PHYSALOPTERA VARANI
STUDIES IN MORPHOLOGY AND
LIFE-CYCLE'

BY

SYLVESTER JOHNSON²

1. Thesis submitted for the degree of Ph.D. of the Aligarh Muslim University.
2. Research Scholar in the Department of Zoology, Aligarh Muslim University.
ACKNOWLEDGEMENT

The author expresses his earnest thanks to Dr. M.A. Basir under whose direction and guidance this work was done. He further wishes to thank Prof. M.B. Mirza for his valuable advice and suggestions throughout the entire course of this study.
## TABLE OF CONTENTS

1. Introduction and classification
   
   (i) Introduction  
   (ii) Historical review  
   (iii) Distinguishing characters of the genus *Physaloptera*  
   (iv) Key to the Indian species of the genus *Physaloptera*

2. Material and Methods

3. General description of *Physaloptera varani*

4. The body wall
   
   (i) Cuticle  
   (ii) Hypodermis

5. Musculature
   
   (i) Somatic musculature  
   (ii) Specialised muscles

6. Nervous System
   
   (i) General plan  
   (ii) Nerve ring and Cephalic ganglia  
   (iii) The nerves  
   (iv) Posterior region of female  
   (v) Posterior region of male  
   (vi) Phasmids

7. Excretory System

8. Digestive System
   
   (i) Cephalic structures  
   (ii) Stoma  
   (iii) Oesophagus  
      (a) Oesophageal glands  
      (b) Nuclear distribution  
      (c) Oesophago-intestinal valve  
   (iv) Intestine  
   (v) Posterior gut  
      (a) Intestino-rectal valve  
      (b) The rectum  
      (c) The cloaca  
      (d) The rectal glands
9. Female Reproductive System

(I) Ovary 81
(II) Oviduct 83
(III) Uterus 84
(IV) Vagina 85
   (a) Vagina uterina 86
   (b) Vagina vera 86

10. Male Reproductive System

(I) Testis 89
(II) Seminal vesicle 90
(III) Ductus ejaculatorius 91
(IV) Spicules 93
   (a) Left spicule 93
   (b) Right spicule 93
   (c) Functions of the spicules 94

11. Life-cycle Studies

(I) Historical review 98
(II) Methods of infection 101
(III) Results 102

12. Key to lettering of figures 105

13. References 110

14. Five plates with 110 figures
INTRODUCTION

The great bulk of work done in nematology is confined either to human parasites or to those parasitizing the domestic animals. Much work has been done on systematics which is usually confined to the descriptions and re-descriptions of the species while little contribution has been made to the detailed studies of the individual members of this group. The pioneers in this field were Schneider (1860-1866), Bastian (1865) and de Man (1886). Their good work was carried over by Looss (1905) and Martini (1916) in their studies on Ancylostoma duodenale and Oxyuris curvula respectively. While Martini (1906-1909) was making one of the most detailed studies of the nemic sub-cuticula, Goldschmidt (1908-1910) was busy with his classical work over the nervous system of the two ascarids, Ascaris lumbricoides and A. megalcephala. Soon after followed Rauther's (1906-1918) study of an aphasmid worm: Mermis albecana. In 1919, Magath published his monograph on Camallanus americanus. Steiner described various worms in detail from 1916-1935. In 1929 Mirza and Mueller made their contribution with the studies on Dracunculus medinensis and Ascaris lumbricoides and A. megalcephala respectively. Since 1930 Chitwood began his tremendous work over the
group and published comprehensive accounts dealing practically with all aspects of nematology.

Considering the vast numbers of nematodes, both parasites and free-living, known at the present time, our information about their detailed structure is fragmentary. It may be one of the reasons that in the absence of this detailed morphological knowledge it sometimes becomes very difficult to solve systematic riddles. Ward realising the importance of such morphological work said "It has been my fixed principle never to make any changes until I ..... know that some change was inevitable and that the proposed modification was defensible on morphological grounds." While recognising a number of groups of family rank in Nematoda, there has been hardly any attempt to correlate them. Ward (l.c.) while desiring such an attempt, opines "I am of the opinion that more precise study of the morphology of these groups will furnish the basis for interpreting their relation to each other."

