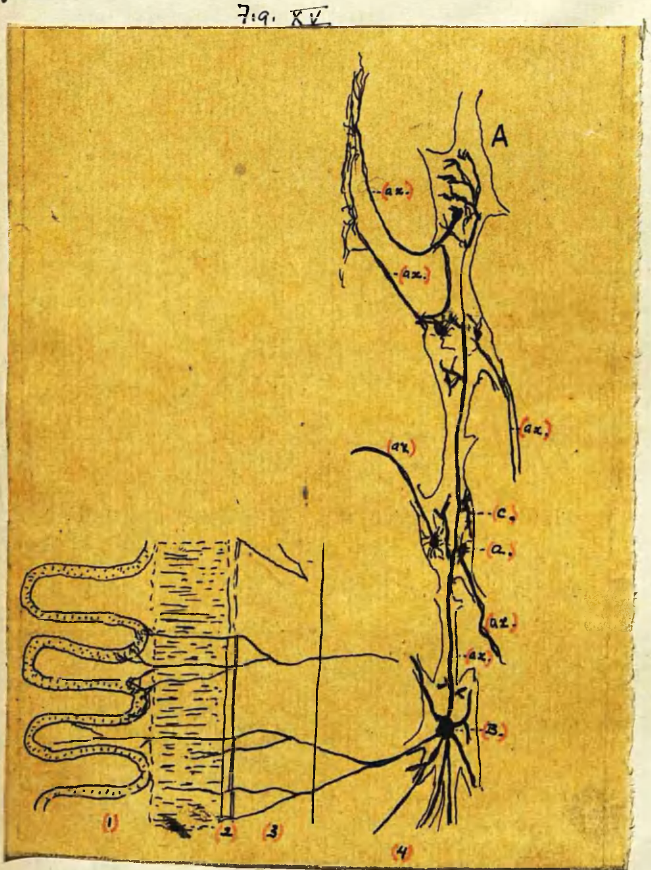
As regards the physiological significance of the two types it seems highly probable that those of the first type are motor in function while the cells of the second type are sensory.This suggestion is made because of the analogy which is seen to exist in the first place between the motor cells of the cerebro-spinal system and the cells of the first type here described.The protoplasmic outgrowths are short and relatively thick while the axis cylinders may be traced to the involuntary muscle fibres.The outgrowths of the sensory cells or the cells of the second type terminate in the various organs,where it is possible they form some end apparatus parallel

Fig. XIV

(B.) Sympathetic Cell Type 2. (Dogiel)

to the arrangement found in the central nervous system.
In this connection Dogiel refers to the work of Sakusseff(36) who demonstrates in the alimentary canal of the fish a delicate network of nerve fibres which pass from the nerve mechanism in the gut wall to surround the epithelial cells lining the gut. The arrangement in the gut therefore resembles closely the relationship between the sensory branches of the cerebro spinal cells and their end organs.
The axis cylinders of the cells of the second type may be traced passing on from one ganglion to another to each of which it gives off collaterals, they therefore resemble in their arrangement the axis cylinders of the central nervous system.
As a result of this investigation of the minute anatomy of the ganglia of the intestinal nerve plexuses Dogiel gives the accompanying diagram which shows the schema of the intestinal reflex (fig. 15)

Fig. XV.



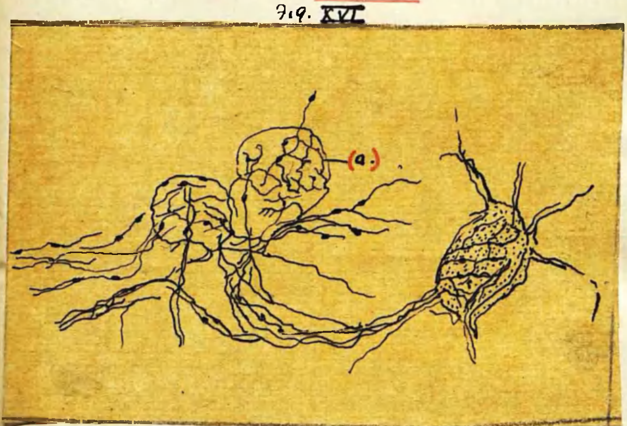
(Dogiel)

Schematic diagram of Intestinal Reflex. formed by intestinal plexuses
(A.) Intestinal plexus.
(B.) Sensory sympathetic cells.
(a.) Motor sympathetic cells
(ax.) axis cylinder.
(1.) Epithelium and villi of gut
(2.) Muscularis Mucosa.
(3.) Submucous Layer.
(4.) Muscular layer with the Intestinal plexus.

Apolant(1) describes two varieties of sympathetic cells in the rabbit unipolar and bipolar. The examination of foetal tissue shows that in the rabbit the majority of the sympathetic cells are uninuclear but when the adult is examined it is found that nearly all the uninuclear cells are replaced by binuclear. It would appear as if the second variety were an evolultion from the first type.
Juschtschenco(22) describes the results of an investigation made by him on the formation of the sympathetic ganglia in mammals. In all the mammals examined the the general construction of the sympathetic ganglia is found to be the same. The cells are chiefly multipolar and all have numerous outgrowths. There is nothing to distinguish the cells which lie at the periphery of a ganglion from those which lie in the centre. The outgrowths of the cell end either by forming the

"nids pericellulaires"of Ramon y Cajal round the individual cells of the ganglion,or they form a fine network which lies between and unconnected with the ganglionic cells.The axis cylinders of the cells pass out of the ganglion to which the cells belong and traverse adjacent ganglia,they do not divide and only give off collateral branches at rare intervals.The nerve fibres which enter a ganglion are seen to break up and form a basket-like network round the cells of the ganglion(fig.16).As regards the general arrangement of the ganglionic cells the, are as a general rule very irregularly disposed but in some cases they are arranged in small groups.From a consideration of the common characteristics of the cells of the sympathetic ganglia the conclusion is come to that beyond the slightly finer build there is nothing to distinguish them definitely from the cells of the cerebro-spinal system.

Fig. XVI



(a) Network formed round sympathetic cells by nerve fibrils. (Jusatlenhenco)

Dogiel (18) investigates the structure of the ganglia in the heart in the human subject and also in other mammals.He is able to distinguish three varieties of cells and two types of nerve fibres in the ganglia. The cells of the first type are round,oval,club-shaped,or angular and form the majority of the ganglionic cells.They have from two to sixteen dendrites,which like the body of the cell have a flattened appearance,and interweave with one another.There is one axis cylinder which sometimes shows varicose swellings on its course.These cells are described by Dogiel as the motor sympathetic cells and correspond exactly with the cells which lie in the intestinal plexuses, (fig.17).The cells of the second type* form the most interesting elements in the peripheral ganglia.In form they are not very different from the cells of the first type,while in the arrangement of their outgrowths multipolar,unipolar,and bipolar forms are seen.Besides the position they occupy in the cardiac plexuses they also lie along the course of the nerves in the subpericardial plexus,either singly or in small groups.The dendrites are long and slender and come off from that portion of cell lying nearest the centre of the ganglion

Fig. XVII

Sympathetic cells. Type I.
(a)- axis cylinder
(b)- dendrites

(Dogiel)

where the cell is situated at the periphery of a ganglion,or from any point in the cell wall if the cell is central.Some of them are seen to be incorporated in a bundle of nerve fibres.The axis cylinder which comes either directly from the cell or a dendrite is long and slender and is non-medullated for a part of its course(fig.18).

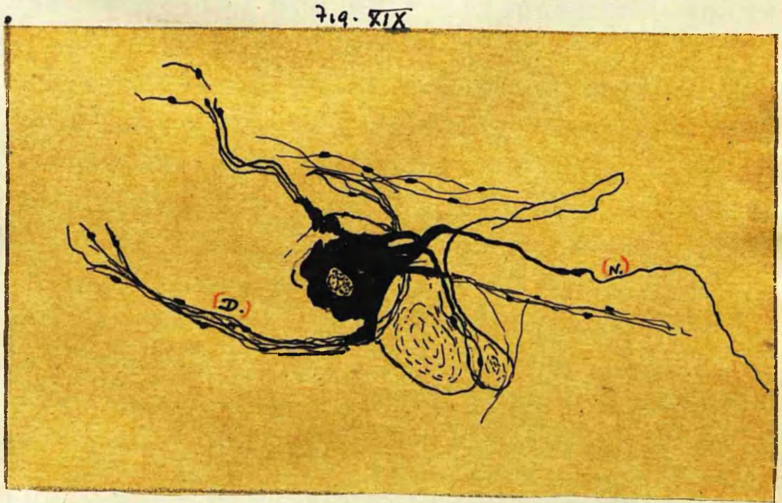
Fig. XVIII

(Dogiel)

Sympathetic cell Type 2.

The third type of cells correspond in the appearance and arrangement with the cells of the second type except in one point that they are all localised in the ganglion to which the cell belongs.The dendrites form a very close network round the various types of cells which is recognised and described by Ramon y Cajal as the"nids pericellulairs". (fig.19).

Fig. XIX



(Dogiel).

Sympathetic cell Type 3.
(N.) axis cylinder
(D.)- dendrites with varicose thickenings.

The fibres of the ganglionic plexus are derived partly from the outgrowths,axis cylinders and dendrites,of cells in adjacent ganglia,and partly from the out-growths of cells lying in sympathetic ganglia outside the heart.

A more complete discussion as to the significance of the various types of cells is given in a later paper in which similar cells are described in the gut and gall bladder.

In a paper which appears ~~a~~ in the same year ~~later~~ Dogiel(16) gives a general account of the formation of the sympathetic ganglia in the gut and gall bladder of the human subject as well as in certain other mammals. Much of the work is already referred to but this paper gives an excellent resume of articles which appeared from time to time on this subject.In the gut Dogiel distinguishes three types of cells. In the first type the cells are star-shaped or angular,and have oval or round nuclei lying either at the centre or side of the cell. The cells as a whole have a flattened appearance,and they constitute the most prominent group in the various ganglia.This is more particularly the case in the plexus of Auerbach.The outgrowths of the cells vary in number from four to twenty .They are comparatively thick and have a flattened appearance,while they break up into numerous thick short branches,which interweave with the dendrites from other cells(fig.20).In some cases the dendrites and axis cylinder of the cell both come off from the same pole of the cell while in other cells the dendrites and axis cylinder come off at opposite poles.The axis cylinders of this type of cells usually give off a number of long thin collateral branches which pass in between the cells in the various ganglia it traverses.This type of cell is the motor cell in the sympathetic ganglia.

Fig. XX

Sympathetic Cells. Motor (Dogiel)

The cells of the second type are angular, star or spindle-shaped with relatively large oval or round nuclei which contain one or two nuclei.From the poles of the cells go from three to ten dendrites,which become slighter in structure at some little distance from the cell divide into numerous branches which ramify between the cells of the ganglion and pass out of the ganglion in one or other of the nerve bundles.In some cases the dendrites have been traced to glandular epithelium and to various intestinal glands.It is just possible that the cells of the second type may influence secretion but this is doubtful,their true function is sensory.In number they are less than the cells of the first type except in the plexus of Meissner where they are comparatively abundant.The grouping of cells of this type in this position is significant of the part they play in the intestinal reflex arc.(fig.21).

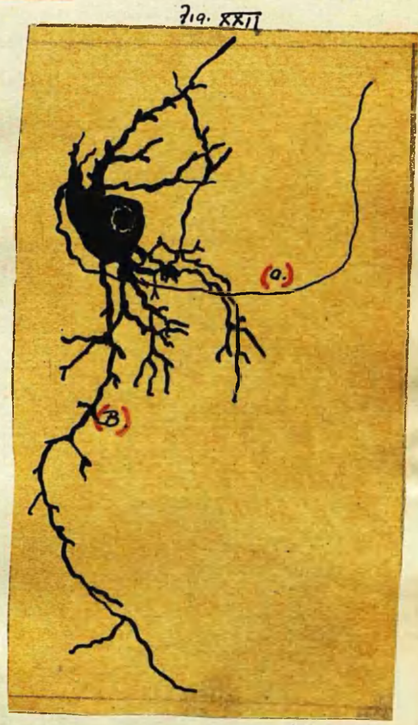
Fig. XXI

Sympathetic cell. Sensory. (Dogiel)

The cells of the third type resemble in size and appearance the preceeding type while in mumber they are somewhat less plentiful than the first type. They generally lie in the centre of a ganglion but they are found at the periphery and along the nerve bundles. In smaller ganglia they are wanting. The dendrites which number from two to twelve branch and ramify amongst the cells of the ganglion, while the axis cylinder is long and slender. In the number, length, and characteristics of the dendrites the cells of the third type resemble the second type while in the arrangement of the dendrites and their limitation to one ganglion they resemble the first type (fig.22).

Fig XXI
(A)- axis cylinder
(B)- dendrites

Fig. XXII



(Dogiel)

Sympathetic cell.

(a)- axis cylinder.
(B)- dendrites.

The fibres of the ganglia are composed of two varieties. One variety is formed by very thin, smooth or slightly varicose fibrils which form the dense network round the cells. They are derived from the ganglia in the intestine and from ganglia lying outside the gut. The second variety is composed of relatively thick fibres which have a medullary sheath for part of their course. In number they are scanty compared with the first variety. Besides these ganglia there are other cells in the intestine which lie along the blood vessels and nerve trunks. As these cells have already been discussed in detail it is not necessary

to describe them further.
In the gall bladder the arrangement and type of cells are the same as in the gut and requires no special description.
Huber(21) describes an investigation on theminute anatomy of the sympathetic ganglia in vertebrates.
In amphibia the sympathetic neuron is a unipolar cell with a straight and spiral outgrowth. In the wall of the intestine however the sympathetic cells are multipolar, and thus form an exception to the general rule. In a typical sympathetic neuronthe cell body is enclosed in a network of fibres which are either smooth or varicose and are in direct connection with the spiral fibre. It would appear that the pericellular network and spiral fibre are parts of a neuron which lies central to the ganglia in which the structures are found. This opinion is based on the fact that medullated fibres may be traced entering the sympathetic ganglia probably from the cerebro spinal system where they give off non medullated collaterals which end in the spiral fibres and pericellular plexuses. The spiral fibre is therefore not an outgrowth of the sympathetic neuron although it closely resembles such a structure. (fig. 22).

Fig. XXII

(Huber)
(a) axis cylinder.
(b) Sheath of axis cylinder.
(c)- capsule.
(d) nodules in pericellular plexus.
(e)- fine endings of plexus fibrils
(s.f) spiral fibrils

In reptilesthe sympathetic cells are either multipolar, bipolar, or unipolar. All the cells have one axis cylinder which is non-medullated near the cell but is probably invested with a medullary sheath at some distance from the cell. Medullated fibres of cerebrospinal origin end in the sympathetic ganglia either in pericellular plexuses round the multipolar or bipolar cells or in the more complex pericellular plexuses and spiral fibres in connection with the unipolar cells (fig. 23). The unipolar cell shown in the photograph is very characteristic of the sympathetic ganglia in reptiles.
In birds the sympathetic cells are multipolar with one axis cylinder and several dendrites while the cell body is enclosed in a nucleated capsule. The non-medullated fibres enter the ganglia and terminate on the dendritic outgrowths of the neurons. The medullated fibres from the cerebro spinal system end in pericellular plexuses round the cells (fig. 24).

Fig. XXIII

(A)- axis cylinder.
(B)- cell body.
(C)- nucleus.
(D)- nucleolus.
(a'a''a''') medullated nerve fibres ending in pericellular network.
(Huber)

Fig. XXIV

(Huber)

(a) – axis cylinder.
(c) - capsules of sympathetic cells.

In fish the sympathetic neurons vary in size and shape, and they may be either unipolar or multipolar. The dendrites vary in number from four to six being a usual number and terminate extracapsularly between the cells of the ganglion. The nuclei which are found surrounding the cells are derived partly from the capsule of the cell while it is possible that the others are the nuclei of branched neuroglial cells. A very few medullated fibres are seen in the sympathetic ganglia but no definite information can be given as to their source(fig.25).

Fig. XXV

(Huber)

(a)– medullated fibre giving off branches ending in capsules of sympathetic cells (A)(B).

In mammals the great majority of the sympathetic cells are multipolar although bipolar and unipolar cells do exist. In preparations made from the solar plexus of the guinea pig excellent demonstrations ~~were~~ are got of binucleated cells. Huber therefore agrees with Apolant( )and does not look on the presence of two or more nuclei in the sympathetic cells of certain mammals as the sign of a degenerative change.

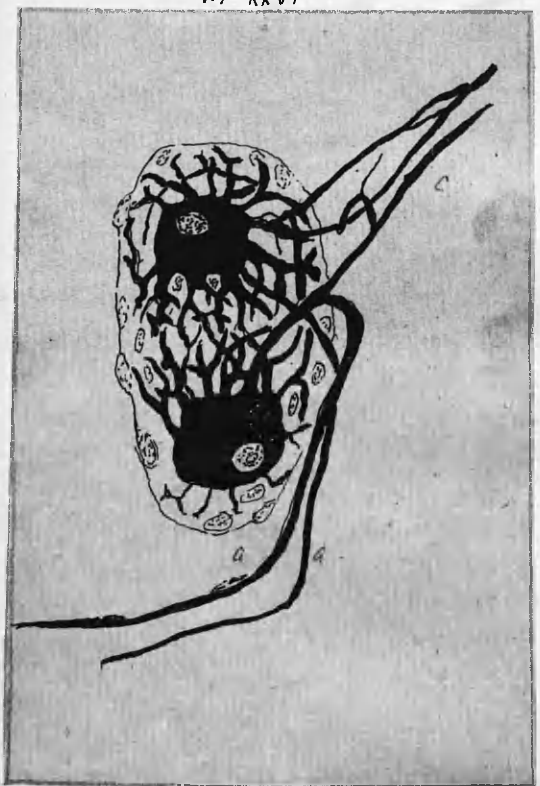
The dendrites of the cells vary in number and arrangement but ultimately form a basket-like plexus round the cells. The axis cylinder which is single arises either from the cell or from a dendrite and may be followed for a considerable distance through the ganglionic network.

In the groundwork of the ganglia both medullated and non-medullated fibres are found. The medullated fibres may be traced from the ~~from the~~ white rami into the ganglia where they branch and terminate in a pericellular network. The terminal branches mayor may not be medullated. In good sections the terminal branches are seen to pass right through the cell capsule. Other medullated fibres are derived from the cells of adjacent ganglia which branch and ramify between the cells.

In many of his observations on the sympathetic ganglia in mammals Huber agrees with Dogiel(15-18) but is unable to confirm Dogiels observation on the presence of a sensory sympathetic cell in the ganglia.

Ramon y Cajal(12)gives a detailed description of the cells in the sympathetic chain in man.These cells he divides into three groups according to the arrangement of their dendrites and axis cylinders. In the first group the cell show an arrangement of dendritic outgrowths below the capsule of the cell.Sometimes these dendrites show a good deal of branching while in other cases they divide close to the border of the cell capsule.Sometimes two or three cells lie within one capsule and the short intracapsular dendrites of each cell interweave to form a very close network(fig.26).Besides these short dendrites there are other long outgrowths which terminate either in small branches which may communicate with the terminations of other dendrites or in small olive-shaped thickenings.The axis cylinders of the cells are easily distinguished from the dendrites by their transparent appearance.

Fig. XXVI

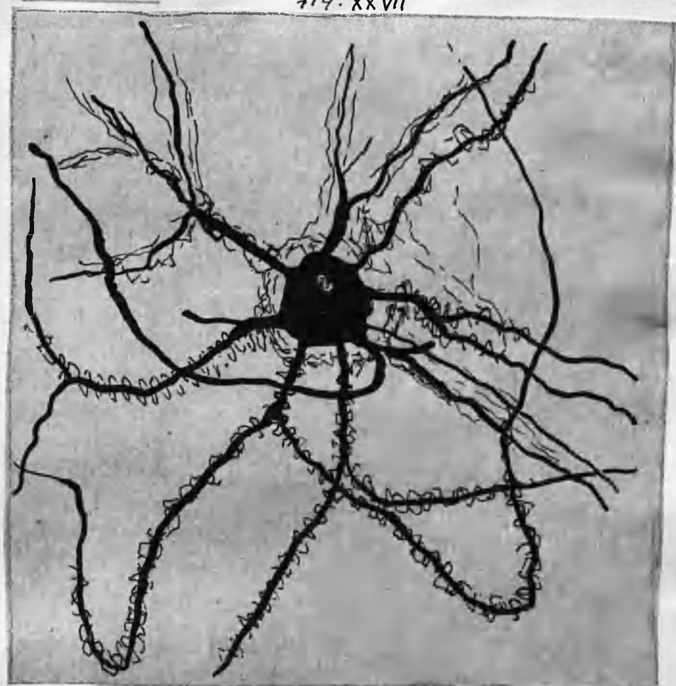


(Cajal)

Sympathetic cells of the first Type.

The cells of the second type are characterised by their long radiating dendrites,many of which are surrounded by very delicate fibrils (fig. 27).

Fig. XXVII



(Cajal)

Sympathetic Cells Second Type.

The third type of cell is also known as the mixed type since it displays some of the characteristics of the first and second types of cells.Thus the cells have an intracapsular network as well as long radiating dendritic outgrowths which are accompanied by numerous fine nerve fibrils(fig.28).
Round the various dendritic outgrowths from the sympathetic cells

Fig. XXVIII

Sympathetic Cells Second Type. (Cajal)

numerous fine fibrils wind as indicated in the figures and while a very complicated network is also formed round the bodies of the cells. This is but a bare outline of a paper which describes in minutest detail the relationship between the different parts of the sympathetic chain as shown by the silver nitrate stain, and it is probably the most complete description extant of this structure.

Warfwinge(40) gives a description of the sympathetic ganglionic cells in the frog. These cells he finds are usually round or oval in shape with a more or less excentric nucleus, which is surrounded by a special band of protoplasm, the endoplasm. This endoplasm is seen to be traversed by many delicate fibrils which are continued directly into the axis cylinder of the cell. Beyond this zone is the ectoplasm which contains numerous granules. On its outer surface lying between the body of the cell and the cell capsule are some coarser fibrils which are directly connected with the spiral fibre which lies in close relationship with the axis cylinder of the cell (fig. 29).

Compared with the cells of the spinal ganglion they are somewhat smaller and less regular in form but a parallel condition is found as regards the arrangement and disposition of the axis cylinder and the intracapsular network with its spiral outgrowth.

Fig XXIX

(Warfwinge)

(X) – Cell capsule.
(Ectopl) – Ectoplasm.
(Endopl) – Endoplasm.
(N) – axis cylinder.
(sp.h) – spiral outgrowth

Michailow(31) describes the sympathetic cells which form the ganglia in the mammalian bladder. He also points ou that the results he describes in connection with the bladder bear out in many points his earlier work on the nerve cells of the heart(31b). In both the bladder and heart ganglionic cells are found which do not correspond with any of the types described by Dogiel. These cells are characterised by the arrangement of the dendrites which are partly limited to the ganglion while some extend beyond it. The dendrites of this type of cell as well as those which belong to cells corresponding to the third and second types of Dogiels classification,all terminate in a special end apparatus.It is an invariable rule that the dendrites of one cell all have the same type of end apparatus.So far four different types of this end apparatus are recognised.

According to the classification of Michailow there are four different types of sympathetic cells .

The cells of the fourth type which are first described vary both in size and form and give off some two or three outgrowths.These outgrowths terminate in small round bodies which are in close relationship with the dendrites of other cells in the ganglion,or they may lie completely outside the ganglion(fig. 30).

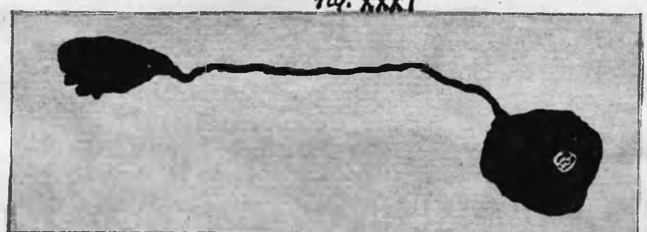
Fig. XXX

(Michailow)

Fig XXX
Fourth Type of Sympathetic cell.

The cells of the third type are exactly the same as those of the fourth type except that the end apparatus of the outgrowths is formed by comparatively large circular or club-shaped bodies(fig. 31).

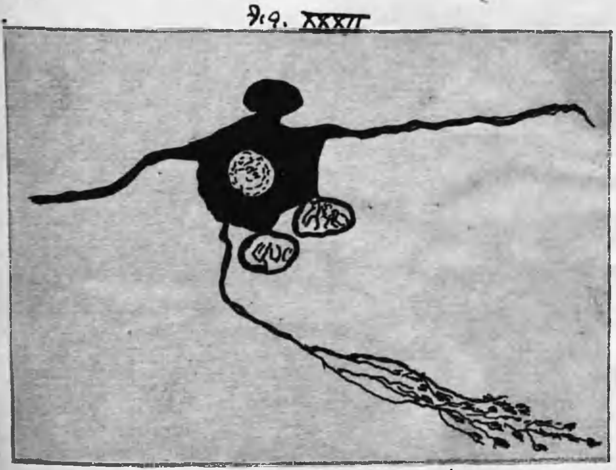
Fig. XXXI



Third Type of Sympathetic cell - (Michailow)

The cells of the second type are somewhat irregular in form but are as a general rule oval or round.They are always multipolar and display an axis cylinder,short and long dendrites.The short dendrites with their end bodies lie wholly inside the capsule of the cell, while the long dendrites terminate in small tufts or brush-like structures(fig. 32).

Fig. XXXII



Second Type of Sympathetic cell. (Michailow)

The first type of cell which is described in the ganglia of the heart is not found in the ganglia of the bladder,it is therefore evident that the construction of all the sympathetic ganglia is not the same.

The fibrous portion of the ganglia in the bladder is composed of fibres which form an intracapsular network,a pericapsular plexus,a pericellular network, and a terminal plexus in the ganglia.

These sympathetic ganglia are regarded by some writers as the fourth centre for the regulation of the action of the bladder.The first two centres lie in the brain,the third in the spinal cord,while the fourth may be constitued by the ganglionic cells,although Michailow points out that the evidence on this point is not conclusive.At the same time he suggests that the inferior mesenteric ganglion may be a fifth centre for the regulation of the bladder in mammals.

From this short description of the more important investigations on the minute anatomy of the sympathetic ganglia in the vertebrates it is evident that although the more modern methods of staining have given us a clearer picture of the individual cells and their relationship to other cells yet many of the earlier descriptions are not entirely superseded.
This is the case with the descriptions of the sympathetic cells in the frog.The early workers among whom are Arnold(3,4,5),Beale(9), Courvoisier(13,14)Schwalbe(35)and others all recognise the presence of a spiral and straight fibre in connection with the sympathetic cells It is not however until the work of Retzius(32) and Ehrlich(19) appears that the significance of the spiral fibre is recognised. They describe the spiral fibres as outgrowths from the cerebro-spinal system which enter into connection with the sympathetic cells by means of the intracellular network so thoroughly described by the earlier workers*.This view is supported by the work of Huber(21)who is able to follow out the course of the spiral fibres from the cerebro-spinal system to the sympathetic cells.
With regard to the structure of the sympathetic cells in mammals the work of Dogiel(15-18b),and Ramon y Cajal(11,12) stands out preeminently. Although they disagree on some points regarding the structure of the intestinal ganglia,and much of their nomenclature is different,yet the comparison of their diagrams shows that to a great extent they are in agreement.Dogiel is probably in advance of Cajal in the conclusions he draws as to the function of the various types of sympathetic cells.Although his theory as to the presence of motor and sensory cells in the various sympathetic ganglia is not actually proved it is none the less evident that such a theory affords a satisfactory basis for the explanation of a peripheral reflex.
The recent work by Michailow(31)supports the work of Dogiel since he suggests that the sympathetic cells lying in the wall of the mammalian bladder may form a fourth centre for the regulation of its action.
Whatever be the exact explanation of the different characters and functions of the sympathetic cells found in the various viscera the fact remains that in vertebrates generally these cells are exceedingly numerous and form extremely complicated plexuses which are further provided with elaborate means of communication.It seems ~~doubtful~~ doubtful that such an elaborate system should be but a shunting station for impulses from the central nervous system,certainly if Dogiels interpretation of the significance of the cells is correct we have in the various sympathetic plexuses a segment which is equipped for independent action.Whether such independent action

is the normal condition or whether it comes into play under certain cicumstances is as yet a matter for speculation.

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Chapter 9.

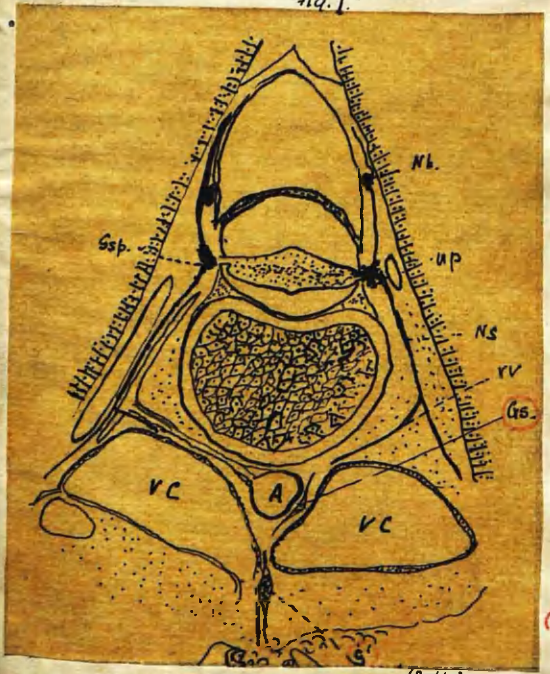
The comparative Anatomy of the Sympathetic System.