In the present work a detailed study of the histological anatomy of Physaloptera varani is made. This is a spiruroid worm found in the stomach of Varanus bengalensis which is easily available in this
part of the country. It is hoped that this contribution to the knowledge of the nematode morphology would be a useful addition to our scanty possessions of such nature.
The genus Physaloptera was established by Rudolphi in 1819. He was, however, somewhat doubtful as to its validity. Dujardin (1845), in accordance with the doubts of Rudolphi, suppressed the genus, transferring the species originally ascribed to it to the genus Spiroptera. In 1851, Dissing re-established the genus and defined it once for all categorically as a genus distinct and separate from other Nematode genera. Since then the validity of the genus has never been questioned. Schneider (1866) even went to the extent of remarking that Physaloptera is one of the best of Rudolphi's genera.

Since Rudolphi's time Physaloptera has gradually become a very big genus parasitising, with a solitary exception, the higher vertebrates: carnivorous species of mammals, birds and reptiles. Rudolphi created the genus only on seven species of which one was a mammalian, four avian and two reptilian parasites. Today we know about a hundred species of Physaloptera ranging from Amphibia on the one hand to man on the other. In 1899, v. Linstow described P. amphibia from an amphibian, Rana macrodon. It is, as yet, the only recorded
occurrence of a member of this genus from amphibians. In 1902 Linstow described P. caucasia, the first human parasite from this genus.

Much work has been done during the 133 years since the birth of the genus, mainly in the taxonomic field. The major contributions were made by Seurat (1914-17), Travassos (1920), Irwin-Smith (1822-23) and Ortlepp (1922-23). The result is not very encouraging and a lot of confusion still prevails. Attempts to sub-divide the genus did not prove very satisfactory.

Seurat (1915-16) tried to sub-divide the genus on the basis of dentition. His study, however, failed to cover all the species as pointed out by Ortlepp (1922). Travassos (1920) relied mainly upon the form of female genitalia and the pedunculated papillae. Ortlepp (l.c.) remarked that this was also untenable. He used the number and mode of origin of uterine branches as the main taxonomic characters and divided the genus into di-, tetra-, and polydelphoid groups, the arrangement proceeding from mammals to birds and then to reptiles. Although in most cases this division holds good, still, there are cases on record where the mode of origin of the uterine branches differs in different individuals.
of the same species. Sandground (1936) showed three modes of origin of the uterine branches in Abbreviate poilometra.

Apart from this instance, which might be regarded as an exception, Irwin-Smith (1922) raised another serious objection to the use of the form and mode of uterine origin as a taxonomic character. She considered it "undesirable to establish a new genus entirely on a character which can be determined only by dissection". In order to avoid this difficulty, Ortlepp (l.c.) searched in vain for other characters that might enable him to split the genus into several genera and had to conclude that "the whole genus is so compact, and its individual species have so many characters in common, that at the present state of our knowledge of Physaloptera, I am compelled to retain all in the same genus.....".

Even during thirty years after Ortlepp, little has been added to our knowledge and Chitwood and Chitwood (1950) are content to conclude that "the Physalopteridae present more taxonomic difficulties than any other group.....".

The present writer is in full accord with Mirza (1935) that "the characteristics of the species
of the genus *Physaloptera* should mainly depend upon the size, shape and the arrangement of the pre- and post-anal ventral papillae. The form of the uteri and the arrangement of the teeth and denticles on the lips should also be taken into consideration." However, we have occasionally to face certain "abnormalities" with regard to the size and shape of the ventral papillae. Mirza himself recorded in the same paper a specimen recovered from the stomach of *Varanus indicus* which had six lateral pedunculated papillae on the left side instead of the usual four. On the right it had only four papillae which is the normal number. Such occurrences should be regarded as abnormalities and should not be allowed to influence the application of these characters in taxonomic studies.