A consideration of the formation of the sympathetic system as it appears in the various classes of vertebrates shows clearly the gradual evolution from a very rudimentary form to the highly specialized system found in birds and mammals.
Starting with the Cyclostomata Muller(14) writing in 1840 points out that in this order an independent sympathetic system does not exist. He suggests that the intestinal nerve which is given off from the vagus and its cardiac branch are partly sympathetic in structure, and that therefore the sympathetic system is present in the Myxine (the type he describes) but is incorporated with the vagus.
Stannius (17) who also describes the sympathetic in the Cyclostomata disagrees with Muller and other anatomists of his time since he regards certain nerve fibres which he finds accompany the vertebral veins as the analogue of the sympathetic system of higher vertebrates.
Ransom and Thompson(16) agree to a certain extent with the work of Muller. Taking the Petromyzon as their type they describe the vagus as arising by four posterior roots which unite to form a bi-lobed ganglion which gives off a dorsal and ventral ramus. The spinal nerves, which in this type do not unite to form a mixed spinal nerve but remain separate, send branches to the vagus where they meet it. The anterior and posterior spinal branches enter the nerve trunk separately. The vagus fibres therefore which supply the heart and other parts contain fibres derived from the spinal branches as well as from the vagus ganglion. The small fibres and clusters of cells which enter the vagus from the posterior spinal nerves are the elements of a typical sympathetic system which is therefore as Muller pointed out incorporated with the vagus nerve. The suggestion is also made that sympathetic elements are fused in the vagus ganglion or in the root of the vagus although they are separate lower down. Further support is given to the view that the sympathetic system is incorporated with the vagus by the fact that their is no trace of the sympathetic below the branchial region.
An investigation made on the Bdellostoma shows that there is no communication between the vagus and the posterior spinal roots, and that there is no representation of the sympathetic chain.
Julin(13) disagrees with the findings of Ransom and Thompson and gives a very different description of the sympathetic system in the Petromyzon planeri. He describes a series of small round bodies lying along the course of the aorta on both the right and left sides, these he identifies as sympathetic ganglia. At first sight these ganglia seem to be irregularly arranged but closer inspection shows that

they lie at the points where the dorsal and ventral spinal nerves emerge.From these ganglia nerve fibres pass to the upper surface of the cardinal vein while other fibres pass inwards and come into contact with more deeply situated sympathetic ganglia. The more deeply situated ganglia are identical with the ganglia just described,or as Julin styles them the superficial ganglia,in both form and structure.They serve as the sympathetic supply for the heart and intestinal tract.The ganglia for the heart form a delicate chain beginning about the level of the jugular vein and besides being connected with the superficial ganglia are also in close juxtaposition to the cardiac branches of the vagus with which they may actually blend.For the supply of the gut a ganglion is recognised at the level of the anterior intestinal artery,this is known as the oesophageal ganglion.From it outgrowths accompany the ramifications of the artery to the various portions of the gut.It is evident from this description that the Petromyzon is furnished with a primitive type of sympathetic system for as Julin points out there is no formation parallel to the sympathetic chain developed in higher vertebrates where the anterior and posterior spinal nerve roots unite.It is possible that if the anterior and posterior spinal nerves are as in higher vertebrates purely motor and sensory the small sympathetic ganglia may share the characteristics of the root with which they are connected,this however is uncertain.

Gegenbaur(7)in his textbook on comparative anatomy refers to the work of Julin(13) and gives a diagram which shows very clearly the position and relationship of the various sympathetic ganglia in the Petromyzon(fig.1).He also points out that it is extremely uncertain whether the vagus forms in this type any connection with the gut.

Fig. 1.



(Julin)

Wiedersheim(20) points out that although in the Amphioxus there is no trace of a sympathetic system yet in the next class,that including the Ammocoetes and Petromyzon,one gets typically arranged sympathetic ganglionic cells lying on the dorsal and ventral branches of the spinal nerves.Generally these ganglia lie at the point where the parietal veins open into the cardinal vein and not along the sides of the aorta as is the arrangement in higher vertebrates

a - aorta
v.c. Cardinal veins
(S', Gs) sympathetic ganglia
Gsp. spinal ganglion
nl - lateral nerve
rv - ventral branch
Ns - spinal nerve
up - parietal branch.

Passing next to the consideration of the formation of the sympathetic system in fish we find one of the earliest descriptions given by Stannius(171).In the Selachian he is able to trace out a series of ganglia which lie along the vertebral column and which represent the sympathetic chain.The upper ganglia are somewhat larger than the others while they are connected by delicate fibres with the corresponding ganglia of the opposite side.The uppermost ganglion on both sides is connected with the vagus ganglion,while the other ganglia are connected by rami communicantes with the spinal ganglia. The splanchnic nerve takes its origin from the upper ganglia and accompanies the coeliac artery to the various parts of the intestine. From certain of the lower ganglia sympathetic fibres pass out for the supply of the sexual glands.

In the Ganoidei of which the sturgeon is taken as a type the sympathetic chain is seen to lie almost concealed in the glandular tissue surrounding the vertebral veins.The uppermost ganglion is connected with the vagus ganglion while branches pass from it for the supply of the gills.In the abdominal cavity the chain gives off branches for the supply of the kidneys and sexual glands,as well as two large branches which supply portions of the gut,and accompany the ramifications of the posterior mesenteric and coeliac mesenteric arteries.

In the Teleosts both the trunk and tail portions of the sympathetic chain are well developed while a cranial portion appears.The cranial portion consists of the connections which link together the vagus, glossopharyngeal,and facial nerves with the sympathetic chain.Sometimes it is possible to trace the connection as far forward as the sixth and fifth nerves and ciliary ganglion.Just below the base of the skull there is a very large sympathetic ganglion which forms the origin of the splanchnic nerve.This nerve accompanies the coeliac mesenteric artery to the gut.In many bony fishes the vagus and sympathetic nerves are connected by means of small branches from the splanchnic.From the abdominal portion of the chain branches pass to supply the ovaries,testes,and bladder.Along the course of these nerve small groups of sympathetic cells are found.Very frequently the lower portion of the sympathetic chain enters the haemal canal where they may unite and form a single band.

Gegenbaur(7) describes the sympathetic chain in Selachians and Teleosts He points out that in the Selachian the uppermost sympathetic ganglion is connected with the vagus ganglion and that a cranial segment of the sympathetic system is lacking.In the Teleosts on the other hand fibres pass upwards forming a communication between the sympathetic in the trunk and the trigeminal.These fibres which terminate in a ganglion which sends branches to the fifth nerve and ciliary ganglion are the cranial part of the sympathetic system.In the trunk in the Selachian the ganglia are somewhat irregularly arranged and there is no formation of a sympathetic chain such as is seen in the Teleosts where the individual ganglia along the side of the vertebral column are all linked together.In Teleosts also a caudal portion of the system is present.Both chains leave the trunk by the haemal canal where they remain separate,or if they have joined in the trunk they divide.For the distribution of the visceral branches of the sympathetic different arrangements are found in the types under consideration.In the Selachians the visceral rami of the first spinal nerves form a plexus which is supplemented by branches from the vagus and cervico-brachial plexus.Nerve fibres from this follow the course of the coeliac artery and along with branches from the vagus supply the intestine.Numerous ganglionic cells are scattered in the interstices both of this plexus and the plexus formed from the lower ganglia for the supply of the urogenital system.In the Teleosts the splanchnic nerve is seen to originate in the upper ganglia of the sympathetic chain and to pass downwards along with the arteries for the supply of the intestine

Hoffmann(11) describes the sympathetic system in the Selachian in great detail,and in recent textbooks on comparative anatomy reference is very frequently made to his work.

In the Selachian Hoffmann finds that ten protovertebrae form the head each of which is furnished with a set of nerves whose relation to the sympathetic system must be understood.The tenth protovertebra shows an anterior or ventral root and at an early stage in development a dorsal root also.This dorsal root however soon disappears.The ventral root is the representative of the hypoglossal nerve in higher vertebrates and is named by Furbringer(5) the spino-occipital.This ventral root forms no communication with the dorsal root and no sympathetic ganglion is formed in connection with it.The same holds good for the arrangement found in the nerves of the eighth anh ninth protovertebrae At the seventh protovertebrae the region of the vagus is entered.This segment possesses a dorsal root which however cannot communicate with the ventral root of the same segment.The sixth segment has no ventral root but it forms a part of the developmental region of the vagus.The fifth segment has as its dorsal root the glossopharyngeal but no ventral root.In the fourth segment the nervus acustico-hyoideo-mandibularis forms the dorsal root,while the abducens is the ventral root of the third segment.the dorsal root of the third segment is also very well developed and forms the ramus ophthalmicus superficialis,and the ramus buccalis,The fifth nerve originates from the dorsal root of the second segment,and also from the dorsal root of the first.The first segment also possesses a ventral root which forms the oculomotor nerve.The ophthalmic profundus which is a branch of the thalamo-ophthalmicus or dorsal root of the first segment joins the ventral root of the same segment,the ciliary ganglion marking their junction.The fifth nerve is a most important structure in the Selachian and is provided with two ganglia which are found fused in higher vertebrates forming the Gasserian ganglion.It is interesting to note that the ophthalmic branch which is seen in the Selachian to be the dorsal root from the first segment preserves its character in higher vertebrates being a purely sensory nerve.It is seen that the cranial nerves are not arranged as the spinal nerves since the union of the anterior and posterior roots is not the regular matter it is along the cord.But this difference in arrangement is only apparent,as it will be shown,It was for long thought that there was no union between the anterior and posterior roots of certain spinal nerves on account of anatomical and developmental conditions,but this explanation is now seen to be incorrect.All along observors have been looking for a union between dorsal and ventral nerve roots outside the neural tube as it occurs in the spinal cord,but the union of the two roots of a cranial nerve takes place inside the brain wall. In cases where no ventral root is recognised outside the brain wall it is highly probable that the ventral root is confined to the brain wall,and is therefore not absent.If this be the case then the cranial nerves may like the spinal nerves develope sympathetic elements and such elements are found in the ganglia of the vagus, glossopharyngeal,acustico-facialis,and trochleo-trigeminus.The ciliary ganglion whose mode of formation has already been described is the only purely sympathetic ganglion and is thus peculiar among the cranial ganglia.In the trunk the sympathetic chain is not arranged as a regular series of ganglia such as seen in higher vertebrates but consists of isolated ganglia in some instances fused in groups of two or three,while in other parts some of the ganglia have vanished Briefly in the Selachian there is one purely sympathetic ganglion in the cranial region,although many of the ganglia in connection with the different cranial nerves contain sympathetic elements,and an

irregularly developed sympathetic chain in the trunk.
Ariens Kappers(23) criticises the deductions drawn by Hoffmann in this paper and regards the evidence in favour of the development of sympathetic nerve elements in connection with certain cranial nerve roots as unsatisfactory. He further points out that in the Teleosts definite sympathetic ganglia develope in connection with some of the cranial nerves. Why therefore should the sympathetic elements in the Selachian be localised in the brain wall?
Wiedersheim(20) gives an account of the sympathetic system in various martebrates and points out that in the Selachian for the first time is the sympathetic a clearly differentiated structure. In the cranial region apart from the ciliary ganglion there are no cranial ganglia in connection with the sympathetic chain and this points to a non-union of the dorsal and ventral roots of the cranial nerves. In the spinal region where the two roots join sympathetic ganglia are developed. The sympathetic chain in the trunk is not the regular structure seen in higher vertebrates since the ganglia are in some wanting, while in other cases two or three ganglia may fuse together. In the Teleosts the three ganglia which develope in connection with the trigeminal facial system include the cranial portion of the sympathetic chain. In the trunk the ganglia are arranged regularly and form two chains one at either side of the vertebral column. These chains ~~xxxxxxxx~~ leave the trunk by the caudal canal where they still remain separate.

Anderson(1) describes the sympathetic system in the Urodela.
In the Salamandra maculosa the sympathetic system may be divided into three parts a cervical,abdominal,and caudal.THe cervical part extends from the ganglion of the vagus to the subclavian artery. This segment of the system is very delicate in structure and has three small ganglia on its course.From the uppermost ganglion a branch passes to communicate with the first spinal nerve,~~and from~~ while a second branch passes upwards to the parasphenoids.From the second ganglion a branch passes to the second spinal nerve.The third ganglion lies practically in the subclavian plexus and sends a twig to the intestinal ramus of the vagus.
The subclavian plexus is built up of two ganglia lying in front of the subclavian artery and two which lie behind it.Outgrowths from the ganglia form a close network round the artery,the plexuses of the two sides are connected by means of commissural branches passing behind the aorta.This commissure is known as the Stannius Commissure. Connection is also established between the plexus and the third spinal nerve.
In the abdominal segment the sympathetic chain courses along the medial aspect of the posterior cardinal vein.The ganglia are arranged regularly but decrease in size as the caudal region is approached. The largest ganglia are the most anterior,they are enclosed in a distinct capsule and are closely in contact with the anterior cardinal vein.The various ganglia are connected to the corresponding spinal nerves by rami communicantes,as a general rule there is but one ramus to each spinal nerve but occasionally the single ramus divides ~~one~~ each branch passing to one ganglion.From each sympathetic chain there go two nerves,the anterior and posterior splanchnics. The anterior splanchnic arises in the posterior subclavian ganglion or sometimes from a ganglion which is developed close to the posterior subclavian ganglion.The branches of this nerve follow the coeliac artery to the stomach.The posterior splanchnic comes from the sympathetic chain about the level of the termination of the posterior cardinal vein.The sexual organs are provided by rami which pass from three or four sympathetic ganglia in the adjacent part of the chain. A very fine plexus is formed round the duct of Muller.A rich plexus is also formed round the iliac artery.
In the caudal region the sympathetic chain consists of two trunks which send branches for the supply of the renal veins and the cloaca and rectum.The sympathetic chain accompanies the aorta and lies with it inside the bony canal formed by the vertebral arches.It diminishes in size steadily although the arrangement of the ganglia and their connection with the spinal nerves is very uniform.

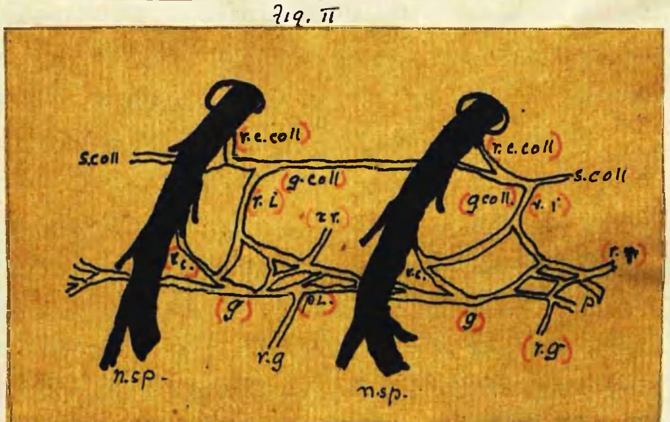
The next type examined, the Menobranchus lateralis, offers many points of contrast. In this type a cranial segment of the sympathetic system appears. From the ganglion of the facial nerve branches pass to the pharyngeal ramus of the vagus with which they unite. From this nerve about the middle of its course goes a branch which unites with the sympathetic chain. This nerve represents the cranial portion of the sympathetic chain.

The cervical portion of the sympathetic is represented by a ganglionated cord which is connected to the vagus by two delicate fibres given off from the vagal ganglion. Rami pass to the first three spinal nerves and to the intestinal branch of the vagus in the same way as in the Salamandra maculosa.

The subclavian plexus is practically similar to the plexus in the Salamandra.

The abdominal portion of the chain is connected to the spinal nerves by rami which show a different arrangement from that described in Salamandra. Two rami come off from each spinal nerve at different levels. The ramus which is given off some little distance from the point where the spinal nerve emerges from the spinal column corresponds to the rami described in the Salamandra and passes directly to the sympathetic chain. The other rami leave the spinal nerves nearer their origin and pass into the canal formed by the two roots of the transverse processes, where they accompany the vertebral collateral artery. The two parts of the sympathetic chain are united by rami (fig. 2). The branches from the main sympathetic are numerous and form rich plexuses.

Fig. II



(Andersson)

(g) - ganglion of the sympathetic chain

(g.coll) - ganglion of the collateral sympathetic chain s.coll.

n.sp. - spinal nerves

(pL) Loops of sympathetic passing to genitalia & kidneys or their arterial supply

(r.c.) Communicating rami from spinal nerves

(r.c.coll) - Communicating rami to collateral chain

(r.g.) Branch to sexual glands

(r.i) - Ramus intermedius

(r.r.) Branch to the kidneys.

From the left subclavian ganglion four branches pass of which the first forms an anastomosis with the sixth spinal nerve. The second is the anterior splanchnic nerve which follows the course of the coeliac artery to the stomach. The remaining two pass along the aorta and form a pair of ganglia about the level of the sixth vertebra. These ganglia are united by a commissural band of nerve fibres which send a branch to the anterior splanchnic nerve. From each ganglion a nerve is given off ,both unite at the level of the origin of the coeliac artery and form the splanchnic medius which terminates in the stomach. The sympathetic chain from about the level of the kidney on the left side divides into two branches a lateral which follows the posterior cardinal vein and a mesial which follows the aorta.The lateral nerve may be traced to the ganglion which receives the rami from the seventh spinal nerve.It divides into two branches which follow the anterior and middle splanchnic nerves to the stomach. The mesial band may be traced to the rami from the ninth spinal nerve. At the level of the twelfth spinal nerve it forms a ganglion and receives a branch from the lateral division of the chain.As a general rule both the rami communicantes and rami intermedii of the twelfth spinal nerve enter this ganglion also.A plexiform arrangement exists between the lateral and medial branches of the sympathetic chain of same side while connection is established between them and the sympathetic chain of the opposite side.The rami from the thirteenth spinal nerve are connected by means of a pléxiform network with both branches of the chain a ganglion marking the point of union. From this ganglion a branch passes down to the point of reunion of the lateral and mesial sympathetic branches.From the upper part of the ganglion which lies at the junction of those two branches the posterior splanchnic takes origin.

In the neighbourhood of the kidney the sympathetic chain sends numerous branches to the kidneys and sexual organs.

On the right side the anterior splanchnic nerve originates in the posterior subclavian ganglion and in the rami communicantes of the sixth spinal nerve.The arrangement of the lower part of the sympathetic chain shows some variaton from the arrangement on the left side, but only in minor details.

The iliac plexus is practically similar in extent and development to the iliac plexus in Salamandra.

Both sympathetic chain are united at four points in the abdominal cavity.These points lie at the eight,ninth,eleventh,and eighteenth vertebrae,but the anastomosis is best marked at the last point.

From the upper part of the caudal segment of the sympathetic chain the nerve passes downwards for the supply of the cloaca.Below this level the chain divides into two parts its point of division being marked by a ganglion.The ganglia of the two sides are connected by the junction of an outgrowth given off by each and which passes upwards to a ganglion lying at the level of the se~~x~~cond caudal vertebra.From this a nerve is sent down to the rectum,while another branch supplies the glandular tissue round the cloaca which is further supplied by two branches from the left caudal sympathetic.From the right side branches pass to the duct of Muller,and the cloaca.As the point of the tail is approached the chain gradually becomes smaller and smaller and eventually disappears.

The arrangement of the sympathetic in the different members of the Urodela class is by no means regular for in the Siredon pisciformis the cranial segment is wanting,while the abdominal and caudal segments differ somewhat from the descriptions already given.

From this account it is evident that in the Urodela there are two types of the sympathetic system,one of which is seen in the Salamandra and the other in the Menobranchus.The first type or that seen in the Salamandra is the simpler and is characterised by the absence of a cranial segment and of the rami intermedii or collateral sympathetic chain.In the Menobranchus type on the other hand both the cranial part and the collateral sympathetic chain are present. Intermediate types are found in other members of the class such as the Amblystoma,and Siredon.As a whole the Urodela show many irregularities in the development of the sympathetic chain,and no general description can be given which will fit into all the conditions found in this class.

It is interesting to note that in Birds and Crocodiles a portion of the sympathetic chain accompanies the vertebral artery in the neck. Whether this sympathetic band bears any genetic relationship to the collateral sympathetic in Urodela,or whether it is an analogous structure it is however impossible to say.

Gegenbaur(7)finds that the sympathetic chain in the Urodela is somewhat plexiform in structure but shows on the whole a more regular arrangement than that seen in the Teleosts.The work of Andersson is referred to very fully,but as an account of his work has already been given further reference is here needless.

In Teleosts the cranial segment of the sympathetic system is developed and extends to the trigeminal nerve and the ciliary ganglion.Sympathetic ganglia are also developed in connection with the facial,glosso-pharyngeal,vagus and hypoglossal.From the ganglion in connection with the last nerve as well as from the first ganglion of the trunk the splanchnic nerve takes origin.This nerve follows the arterial supply to the gut and supplies the viscera.

A very clear description is given by Ecker and Wiedersheim (4) of the sympathetic system in the next class of vertebrates namely the Amphibians.They have selected the frog as their type and the description given by them shows very clearly the advance in the structure of this segment of the nervous system.
In the frog there is a well fromed sympathetic system which extends from the ganglion Prooticum to the coccygeal region.The most anterior part of the chain lies intracranially and is represented by a nerve which connects the Prootic ganglion with the sympathetic ganglion formed in connection with the second spinal nerve.This nerve is joined at the jugular foramen which serves to unite the jugular ganglion to sympathetic ganglion already referredto.Since the first true sympathetic ganglion is formed in connection with the second spinal nerve the plan is adopted of referring to this ganglion as the second sympathetic.From the second down to the tenth spinal nerves the arrangement of the sympathetic ganglia is perfect,one ganglion being connected with each spinal nerve.As a general rule there is one ramus from each spinal nerve to the sympathetic ganglion in connection with it but in the lower nerves there may be two or more.
Since there is some evidence to show that the prootic and jugular ganglia both contain sympathetic elements the outgrowths which connect them ~~with the second sympathetic ganglion~~ may be regarded as rami communicantes.For purposes of description the sympathetic chain is divided into a cephalic,a cervico brachialis,a pars abdominalis, a pars sacro coccygea,and a caudal part.
The cephalic part consists of the nerve fibres which connect the prootic and jugular ganglia with the second sympathetic ganglion.
The cervico brachialis portion consists of the upper three sympathetic ganglia.The first or second sympathetic ganglion corresponds to the anterior subclavian ganglion described in Urodela by Anderson(1)
It is connected to the second spinal nerve by a very short ramus.
From its anterior part spring the two fibres connected with the cranial ganglia while from its posterior part fibres pass off to form the ansa Vieussens.The second sympathetic ganglion or more correctly the third,is connected by a very short ramus with the spinal nerve and corresponds to the posterior subclavian ganglion of Anderson(1).
The fourth sympathetic ganglion corresponds to the ganglion cardiacum basale described by Gaskell and Gadow(6).
In the pars abdominalis the sympathetic ganglia lie on the ventral surface of the vertebrae instead of at the side and therefore the rami are correspondingly longer and more prominent.The fifth ganglion which is the first of this segment,is with the possible exception of the eleventh the smallest of all the ganglia.The sixth ganglion is large and lies at the level at which the intestinalis communis artery

is given off.The seventh ganglion is the last of this segment and shows nothing peculiar in its structure.
The sacro coccygeal segment lies between the lumbo sacral plexus and the coogyx .The eighth ganglion lies at the most anterior part of the coccyx,while the ninth and tenth lie on its ventral aspect.The tenth ganglion is very long and has three or four rami entering it. The eleventh ganglion is sometimes wanting or it may be very small. It lies very close to the tenth with which it is often connected by a special ramus.
The caudal part consists of the thin nerve fibre which goes down from the eleventh ganglion along the aorta.Sometimes an anastomosis is formed between the fibres derived from the two chains while a ganglion marks the point of union.
The peripheral branches and ganglia of the sympathetic chain are very numerous.From the second and third ganglia branches pass to the occipital vertebral artery and to the subclavian.The splanchnics originate in the fourth to the seventh sympathetic ganglia and are distributed to the stomach,liver,pancreas,and spleen.A very rich plexus is formed in the region of the stomach the plexus solaris and from it branches pass to the gut as well as to the viscera including the upper part of the kidneys,ovaries,and oviduct.The urogenital plexus is derived from the seventh,eighth,ninth, and tenth ganglia.It supplies the kidneys,and sexual glands.
An examination of the cranial nerves shows that the vagus contains numerous sympathetic elements.According to Strong(18)many of the sympathetic nerve elements pass along the auricular branch of the vagus, while Ranvier(15)finds sympathetic cells on the vagal branches to lungs.The cardiac supply is derived from the vagus together with a branch from the fourth and probably also from the second and third sympathetic ganglia.It is probable that all the sympathetic elements in the vago sympathetic branch are not derived from the sympathetic ganglia but are also supplied from the sympathetic elements in the vagus
The work of Ecker and Wiedersheim supports the observations made by Steinach and Wiener(21)on the distribution of the nerve fibres in the trunk of the frog.The recent work of Langley and Orbeli(22)on the sympathetic and sacral autonomic system in the same animal further confirms their work.In many points Steinach and Wiener and Langley and Orbeli are in agreement but they come to different conclusions regarding the distribution of motor fibres in the posterior nerve roots,Steinach and Wiener describing this as a common occurrence in the frog,while Langley and Orbeli consider it exceptional

Hoffmann(12) also records observations on the Urodela. He selects the Salamander and Triton as types. In both a regularly arranged chain of sympathetic ganglia are seen in the trunk. For the most part this chain is cellular but here and there fibrous portions appear, these are the beginning of the development of the fibrous bands which are found connecting the different ganglia in higher vertebrates. At the cranial end the chain is found connected with the accessory vagal nerve, but indirectly and not directly as Anderson( ) describes. The vagus speedily unites with the glossopharyngeal and is thus brought into contact with the facial nerve by means of its ramus to glossopharyngeal. It is interesting to find the same arrangement in Urodela as in the ~~Salamander~~ Selachian as regards the formation of the ciliary ganglion. A special ramus connects the trigeminal and therefore the ophthalmic branch with the cilary ganglion to the facial nerve, and as has already been shown this nerve is linked up with the vagus which is in turn connected with the ganglion of the sympathetic chain. This complicated network terminating in connection with the trigeminal may therefore be regarded as the cranial sympathetic system

Wiedersheim(20) in his note on the sympathetic chain in Amphibians describes a well marked bilateral sympathetic chain in the trunk which is united with the cranial ganglia by nerve loops which terminate in the ciliary ganglion. The caudal portion of the chain is also well developed.

In the next class or Reptilia the close relationship between the sympathetic chain as it appears here and in the Amphibians is very evident. Anderson(1) who describes the collateral sympathetic in certain members of the Urodela points out that in the crocodile this collateral sympathetic is probably represented in the neck by a part of the sympathetic chain which divides from the main stem at the upper part of the neck and accompanies the vertebral artery.

Gegenbaur(7) agrees with this note made by Anderson and points out further that in the Sauropsida the cranial portion of the sympathetic system is as extensive as in mammals. As regards the caudal portion of the chain it is somewhat uncertain whether it is continued along the caudal canal, but any evidence which is forthcoming is in favour of its so doing.

Wiedersheim(20) also describes a double cervical sympathetic segment of which one part accompanies the vertebral artery while the other is the main sympathetic chain which lies at the side of the vertebral column.

Probably the best description of the sympathetic system in the next class of vertebrates, namely Birds is that given by Thebault(19) He describes the formation of the sympathetic system and its relation to the cranial nerves in a large series of birds. In some of them slight and comparatively unimportant variations are seen but a general description serves fairly accurately for all.

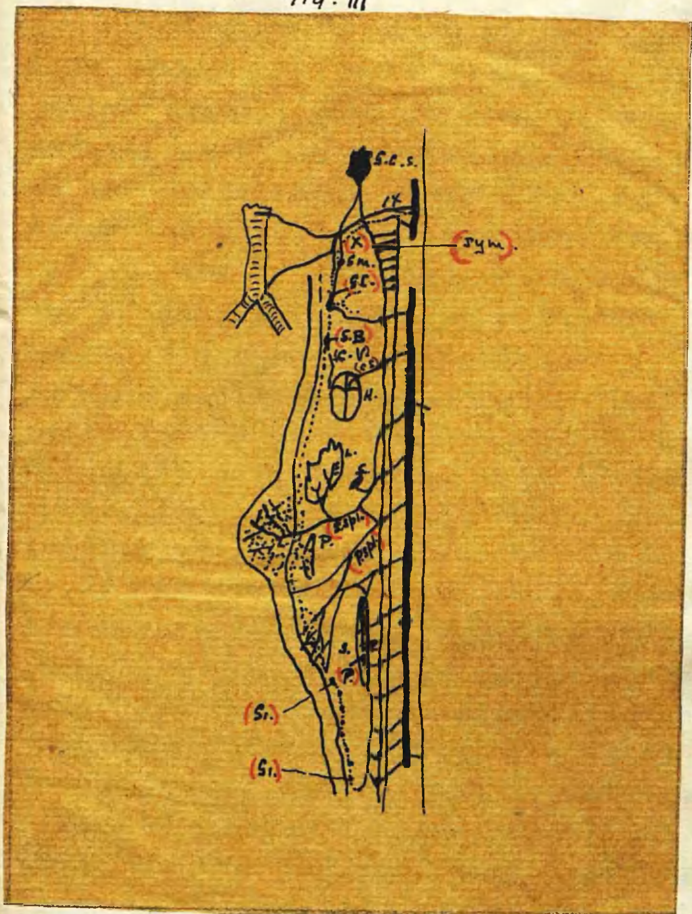
Taking the Linnet as a type the lower four cranial nerves are seen to be closely associated anatomically. The hypoglossal is however a very prominent nerve while the vagus is comparatively insignificant, this is a general rule with the singing birds. The last three cranial join to form the jugular ganglion. From this common trunk and from the glossopharyngeal a nerve goes which divides into two parts. One part passes up to the auditory region, while the other which is very long and thinpasses above the superior cervical ganglion and comes into contact with the glossopharyngeal where a ganglion is formed. From this ganglion fibres pass upwards to the facial muscles while those passing downwards constitute the glossopharyngeal trunk. The glossopharyngeal supplies the tongue and glottis. At the bifurcation of the carotids a small ganglion is seen on its trunk while at the level of the trachea the pharyngo-oesophageal nerve is given off.

The hypoglossal nerve which is very large lies at its origin near the sympathetic chain, it divides into numerous branches for the supply of the larynx, tongue, and syrinx. The pneumogastric separates off from the common trunk and accompanies the jugular vein along the neck. At the lower part of the neck it forms the ganglion of Couvreur from which fine nerve twigs pass to the thyroid gland. A little below this level another ganglion is formed from which the recurrent, and cadiac nerves. The ganglion receives a number of nerve fibres from the sympathetic which accompany the vagal branches to the heart. Below the level of the heart the vagus supplies the oesophagus, stomach and part of the gut.

The sympathetic chain has at its upper end a large fusiform ganglion which is connected with the cranial nerves and sends off branches which ramify round the carotids. From this point the sympathetic chain sends off a branch which dips into the transverse canal ~~of the transverse process~~ where it accompanies the vertebral artery. From the sympathetic chain fibres pass out to supply the different viscera. Many of the viscera are like the heart supplied from both the vagus and sympathetic, but the liver, kidneys, spleen, and sexual glands are all supplied from the sympathetic chain only. (fig. 3.4).

It is interesting to note that Anderson(1) and Gegenbaur(7) both regard that portion of the sympathetic which accompanies the vertebral artery as the homologue of the collateral sympathetic chain seen in the Urodela.

Fig. III



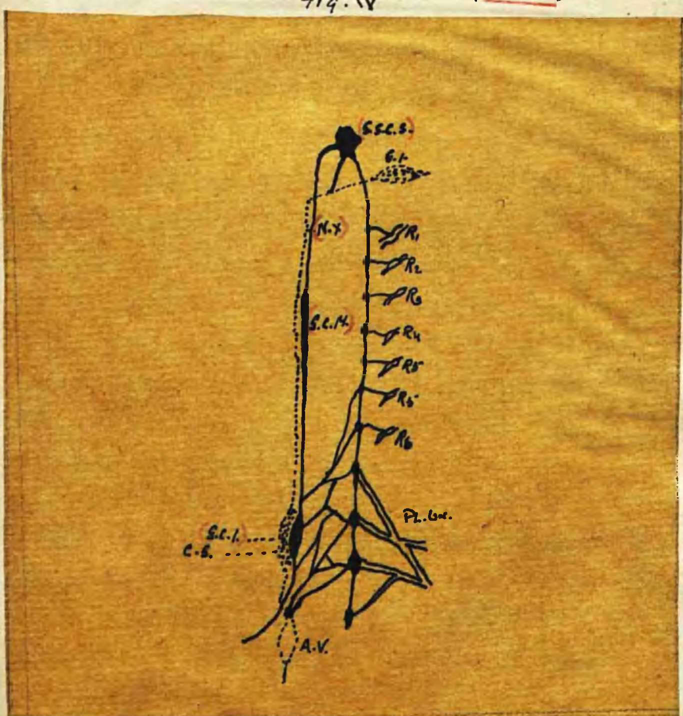
(Thebault)

Fig. III

S.C.S. Superior cervical ganglion
IX . glossopharyngeal.
(X) – Vagus. (dotted line)
S – Spleen
L . Liver.
H . Heart
S.C . Suprarenal.
P — Pancreas.
S m — middle cervical sympathetic ganglion

(S. Spl) – Splanchnic nerve
(C. V) – Cardiac vagal branch.
(C. S) Sympathetic cardiac branch
(sym) — Sympathetic chain lying in the transverse bony canal.
(P. spl) — Lesser Splanchnic nerve
(P) — Plexus round suprarenal
(S1) – Intestinal ganglia
(S.C) – Lower ganglion of Vagus G. Convexur.
(S.B) — Small ganglion on vagus.

Fig. IV



(Thebault)

Fig. IV

(S. S. C. S.) Superior cervical ganglion
(N X) — Vagus.
G 1 – Jugular ganglion of Vagus.
(G C M) — Middle cervical ganglion
(G. C. I) — Inferior cervical ganglion
C. G – Convexur ganglion or lower cervical ganglion of vagus.
A. V. – Ansa Vieussens –
PL. br – Brachial plexus.
R¹ – R⁷ – nerve roots.

His jr.(9) in discussing the morphology of the sympathetic system points out that in certain cranial ganglia in teleosts and selachians two varieties of cells are found. In one variety the cells are large and bipolar, while in the other they are small and unipolar. The small cells are sympathetic cells which are in this type of animal enclosed in the cranial ganglia. This view is further supported by the fact that the fibres which connect the vagus, glossopharyngeal, and trigeminal to the sympathetic chain all come off from the ganglia at the points where the small cells are located. In the early stages of development some of the sympathetic cells accompany the fibres. Further in the spinal ganglia which are originally composed of bipolar and unipolar cells only bipolar cells remain after the development of the sympathetic ganglia. The examination of the cranial ganglia in frogs also leads to the same conclusion that some of the sympathetic cells are permanently enclosed in some of them. His points out how these observations made by him bear out the early work of Muller(1). Muller(1) records observations made on the amphioxus and myxine. In both those types the sympathetic as an independent system is absent but numerous sympathetic cells lie enclosed in the spinal and cranial ganglia. In animals a little higher in the scale the sympathetic chain is partially developed, that is the sympathetic cells already developed in the amphioxus and myxine begin to travel to the periphery.

In the higher vertebrates sympathetic cells are found in the ciliary, otic, and spheno-palatine ganglia in adult life but not in the ganglia of either the vagus or glossopharyngeal, although the ganglia of both those nerves contain many sympathetic cells in the early stages of development. The sympathetic cells from those ganglia migrate during development and become incorporated with the cells from the spinal cord which form the superior cervical ganglia. The vagal, glossopharyngeal, and spinal ganglia in the mammal are therefore alike as they both show an absence of unipolar or sympathetic elements after the development of the sympathetic chain. In the other ganglia the condition found in the lower types is represented as the migration is incomplete sympathetic cells remaining permanently in the ganglia. In birds an interesting and intermediate stage in development is seen. In the upper part of the neck two superior cervical ganglia are found, One of these is formed from the spinal ganglia along with the other parts of the sympathetic chain, while the other is developed from the sympathetic cells which migrate from the vagal and glossopharyngeal ganglia. As in the mammal the sympathetic cells migrate from the ganglia of those nerves but owing probably to the developmental peculiarities in the chick they fail to unite with the secondary sympathetic ganglia and form an independent ganglion, which is however united to the superior cervical ganglion of the secondary sympathetic. In later work on the sympathetic supply of the abdominal region in the chick His(10) describes the connections between the various pre-vertebral ganglia and the sympathetic chain. Branches pass from the thirteenth to the twenty-second segment to the plexus lying in front of the aorta, which in turn gives off the ganglion and mesenteric nerve. From the aortic plexus nerve elements are also derived~~xxx~~ which when joined by the vagal branch from the right side form the ~~xxxxxx~~ coeliac plexus and nerves. The intestinal nerve is connected to the twenty-sixth, twenty-seventh, and twenty-eighth segmental portions of the sympathetic chain, in many cases the union between the two structures is so close that they seem to fuse. The complete developmental condition which is represented at the tenth day of development is shown in the accompanying diagram (fig. 5). Fig. V

(His)

Syg - Sympathetic Chain
R.V. Right Vagus
Ao - Aorta
Oe - Oesophagus
13-33 - Spinal nerve roots
1 - Aortic plexus
2 - Coeliac plexus
3 - mesenteric ganglion
4 - Remaks intestinal nerve
5. 6. - Portions of this nerve
7 Pelvic Plexus
M - stomach
D'. D''. D''' - Intestine
Py. Pylorus.
Doe - Omphalo mesenteric duct
R - Rectum
Sug. Sinus urogenitalis
Vm. Sm. — Gastric vagal branches
S.m. vagal ganglia.
Ans. And. Umbilical arteries

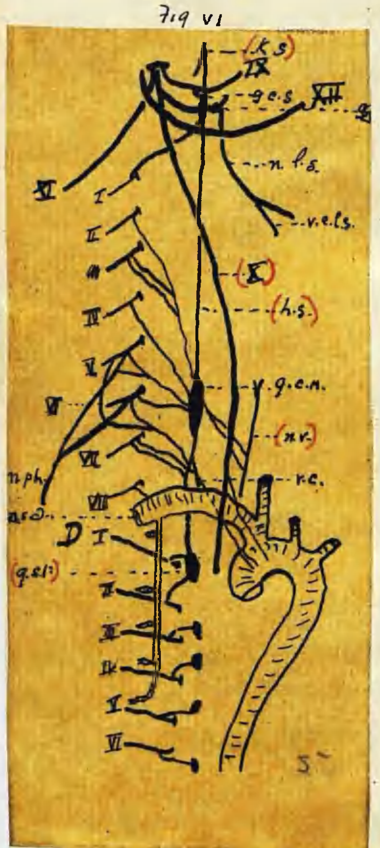
Gegenbaur(7)points out that in the highest class of vertebrates the Mammalia the origin of the splanchnic nerves is as Birds relagated the posterior part of the trunk.He further suggests that the sympathetic nerve which accompanies the vertebral artery is a homologue of the collateral sympathetic described by Anderson( ) in the Urodela and recognised in the Reptilia and in Birds.

Van den Broek(2)describes the formation of the sympathetic system in a long series of mammals.This description which is extremely detailed can only be summarised here,and the more important points of contrast in the different mammals referred to.

In the cervical region the sympathetic chain in the mammal shows three ganglia a superior,middle,and lower.The lower or inferior ganglion is frequently fused with one or more of the first thoracic ganglia and forms the prominent ganglion stellatum.This arrangement is the typical one but several departures from it are found in some of the mammals.In the Echidna the superior and middle ganglia fuse, while in the Cuscus orientalis,and Lepus cuniculus the middle and inferior ganglia fuse.In other cases the three ganglia are subdivided and form a row of tiny ganglia,this however is uncommon.

The superior cervical ganglion lies immediately under the base of the skull,the only exception to this rule being seen in the Echidna where it lies far down the neck(figs. 6·7).

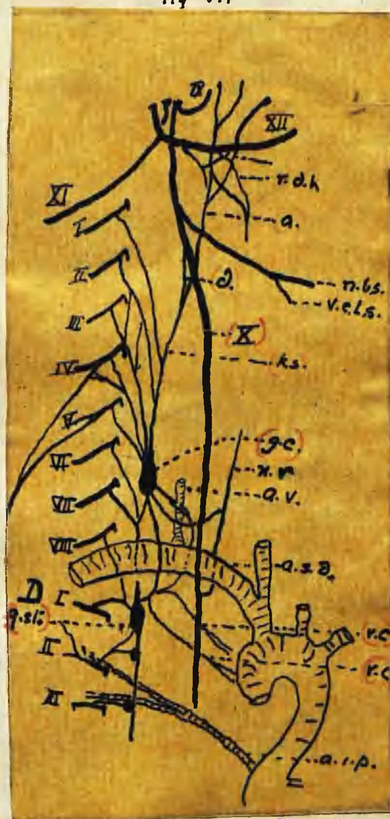
Fig VI



(Broek)

G.c.s. Superior Cervical ganglion
G.c.m. Middle cervical ganglion
(G.st.) Ganglion stellatum
IX - Glossopharyngeal
(X) - Vagus.
XI - Spinal accessory
XII - Hypoglossal
I-VIII - Cervical nerves.
I-VI - Thoracic nerves.
(k.s.) Cranial part of sympathetic
(h.s). Cervical part of Sympathetic
n.ph. Phrenic nerve.
(n.r.) Recurrent nerve.
r.c. Cardiac nerve.
v.e.l.s. External ramus of Supr. laryngeal nerve.
n.l.s. Superior laryngeal
g. ganglionic swelling on the Supr. laryngeal.
a.s.d. Right subclavian

Fig VII



(Broek)

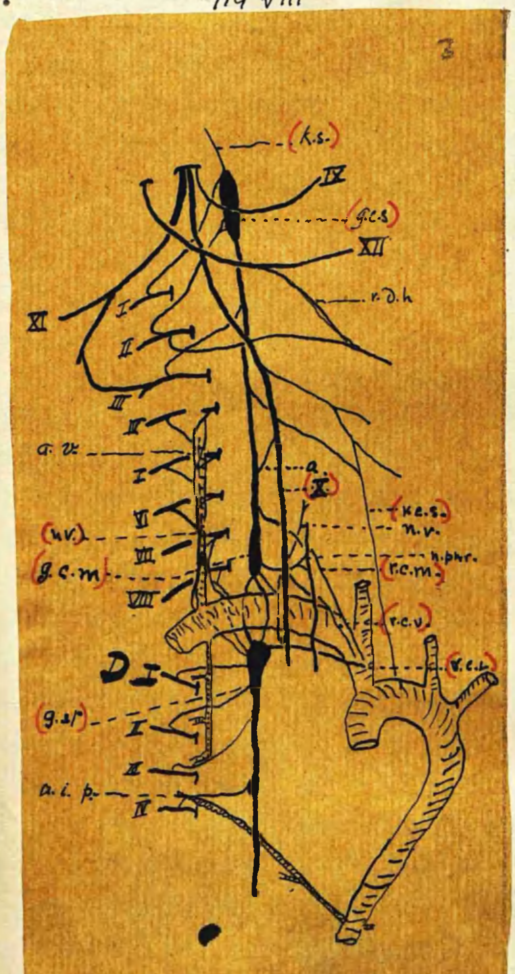
IX - Glossopharyngeal.
(X) Vagus
XI. Spinal accessory
XII - Hypoglossal
I-VIII. Cervical nerves
I-III - Thoracic nerves
(g.c.) Superior & middle Cervical Ganglia
n.r. Recurrent.
r.d.h. - Descendens hypoglossi
(a) cranial part of Sympathetic
(d.) Link between vagus and Sympathetic
(g.st. G) Stellatum
a.s.d. - Right Subclavian
(r.c.) Cardiac rami
a.i.p. First intercostal artery
(k.s) Cranial part of Sympathetic

It is important to note that in no case is this ganglion fused with vagal ganglion, and in only two cases does the vagus trunk enter or become joined to the superior cervical ganglion. As a general rule the shape of the ganglion is like a spindle* but there is a certain amount of variation to this rule

The connections between this ganglion and the cranial nerves is also subject to variation. In the Didelphys, Coelogenys, Lepus cuniculus, and Lemur no connection seems to exist at all (fig. 8). In the Cuscus orientalis, Phascolarctos cinereus, Mus rattus, and Canis familiaris the glosso-pharyngeal alone is connected with the ganglion, while in the Trichosurus vulpecula, Dasypus novemcinctus, Ursus and Mustela the vagal nerve is connected with the ganglion. In Felis leo, Cercopithecus, Cynocephalus, Gorilla, Orang, and in Man the three nerves, namely the glossopharyngeal, vagus, and hypoglossal, are all connected with the first cervical ganglion (fig. 9)

It is evident therefore that the connections between the superior cervical ganglion and the cranial nerves become gradually developed in the various orders of the mammalia until the arrangement found in man appears. There is however no regular progress of this connection through the various orders of mammalia the process of evolution being very irregular.

Fig VIII



(K.S.) Cranial part of sympathetic: I-VIII cervical nerves.
(S.c.s)(S.c.m)(S.s1.) upper, middle, and lower cervical ganglia
(R.c.s)(R.c.m)(R.c.l). upper, middle, and lower cardiac rami
(R.c.v.) Vagal cardiac ramus; n.phr. Phrenic nerve.
(X) vagus. XI Spinal accessory, XII Hypoglossal.

a - Link from Vagus to Sympathetic
r.D.h. Descendens hypoglossi
DI-IV - Thoracic nerves.
a.i.p. first inter costal artery
(n v.) Vertebral nerve.

The number of cervical nerves which communicate by their rami communicantes with the superior cervical ganglion varies to a great extent not only in the different orders of the mammalia but also in the same animal.

Fig. IX

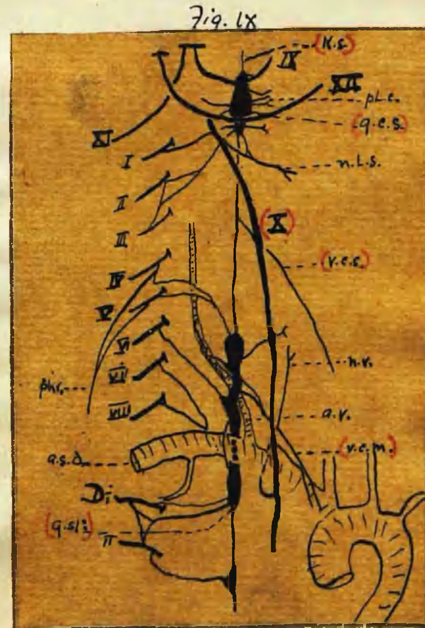


Fig.
(K.S.) Cranial Sympathetic
IX-XII Cranial nerves
I-VIII Cervical nerves
DI-II Thoracic nerves
(g.c.s) Supr. Cerv. ganglion
(g.s1.) Stellate Ganglion
phr. Phrenic
(r.c.s) Supr. Cardiac ramus
a.s.d. Right subclavian
n.L.s. Supr. Laryngeal.
n.r. ~~Lateral nerve~~ Recurrent nerve.
(r.c.m.) Middle Cardiac Ramus.

the nerve trunks a branch passes to it from the vagus in some mammals while in others the recurrent nerve supplies the communicating twig. In other cases especially in the rodentia a branch joins the phrenic and this ganglion.It is interesting to note that in some of the mammals a branch passes from the middle ganglion to the heart.This branch may course alone or it may be joined by a twig from either the vagus or the ganglion stellatum.The connection between the middle and inferior cervical ganglia is in the majority of mammals represented by a double cord which passes ventral and dorsal to the subclavian artery and forms the Ansa Vieussens.In the Trichosurus,Cuscus,and Ornithorhynchus the cord is single and lies behind or posterior to the subclavian artery,but these are the only mammals which show any variation from the arrangement as found in Man.

The ganglion stellatum is composed of the inferior cervical ganglion and one or more of the thoracic ganglia.It lies about the level of tubercle of the first rib and extends cranially to the dorsal surface of the subclavian artery,caudally it extends to the first costal interspace.A delicate furrow divides the ganglion into an upper part which is connected to the lower cervical nerves,and a lower part which is connected to the thoracic nerves.The vertebral nerve which is built up of rami from the upper five or six cervical nerves emerges from the foramen of the transverse process of the sixth cervical vertebra and joins the ganglion stellatum at its upper part.The eighth and sometimes the seventh cervical nerves send special branches to the ganglion This arrangement is however subject to great variation.

The number of thoracic nerves which send rami to the lower part of the stellate ganglion varies but as a general rule rami are received from the upper three.

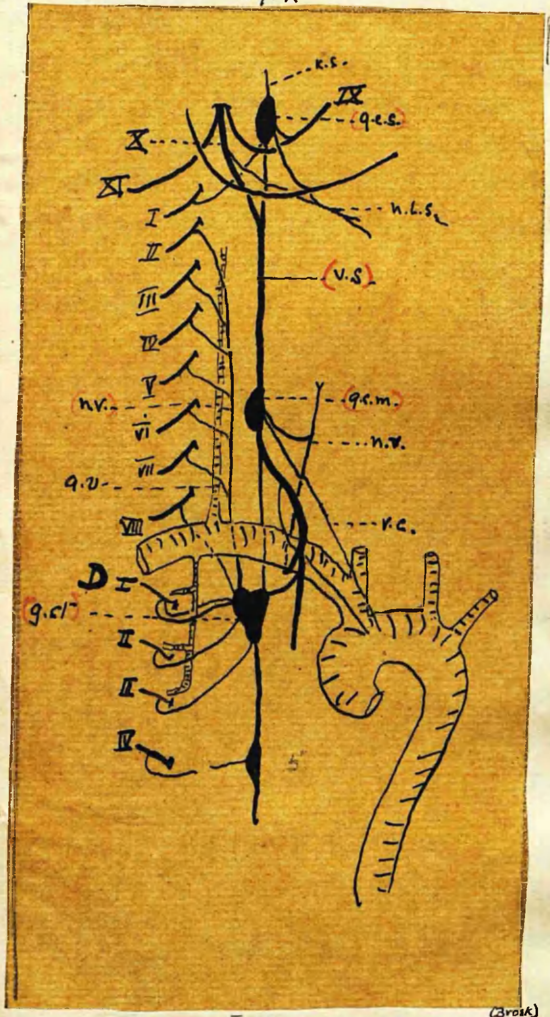
From the middle of the ganglion a well developed branch passes to the heart.The caudal pole is directly continuous with the thoracic portion of the sympathetic chain.

From a consideration of the embryological conditions described by His sen. and jr.(9,10),and Onodi(24) in the mammal and bird the following suggestions are made.In the bird the primary sympathetic chain is either wholly or partly absorbed in the cervical region by the vagus.In the mammal the sympathetic chain sends a proportion of its cells to the vagus but is not entirely absorbed so that there is no need of a secondary chain as in the bird.The vertebral nerve in the mammal may be the homologue of the secondary sympathetic chain in the bird since it serves to link the cervical sympathetic ganglia and the spinal nerves.In the bird a part of the sympathetic chain in its primary form survives in the upper part of the neck and this is connected later with the secondary chain and the spinal nerves.

As a general rule the upper three or four cervical nerves send branches to the ganglion, but where as in the Echidna the superior and middle cervical ganglia fuse rami from the upper five nerves pass to the compound ganglion.

Below the superior ganglion the sympathetic chain is in many cases joined to the cervical portion of the vagus a vago-sympathetic cord being formed. This is seen in the Dasypus novemcinctus, Ursus, Canis familiaris, and Bos taurus(fig. 10). The extent and intimacy of this

Fig. X



(Brosk)
K.S. Cranial sympathetic. IX – XII Cranial nerves.
I – VIII – Cervical nerves – D I – IV Thoracic nerves
(g.c.s.) (g.c.m) (g.sl.) Superior, middle, and stellate ganglia
R.C. Cardiac ramus. n.R. Recurrent nerve. (V.S.) vago sympathetic. n.L.S. Supr. Laryngeal nerve. (n.V.) Vertebral nerve

union varies in the different animals but as ageneral rule it does not exten below the middle cervical ganglion.

The middle cervical ganglion is extemely variable both as regards its position and its formation, but in animals not showing the union of the vagus and sympathetic already described it usually lies just above the subclavian. Where the vagus and sympathetic unite its position is so variable that no rule can be given.

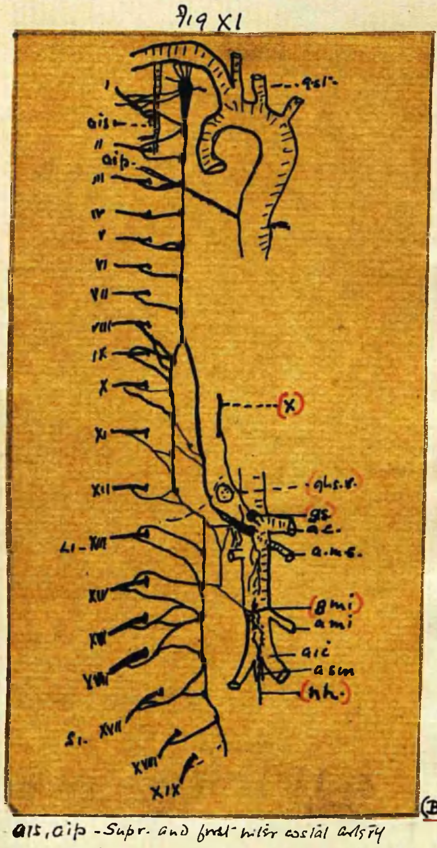
The connections which exist between this ganglion and the cervical nerves may be classified under three divisions as they appear in the Echidna, Ornithorhynchus, and in Man. In the Echidna the middle ganglion and the superior fuse so that the middle ganglion is brought into contact with the upper five cervical nerves(fig.). In the Ornithorhynchus the middle ganglion is connected with the second to the sixth cervical nerves. In Man the ganglion is connected with either the fourth and fifth or the fifth and sixth cervical nerves or there may be no communication at all between the cervical nerves and this ganglion.

In the other animals examined there is no connection at all between the middle cervical ganglion and the cervical nerves except in those cases where the middle and inferior ganglia have fused.

As regards the connections between the middle ganglion and some of

The thoracic,abdominal,and pelvic portions of the sympathetic chain extend from the ganglion stellatum to the sacral region,where it either ends in the ganglion impar or is continued as a slender cord into the tail.In the thorax it lies along the side of the tubercles of the ribs,in the abdomen it rests on the points of origin of the psoas muscle,while in the pelvis it approaches more nearly the middle line.Along its course it gives off branches to the segmental arteries,and at certain points to the viscera,while rami connect it with the various spinal nerves.In the thoracic region the ganglia are usually angular,while in the abdominal region they are ovoid. At the beginning of the lumbar portion of the sympathetic chain there is often a specially large ganglion which is connected by rami with several spinal nerves.Just below the region of the diaphragm the sympathetic chain shows several exceptionally large ganglia but whether these are developed in connection with the intestinal nerves or whether they are ontogenetically related to the diaphragm is uncertain.At the lower part of the thoracic portion of the sympathetic chain the splanchnic branches are given off,and the appearance presented is very similar to that seen in the neck where the chain divides to form the Ansa Vieussens(fig.11).

Fig XI



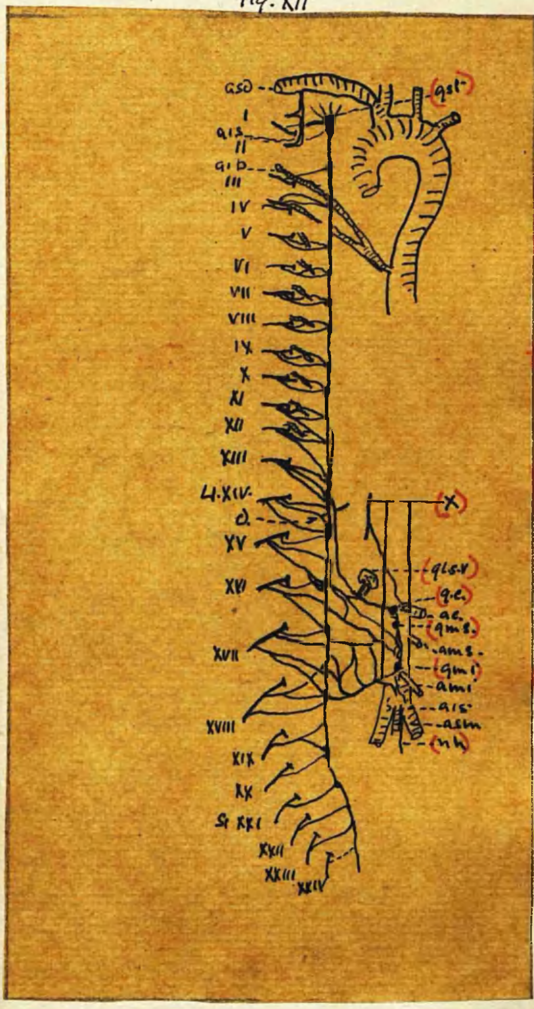
(Brock)

ais, aip - Supr. and first inter costal artery
I - XII - Dorsal nerves - L1 XIII - XVI - Lumbar nerves
S1 - XVII - XIX Sacral nerves - (X) - vagus -
(gmi) Inferior mesenteric ganglion - (h.n.) Hypogastric nerve
(S.S.) Solar ganglion - (gl. s. r.) S ganglion
a.m.i. Inferior mesenteric artery - a.c. Coeliac artery

As regards the arrangement of the rami communicantes it is found that they do not as a rule correspond with the description given by Gaskell( )for the dog.In his account of the rami communicantes he describes a double set between the second thoracic and second lumbar .Now in the present investigation it is found that single rami are interspersed with the double in the Erinaceus europaeus,Tatusia novemcincta,andFelis leo neonatus,while in the Phoca vitulina many of the single rami divide after leaving the spinal nerves and after enclosing a small piece of muscular tissue join and reach the sympathetic chain as a single band.In the Dama vulgaris this arrangement is slightly modified as the rami although single on leaving the spinal nerves branch and enter the sympathetic ganglia by two sets of fibres.As a general rule the connections between the sympathetic ganglia and the spinal nerves are very regular in the upper thoracic and sacral regions but in the intermediate region the connections are irregular, rami from the spinal nerves of a special region passing downwards to join sympathetic ganglia at a lower level.

The branches of the sympathetic chain are not arranged in the same way in all mammals. In many types including Man the branches to the solar plexus are given off from the thoracic region as well as from the sympathetic chain below the diaphragm (fig. 12). In some types on the other hand the branches from the sympathetic chain to the solar plexus come off wholly below the level of the diaphragm (fig. 13).

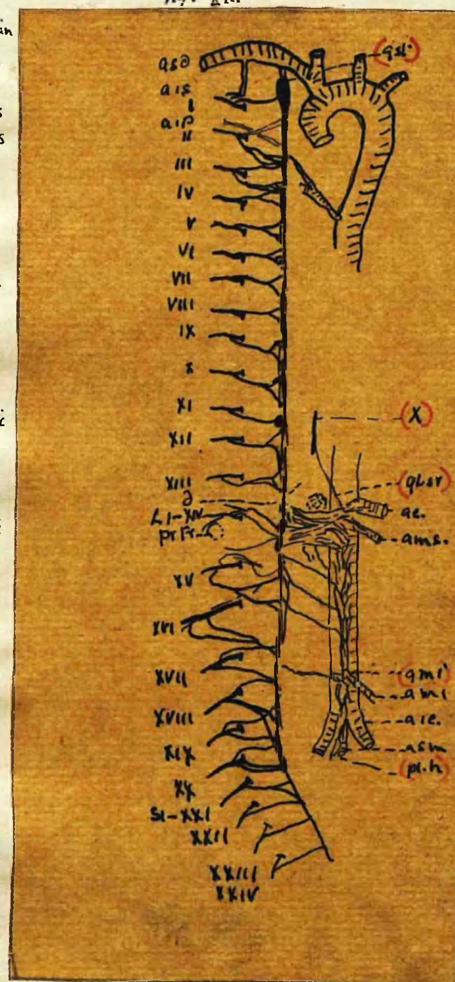
Fig. XII



(Brosk)

a.s.d. Right subclavian
g.st. Stellate ganglion
I-XIII Dorsal nerves
XIV-XX lumbal nerves
XXI-XXIV Sacral nerves
(X) – Vagus
(g.st.) Stellate Gang.
(gl.s.v.) Ganglion
(g.c.) Coeliac ganglion
a.c. Coeliac artery
(g.m.s.) Supr. mesenteric G.
a.m.s. Supr. mesenteric artery
(g.m.i.) Infr. mesenteric Ganglion
a.m.i. Infr. mesenteric artery
a.i.s. Iliac artery
a.s.m. medial sacral artery
(h.h.) Hypogastric Nerve.

Fig. XIII



(Brosk)

Up to the present time no exact information is forthcoming as to the ~~exact~~ highest level from which those sympathetic branches to the solar plexus comes off, but the lower limits are determined in many cases and a table, which is given on the next page, shows the relative position of this point in different mammals.

Animal	Thoracic	Lumbar	Caudal limit of Splanchnics.
Echidna aculeata	15	4 = 19	18(17.18.).
Ornithorhynchus	17	2 =19	18(18.19.)
Didelphys marsupialis	12	6 = 18	16
Halmaturus speciosus	13	6 = 19	18(17.18.)
Erinacaeus europaeus	15	8 = 23	20(20.21.)
Tatusia novemcincta	9	5 = 14	14.
Coelogenys paca	13	7 = 20	16(15.16.)
Mus rattus	13	5 = 18	16(16.17.)
Lepus cuniculus	12	8 = 20	17(18.
Phoca vitulina	15	5 = 20	18
Felis leo	13	7 = 20	18
Canis familiaris	14	6 = 20	19(18.19.)
Bos taurus	13	7 = 20	19(19.20.)
Dama vulgaris	13	7 = 20	17
Lemur macaco	12	5 = 17	14?
Nycticebus javanicus	15	8 = 23	20(19.20.)
Cebus hypoleucus	14	5 = 19	17
Hapale jacchus	13	6 = 19	16(15.16.)
Cercopithecus cynomolgus	12	6 = 18	17
Cynocephalus hamadryas	13	6 = 19	17(16.17.)
Hylobates lar	13	5 = 18	16
Orang	12	4 = 16	14
Homo	12	5 = 17	15

From this table it is seen where the number of the ganglia of the trunk are fewer the lower limits of the splanchnic roots are higher. It is further evident that no rule exists in the vertebrates for the lowest point ~~xxxxxxxx~~ from which the splanchnic nerves originate In three cases a ganglion is found on the course of the splanchnic lying just below the diaphragm.

In the abdominal cavity the splanchnic breaks up into several branches Some of them pass to the suprarenals,they are often provided with a small ganglion,while a few pass to the kidneys.The majority of the fibres however join the solar ganglion or plexus.This plexus usually lies at the origins of the coeliac and mesenteric ganglia,in some cases it lies below this level.This plexus is augmented by a branch from the vagus.In most cases this vagal branch comes off below the diaphragm but in the Erinaceus and Hylobates it leaves the vagus

above the diaphragm which it penetrates through a special opening
The aortic plexus is connected with the solar plexus and also with the inferior mesenteric plexus while it is augmented by branches from the lumbar chain.The hypogastric plexus lies at a lower level and gives off a branch the hypogastric which supplies the bladder and upper genital tract

As a result of this extensive investigation of the structure of the sympathetic system in different mammals v.d.Broek draws the following conclusions.

(1).The sympathetic chain as it appears in the various classes of vertebrates is a homologous structure.

(2).The rami communicantes are also homologous if they develope in the same way.This question can not be settled by an investigatinn of the conditions in the adult as apparently double rami may be developmentally single but split up by an artery or band of muscle.

(3).Although the splanchnics are generally described as an outgrowth from the sympathetic chain the developmental conditions of the various arteries and of the diaphragm are not clearly enough understood to allow of the mode of development of the splanchnics being considered as settled.

In Man the general arrangement of the sympathetic chain is as follows. The superior cervical ganglion is the uppermost of the ganglia of the chain and lies opposite the second and third cervical vertebrae.It gives off a superior branch which divides into two and forms the carotid and cavernous plexuses.The carotid plexus communicates with the Gasserian ganglion,sixth nerve,spheno-palatine ganglion,and Jacobsons nerve.The cavernous plexus communicates with the third, fourth,ophthalmic division of the fifth, and sixth ~~and~~ nerves,as well as with the ophthalmic ganglion.The inferior branch of the superior ganglion connects it with the middle cervical ganglion,while the external branches pass to some of the cranial nerves and the four upper spinal nerves.Three branches pass from the inner side of the ganglion the pharyngeal,laryngeal,and superior cardiac.Anterior branches also are developed which ramify along the carotid artery.The middle cervical ganglion is the smallest of the three cervical ganglia and sends branches to the superior and inferior ganglia as well as to the thyroid and the heart.The inferior ganglion is connected to the middle cervical and first thoracic ganglia while it gives off the inferior cardiac branch.Both the middle and inferior ganglia are connected to the spinal nerves from the fifth to the eighth.

In the thoracic portion of the sympathetic chain consists of a series of ganglia which generally correspond with the number of the vertebrae.

The external branches from each ganglion, usually two in number, communicate with each of the dorsal spinal nerves. The internal branches from the upper five or six are usually very small and pass to the aorta, to the bodies of the vertebrae and their ligaments. Some branches from the third and fourth enter the posterior pulmonary plexus. The internal branches of the lower six or seven are larger and unite to form the great, lesser, and least or renal splanchnic nerves.

In the lumbar portion of the cord the ganglia are of small size and lie near the median line. The external branches pass to the lumbar spinal nerves, while the internal branches pass into the aortic and hypogastric plexuses according to their level.

The pelvic portion of the chain lies in front of the sacrum, while both chains unite at the coccyx in the ganglion impar. The internal branches communicate with those of the opposite side and either join the pelvic plexus or form a plexus which accompanies the middle sacral artery.

Four great plexuses are formed by the sympathetic they are the cardiac, solar, hypogastric, and pelvic. From them are derived the branches which supply the different viscera (Grey 8).

It is evident from this consideration of the formation of the sympathetic system in the different orders of vertebrates that a certain relationship exists between the various types. In some particulars however this relationship is somewhat difficult to follow out.

In the Urodela Andersson(1) shows that a collateral sympathetic chain developes which is connected by rami with the true sympathetic chain, while it has on its course numerous ganglionic swellings. Andersson suggests that the sympathetic supply which accompanies the vertebral artery in the neck of Birds and Reptiles is probably a homologue of the collateral sympathetic chain in Urodela.

Van Broek(23) who worked on the sympathetic system in Mammals also suggests that the sympathetic branch which accompanies the vertebral artery may be homologous with the secondary sympathetic chain in Birds.

It is a matter of great difficulty to establish a homology between structures which present so many points of contrast as the collateral sympathetic chain in Urodela, the so-called secondary sympathetic chain in Birds, and the sympathetic branch accompanying the vertebral artery in Reptiles and Mammals, but from the point of view of development such a homology seems at least probable.

From my own observations on the development of the sympathetic chain in the Bird, recorded in chapters three and four, the conclusion is arrived at that the chain of sympathetic ganglia lying close to the anterior roots, and described by His jr. and other workers as the secondary sympathetic chain, is not in reality an independent structure but a stage in a more or less continuous migration of sympathetic cells. The cells which migrate from the spinal cord at the earliest stages of development form ganglionic enlargements at either side of the notochord, that is they occupy the position of the sympathetic chain in Reptiles and Mammals, and of the true sympathetic chain in the Urodela where a collateral chain also exists. This chain is excellently develop ed in the Bird at the fourth day of incubation but already it is evident that it forms but a station on the course of a peripheral migration of the sympathetic cells. The appearance presented being that of a band of sympathetic cells lying at either side of the notochord connected with the spinal roots by cell chains while chains of cells stream out from ~~them~~ it to the periphery.

This chain evidently, therefore, corresponds with the ordinary sympathetic chain in other vertebrates. As has just been pointed out it is not isolated from the spinal nerve roots but the cells gradually diminish in number owing to the continual drain for the supply of peripheral parts and also because the cells from the spinal nerve roots no longer migrate in large numbers. At the sixth day the sympathetic cells in the region of the notochord begin to disappear while well marked clusters of sympathetic cells appear in the close vicinity of the point of union of the spinal nerve roots. It seems highly probable that the cells from the thoracic portion of the sympathetic chain are drawn into this secondary chain since they do not migrate peripherally early in development as do those of the abdominal region. The only parts of the primary, or what I am attempting to show is the true sympathetic chain, which remain are the superior cervical ganglion and the pelvic portions, and both of these are connected with the secondary chain of sympathetic ganglia by rami. There are several points directly in favour of this theory which deserve mention.

First, in all other vertebrates the sympathetic chain is the first segment of the system to be developed, and it thus forms a basis from which the peripheral portions of the system originate.

In the Bird this is the case for the sympathetic chain which developes at the fourth day, for from it peripheral ganglia and plexuses originate. It therefore corresponds both in position and function with the sympathetic chain in other vertebrates.

Second, if the sympathetic chain in the region of the notochord remained intact there would be no difficulty in recognising in the chain of ganglia lying close to the spinal nerve roots a structure which corresponded to the collateral chain of the Urodela. The difficulty however arises from the fact that the primary chain disappears in the thoracic and abdominal regions. In Fish the same condition is met with for numerous ganglia of the sympathetic chain have been shown by Hoffmann (11.12) to vanish completely as development proceeds. In the Bird therefore there seems to be a reversion to the condition seen in Fish and Urodela with of course certain modifications. The true sympathetic chain in the Bird seems therefore to be represented by the superior cervical ganglion and the pelvic portion while the well marked ganglionated cord found inside the bony transverse canal of the adult is the collateral chain.

Third, the connections which are seen in the adult to exist between this chain and the splanchnic and other sympathetic nerves do not in any way prejudice the view that it is a collateral chain, since in the early stages of development both sympathetic chains were connected by cell chains, any connections or branches of the true chain being thus transmitted to the collateral.

Fourth,this explanation of the formation of the sympathetic chain based on developmental observations serves to bring the Bird into line with ~~the~~ other classes of vertebrates.If on the other hand the view be taken that the sympathetic chain lying in the bony canal in the vertebral column is the true sympathetic chain a condition exists in the Bird which stands quite alone,and for which no homology can be established.It seems at least extremely unlikely that such a condition does exist.

As regards the possibility of a homologue existing between the secondary sympathetic or collateral sympathetic chain in the Bird and the sympathetic supply accompanying the vertebral artery in Reptiles and Mammals The observations made by Van Broek(23) and Andersson(1)certainly suggest that such a homologue does exist,but more work on the process of development in the Reptile and Mammal is required before certain conclusions can be drawn.

I therefore content myself with pointing out the extreme probability of a parallel condition in the development of the Urodela and Bird as regards the formation of a collateral sympathetic chain and the partial disappearance of the true sympathetic chain.

If later work should demonstrate the homology of the sympathetic supply accompanying the vertebral artery in Reptiles and Mammals with the collateral sympathetic chain of either the Urodela or Bird then the riddle of the formation of the sympathetic chain in vertebrates will be solved.

From this consideration of the formation of the sympathetic system in the various orders of vertebrates the following facts may be classified.

1.In the Cylostomata the sympathetic system although present is in a very primitive form.The spinal nerves are in this class also very primiti e since there is no union between the anterior and posterior nerve roots.

2.In the next order or in Fish different degrees of development of the sympathetic system are represented.In the Selachians the Selachians the sympathetic chain is represented by an irregůlar series of ganglia in the trunk,while the cranial segment of the system seems to be represented by the connection between the uppermost ganglion in the trunk and the vagus ganglion.Hoffmann(11,12) has called attention to the sympathetic character of the ciliary ganglion,but whether a definite connection exists between it and the rest of the sympathetic system is uncertain.In the Ganoidei the arrangement is much as in the Selachians,but in the Teleosts a cranial and caudal sympathetic segment is developed while the ganglia of the chain are more regularly arranged.

3.In the Amphibians there are several stages of developmentfound in the different species.Andersson(1)describes two types in the Urodela which are represented in the Salamandra and Menobranchus respectively.In the Salamandra there is no cranial portion of the sympathetic system but the ganglia in the trunk are regularly arranged.In the Menobranchus a cranial segment is present while a collateral sympathetic chain is recognised.In members of this group which occupy intermediate positions in the zoological scale the gradual evolution of the one type into the other may be followed out.It must however be noted that Hoffmann(12)recognises a cranial segment in Salamandra.If this be present then the two types are not so distinct as Andersson conceived them to be.
In the frog the sympathetic chain is well developed,both cranial and caudal segments being present.

4.In Reptilia the sympathetic system is fairly complete in its development,Inthe sympathetic branch accompanying the vertebral artery in the neck it is possible that a homologue of the collateral sympathetic of the Urodela is represented,but this is uncertain.

5.In Birds the sympathetic chain lies enclosed in the canal formed by the transverse processes and the costal processes. This chain appears to be a collateral sympathetic chain while the true sympathetic chain is represented by the superior cervical ganglion and a pelvic segment,both of which lie outside the bony canal in the position of the true sympathetic chain in other vertebrates.A relationship therefore exists apparently between the Bird and Menobranchus.

5.In the Mammal the sympathetic chain reaches its highest stage of development and consists of a very highly organized and complex arrangement of nerve fibres and ganglia,arranged much in the same way as in some of the lower vertebrates.

6.As regards the suggestion made by some writers that there is some developmental connection between the collateral sympathetic chain in Urodela,the secondary or permanent sympathetic chain in Birds,and the nerve supply accompanying the vertebral artery in the Reptile and Mammal it is impossible to give a definite opinion. From a developmental point of view there are certainly many points in favour of regarding the ~~xxxxxx~~ so-called secondary sympathetic chain in the Bird as a true collateral chain and thus establishing a homology between the Bird and Urodela,but whether this homology can be extended to the Reptile and Mammal is a different matter.At the present time there is not sufficient developmental evidence to allow of any definite decision being formed as to the true relationship of the sympathetic supply accompanying the vertebral artery in Reptiles and Mammals to either the collateral sympathetic chain in Urodela,or to what is evidently the same structure in Birds.

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General Conclusions.

General Conclusions.

From this general survey of the development,structure,and comparative formation of the sympathetic system in the vertebrates certain conclusions may be drawn up,while certain suggestions may be made.

(1). The balance of evidence is in favour of the sympathetic system being an ectodermic structure developing as an outgrowth of the central nervous system.The two systems are therefore developmentally related,as they also are anatomically in the adult.

(2). The cells which migrate from the central nervous system form not only the sympathetic chain but the various peripheral plexuses. These cells,which multiply enormously after leaving the sympathetic chain,are recognised in large numbers not only in the plexuses and ganglia developed in or in connection with the different viscera but also along the course of the blood vessels.

(3). These sympathetic cells vary in type and in the extent of the distribution of their outgrowths,and various writers have classified them according to those characteristics.As to the exact significance of the different cells all workers are not agreed,but the explanation given by Dogiel seems at least plausible,and the recognition of a motor and sensory type of sympathetic cell helps at least to explain the action of a peripheral reflex.

(4). That the various sympathetic ganglia and plexuses have some reflex action seems highly probable.Bayliss(and Starling(1)describe the peristaltic action in the intestine as due to the Auerbach plexus. They formulated the theory that the ganglia in Auerbach's plexus formed a nervous system with two reflexes-augmentation and inhibition-with the propulsion of food as the object.These peristaltic or true co-ordinate movements are induced through mechanical stimulation.The pendulum movements they however regard as myogenic.Magnus(6)working later on the subject is able to show quite satisfactorily that the pendulum movements as well as the peristaltic movements are co-ordinate reflexes of the arc formed by the ganglia in Auerbach's plexus.
The work of Langley(4)and Langley and Anderson(5)on the collateral sympathetic ganglia is however suggestive of these ganglia being shunting stations for impulses from the central nervous system and not true reflex centres.

The evidence on this aspect of the physiological significance of sympathetic system is at present too conflicting and in many cases too unsatisfactory to allow of definite conclusions being drawn. As far as the movements of the intestine are concerned the evidence is clearly in favour of there being an actual reflex centre in the ganglia.This is also supported by the work of Dogiel who describes both sensory and motor cells in the ganglia in the intestine. It seems somewhat improbable that sympathetic cells derived from the same souce and passing through the same cycle of development should develop certain characteristics in certain situations,and be absolutely devoid of them in others.

If Dogiels work be accepted as correct, and also the work of Magnus, then we are met by the fact that the viscera as also the various blood vessels are supplied by large numbers of sympathetic cells both motor and sensory in function which are capable of governing and directing the functional life of the viscera.

Whether this influence normally exerted is the ordinary regulating mechanism for the functional life of the viscera,and how far it is controlled by the central nervous systems are questions yet to be settled.

(5) From an examination of the comparative anatomy of the sympathetic system in vertebrates it is evident that the system becomes more and more complex as the zoological scale is ascended.It seems probable that the increase in complexity of the sympathetic system is associated with the development of the brain,or what might be termed the intellectual functions as contrasted with the purely vegetative functions.

Gaskell(2) in his book on the Origin of Vertebrates describes the central nervous system of the vertebrate as the homologue of the central nervous system of the annelid or arthropod.In such species the cycle of life is composed of seeking food,mating,and avoiding enemies,functions purely associated with the vegetative or non-intellectual side of life.In these species one finds no sympathetic system but a comparatively well developed central nervous system.In higher species such as the Cyclostomata and Urodela the sympathetic chain appears.At first it is extremely primitive but in the Urodela has reached a considerable degree of complexity. Is this shedding off of cells for the supply of the viscera a method by which the central nervous system is relieved from the constant regulation of the functional life of the viscera so as to meet the demands made on it by a more complex life?

If this be the case the sympathetic system is phylogenetically secondary to the central nervous system,and is developed as a method of allowing freer action on the part of this latter system.

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Wil. 1913 (1)

The Arrangement of the longitudinal and circular musculature at the upper end of the oesophagus.

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At the upper end of the oesophagus the two muscle layers which may be followed throughout the entire alimentary canal begin,it is therefore a region of special interest including as it does the transition from the pharyngeal to the intestinal type of musculature.As is well known the muscle layers in the upper part of the oesophagus are composed of striated fibres which are gradually replaced by non-striated fibres in the lower part of the oesophagus.An oppurtunity is here afforded of ascertaining how far the muscle layers of the upper oesophagus follow the usual rule with striated muscle and form some definite point of attachment,and how far they adopt the arrangement found in non-striated muscle and have no fixed point of attachment.The peculiarly rapid action of the upper part of the oesophagus as displayed in ~~the~~ swallowing either liquids or solids is probably associated with the mechanical advantages afforded by the attachments of this part of the oesophageal musculature as well as with its histological characteristics.Further in this region diverticula occasionally develope and it is of interest to find what anatomical conditions may be associated with the development of such an abnormality.

It is evident therefore that a clear conception of the arrangement of the musculature at the upper end of the oesophagus is a matter of some importance.With this end in view various textbooks were consulted but the descriptions given were found somewhat unsatisfactory.It was therefore suggested to me by Dr.Brown Kelly that dissections of this region should be made in order to obtain first hand evidence on this point.Before giving an account of the results of these dissections a short resumè of some of the descriptions from the textbooks may be given,and of a paper published some fourteen years ago by Birmingham on this subject.

Macalister(4)describes the longitudinal muscular coat of the oesophagus as dividing into three strands at the upper end of the oesophagus. Of these the anterior is the strongest and is attached to the ridge on the posterior surface of the cricoid cartilage.The other two strands are attached to the elastic tissue in which the palato pharyngeus muscle ends.The circular coat is composed of transversely arranged muscle fibres some of which are apparently continuous with the inferior constrictor muscle.

In the edition of Quains Anatomy for 1896(5) the longitudinal muscular coat of the oesophagus is described as forming at its commencement at the upper part of the tube three bands, an anterior, and two lateral. The anterior band arises from the back of the cricoid cartilage at the prominent ridge between the posterior crico arytenoid muscles, as it descends it spreads out and blends with the fibres of the lateral bands thus forming a continuous layer round the tube. The lateral bands are continuous with the inferior constrictor of the pharynx. The internal or circular muscular coat is separated from the fibres of the inferior constrictor by the longitudinal bands just described. A few fibres turn downwards from the lower border of the inferior constrictor to join the longitudinal coat of the oesophagus.

Cleland and Mackay(2) describe the longitudinal coat of the oesophagus as taking origin anteriorly from the cricoid cartilage, and from the inner surface of the inferior constrictor laterally and posteriorly. The circular fibres are surrounded by the longitudinal fibres which also separate them from the constrictors of the pharynx.

In the latest edition of Greys Anatomy(3) which appeared in 1909 there is no alteration made on the description given in earlier editions for the upper part of the oesophagus. The longitudinal coat is described as forming at the commencement of the tube three fasiculi, one in front and one at either side. The one in front is attached to the vertical ridge on the posterior surface of the cricoid, while the lateral fasciculi are continuous with the muscular fibres of the pharynx As they descend the three fasciculi blend and form a uniform layer covering the tube. The circular layer is continuous with the fibres of the inferior constrictor.

It is evident from this resumé that there is a certain similarity in the accounts; thus in all the descriptions except that given by Cleland and Mackay it is expressly stated that the longitudinal muscular layer originates in three strands, an anterior and two lateral. All agree in tracing the anterior strand to the posterior surface of cricoid cartilage, but the lateral strands are described as originating either from the inferior constrictor or the elastic tissue in which the palato pharyngeus ends. The relation of the circular fibres to the inferior constrictor is also a point upon which textbook descriptions do not agree.

While working at this subject I came across a paper by Birmingham(1) already referred ~~to~~ which I briefly summarize. According to this writer the longitudinal coat of the oesophagus does not divide into three bundles but into two lateral bundles.These lateral bundles diverge from one another about one to one and a quarter inches below the cricoid cartilage.From this point they pass forwards and inwards under cover of the inferior constrictor,with which they are however quite unconnected,to the lower border of the cricoid.At this point both bundles meet but do not fuse and are inserted into a common tendon which is attached to the vertical ridge on the posterior surface of the cricoid.This tendon is about a quarter of an inch in breadth at its upper level and a little broader at its lower level where the muscle bundles are inserted.In some cases a few of superficial longitudinal fibres pass up and terminate in the inferior constrictor evidently with the intervention of connective tissue. In other cases a few of these superficial fibres are found forming an independent bundle which is inserted into the lower border of the cricoid.Quite frequently a small bundle of fibres from the inferior constrictor at its lowest point of attachment to the cricoid is inserted into the lateral bundles of the longitudinal coat at either side.The v shaped space formed on the posterior surface by the diverging lateral bundles is filled in by the fibres of the circular coat,and also to a very slight extent by fibres given off from the lateral bundles.This space usually measures about one and a quarter inches from above downwards and is overlapped at its upper border by the lower portion of the inferior constrictor for about half an inch.The circular fibres on the posterior surface of the oesophagus are directly continuous with the fibres of the lower portion of the inferior constrictor,which is distinguished from the upper portion by the horizontal direction of the muscle fibres and the absence of a raphé.On the anterior surface it is seen that the uppermost circular fibres do not go all the way round but are inserted into the margins of the common tendon for the lateral longitudinal bundles.In some instances delicate muscular slips pass from the circular fibres on the posterior aspect ~~and~~ to blend with the pharyngo oesophageal muscle,while in other cases delicate muscular slips pass from the margins of the anterior common tendon to the circular fibres.Both these muscular slips when present serve to bring the circular layer into close relationship with the pharyngeal musculature.

It is evident from this resumé that Birmingham disagrees on many points with the descriptions given in textbooks of the upper oesophageal musculature and its relationship to the pharynx.

Results of the present investigation.

1.The arrangement of the longitudinal muscular layer in the upper part of the oesophagus.

The examination of the upper part of the oesophagus shows that the longitudinal muscle fibres are differently arranged from elsewhere in the oesophagus.On the posterior surface two bands of longitudinal muscle fibres are seen emerging at either side from under cover of the inferior constrictor.These bundles pass downwards and inwards and unite some 3.5 to 3.8 c.ms. below the lower margin of the inferior constrictor.Below this point of union the longitudinal fibres become evenly distributed over the surface of the oesophagus and form the outer of the two oesophageal coats.A v shaped space is enclosed between the two bundles on the uppermost part of the posterior surface.This space is bounded above by the lower border of the inferior constrictor below by the point of junction of the two lateral bundles.It is usually some 3.5 to 3.8 cms. in length and is filled in by circular fibres belonging to the inner muscular coat.A few longitudinal fibres cross these circular fibres, They are given off from the lateral bundles as they form the sides of this space.A very few longitudinal fibres are also seen in some specimens passing up from the longitudinal coat proper to end apparently in the inferior constrictor(fig. 1).In many cases a small group of fibres passes from the cricoid attachment of the inferior constrictor to be inserted into the longitudinal or lateral bundles just as they pass from under cover of this muscle(fig.2).In one case examined a few longitudinal fibres were seen passing as a detached group to be inserted independently into the lower part of the cricoid and the upper part of the trachea.(fig.3)

On the anterior surface the contrast between the arrangement of the longitudinal muscle fibres in the uppermost part of the tube and in the remainder of the oesophagus is even more striking than on the posterior surface.

On the posterior surface of the cricoid is a ridge to which is attached a tendon.This tendon, which is generally about 1.5cms. in length, extends to the lower border of the cricoid cartilage where it is joined by the two lateral bundles already described on the posterior surface.These two bundles meet but do not fuse just below their insertion into this tendon, which is about .9 cm. wide at its lower margin.From the point of insertion into the tendon the two longitudinal bundles pass downwards and somewhat outwards under cover of the inferior constrictor, with which however they are not connected, and so reach the posterior surface.

As these bundles diverge on the anterior surface they enclose a narrow triangular space which is continuous with a narrow slit like space which is found in the middle of the anterior wall for the upper 5 or 6 cms The triangular space is filled up by the circular fibres of the inner laye longitudinal fibres are practically absent.The narrow slit is occupied by both circular and longitudinal fibres but the longitudinal fibres are comparatively scanty especially at the upper end.
The comparative scarcity of longitudinal fibres in the upper part of the anterior surface is interesting since a special anterior bundle of longitudinal fibres is frequently described.
Briefly therefore the longitudinal muscular layer originates in two muscular bundles attached to the posterior surface of the cricoid,the fusion of these two bundles resulting in the uniform outer muscular coat of the oesophagus.
2.The arrangement of the circular muscular layer in the upper part of the oesophagus.
On the posterior surface of a preparation including the pharynx with the oesophagus it is evident that the horizontal or lower part of the inferior constrictor is very closely connected with the oesophageal musculature(fig.4).On dissection it is found that there is no interruption between the uppermost part of the circular musculature of the oesophagus and the lowest fibres of the inferior constrictor,but the one simply merges into the other.Further since the fibres of the upper part of the circular coat of the oesophagus are striated the continuity between the two structures is histological ~~xxx~~ as well as anatomical.
On the anterior surface the uppermost circular fibres do not form complete loops but are attached to the margins of the common tendon for longitudinal muscles ,at the level of the lower border of the cricoid.

The circular layer is therefore continuous with the fibres of the inferior constrictor posteriorly,while anteriorly it participates to a certain extent in the attachment of the longitudinal fibres.

Discussion.
It is evident from this description that the results of this investigation do not support the accounts quoted from the textbooks,but they agree very fully with the work of Birmingham.
If the description given by Birmingham be compared with the description given in this paper it is seen that in both the longitudinal musculature is recognised as orginating in two bundles attached to the cricoid cartilage,this is of course very different from the usual account where two-thirds of the longitudinal fibres are traced to the inferior

constrictors. Again the attachments of the circular muscle coat is much more satisfactorily accounted for in the descriptions given by Birmingham and myself, since we show that it is ~~connected~~ continuous with the inferior constrictor and ~~also~~ attached to the common tendon for the longitudinal muscle bundles. In the usual accounts there is some doubt as to the extent of the connection between the inferior constrictor and the circular coat, while no suggestion is made that it may share to a certain extent the attachment of the longitudinal coat to the cricoid cartilage.

In his description however Birmingham does not refer to the small triangular space on the anterior surface nor to the slit which is seen in the middle of the upper part of the anterior wall.

Further in this investigation I have failed to get any traces of the muscular slips described by Birmingham as extending between the circular coat and the pharyngeal musculature and the common tendon. It is possible however that this is simply because the specimens examined were not suitable, for Birmingham points out that these slips do not occur in all specimens.

As is well known the musculature of the upper part of the oesophagus is striated and it is especially evident that in the longitudinal coat the arrangement follows the usual rule for striated muscle since the fibres have a definite attachment to a fixed point. In the circular coat this is not so evident and here there is an apparent compromise in the arrangement. The uppermost fibres, which are striated, are continuous with the inferior constrictor, in this point they follow the arrangement seen in non- striated muscle as seen in the intestine. At the same time they are attached to the common tendon for the longitudinal fibres and so to the cricoid cartilage, in this they follow the arrangement found in striated muscle.

It is evident that the conception that the longitudinal muscle bundles end partly in the inferior constrictor is unsatisfactory since it necessitates the anomalous arrangement in which striated muscle fibres are inserted into adjoining muscles of the same type. For the circular fibres the same criticism can not be made, for here it is not the attachment of one set of striated fibres to another but the blending or fusing of two muscles the inferior constrictor and the circular oesophageal coat. The only point of attachment of the circular coat is at the margins of the common tendon.

The mechanical conditions for the propulsion of food through the oesophagus are favoured by the attachment of the stronger or longitudinal coat to a comparatively fixed point such as the cricoid cartilage.

It is easily seen that if the longitudinal musculature were inserted even partly into the pharyngeal tissue a certain amount of energy would be ~~xxxxxxxxxxx~~ necessarily wasted in overcoming this elasticity. The connection of the circular coat to the inferior constrictor ,or rather the blending of those two muscles,does not constitute any obstacle since the direction of the fibres and their mode of action is the same. It is seen from the description that the uppermost part of the posterior oesophageal wall is decidedly weak.The v shaped space lying between the bundles is very poorly provided with longitudinal fibres,and the lateral bundles are so arranged that they do not protect this area from the effect of any undue pressure,which fall on the widest and weakest part.

On the anterior surface there is also a triangular space uncovered by longitudinal fibres but it is much smaller and is very efficiently protected by the two lateral bundles.

The anatomical conditions therefore on the uppermost part of the posterior wall are on the whole such as would allow of the development of diverticula due to pressure.

Summary.

1.The longitudinal muscle layer of the oesophagus forms at its upper part two bundles which are attached by a common tendon to a ridge on the posterior surface of the cricoid cartilage.

2.Enclosed between the diverging bundles are two spaces one on the anterior the other on the posterior surface.In addition to this space on the anterior surface a narrow slit extends downwards between the two bundles of longitudinal muscle fibres for some distance.The two spaces and the slit are filled up by circular fibres crossed by a few longitudinal fibres,except in the upper part of the anterior space where they are wanting.

3.Below the point of separation of the two bundles the longitudinal fibres are evenly distributed over the surface of the oesophagus and completely envelope the circular layer.

4.There is no connection between the longitudinal coat and the inferior constrictor with the exception of the few fibres which pass from the cricoid attachment of this muscle to blend with the two lateral bundles of longitudinal fibres.

5.The circular fibres are continuous with the inferior constrictor posteriorly,while anteriorly the uppermost fibres ~~xxxxxxxxxxxx~~ are inserted into the margins of the tendon for the longitudinal bundles.

6. The arrangement of the upper part of the oesophageal musculature follows to a certain extent the rule for the arrangement of striated muscle tissue in other parts of the body. Further the arrangement offers conditions favourable to the propulsion of food at a rapid rate at least as far as the lower part of the oesophagus.

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