Parona (1899b) first described *P. varani* from the stomach of the Indian monitor (*Varanus monitor = Varanus bengalensis*) at Palon, Pegu, Burma. Parona's description is very incomplete and fragmentary so much so that, according to Ortlepp, it can be applied to quite a number of species of the genus *Physaloptera*. v. Linstow (1904) recorded the species from *Varanus bengalensis* at Bolgoda, Ceylon. He, however, did not give any description.
Johnston (1909) indicated the occurrence of P. varani on the Australian mainland and wrote "I have seen Varanus indicus near Gladstone in Queensland, and hence it may be expected that before long .... P. varani .... may be added to our known Australasian Entozoan fauna." In the same paper (1909,a) he recorded, "a few specimens of a Nematode, Physaloptera sp. perhaps P. varani Paronna" found along with a Cestode in the stomach of Varanus varius from the vicinity of Bathurst, N.S.W. Three years later he again recorded P. varani from Varanus gouldii in Queensland, Western Australia, Victoria and N.S.W. (1912,a). Again in the same year (1912,b) he reported P. varani from Varanus bellii at Eidsvold, Burnett River, Queensland. No figures or descriptions accompany these records and they are apparently open to question. Dr. Willey also collected P. varani in the Western Pacific Isles and it was included by Johnston (1912) in his "Census of Australasian Entozoa".

Seurat (1917) described P. varani from various North African reptiles. Hsu and Hoeppli (1831) have described P. varani from a snake, Zaccys dhumnades, in China. Both these records are, however, doubtful and uncertain.

Presuming that all these records are correct it would appear that P. varani enjoys a fairly wide
distribution ranging from Australia to North Africa including China.

In 1922 Ortlepp gave a somewhat better description of *P. varani* in his comprehensive survey of the whole genus. His description is based on three males from *Varanus bengalensis* and two females collected from *Varanus indicus*.

Schulz (1927) described *P. varani* as *Abreviata (Abbreviata) varani*. The two are now considered as synonyms.

*Physaloptera varani* is very closely related to *P. paradoxa* and *P. quadrovaria* and can only be distinguished from these by relative measurements of oesophagus, tail of the female and mode of origin of the uteri. In fact, the similarity between *P. varani* and *P. paradoxa* is so great that Mirza (1934,a) while recording an unnamed species from *Varanus indicus* could not decide whether it was *P. varani* or *P. paradoxa*. The main difference between the two is in the mode of origin of the uteri. In the former it is dichotomous while in the latter all the four arise simultaneously from the common trunk.
The spiruroid genus Physaloptera includes fairly long worms which taper gradually towards the extremities. According to Ortlepp (1922), the largest known specimens measure about 10 cm. in length and 3 mm. in thickness. The worms are covered externally by a thick cuticle which invariably shows fine transverse striation.

Two lateral, semicircular or triangular, lips are always present. The inner side of each of these lips bears a number of teeth which are arranged as follows:

1. an outer median tooth,
2. an inner median tooth,
3. two inner lateral teeth, and
4. a number of small denticles lying in between the lateral and the median teeth.

Of these the external median tooth is always present. The rest may or may not be found.

In addition to the teeth, each lip bears two papillae and one amphid. Each of these papillae represents two fused papillae.
The buccal cavity is almost absent. The oesophagus follows the lips immediately. It can always be divided into two parts: a short anterior muscular portion and a long posterior glandular region. The oesophageal lumen is triradiate. The intestine is more or less a straight tube. The oesophagus communicates with the intestine through a bicuspied oesophago-intestinal valve. The intestine opens to the exterior through a short rectum.

The excretory system is generally of the inverted-U type and opens to the exterior by means of a ventrally situated excretory pore. The nerve ring surrounds the posterior portion of the muscular region of the oesophagus.

In the female the vulva is pre-equatorial in position. It communicates internally with a thick-walled muscular ovijector which is generally divisible into three portions:

1. vagina vera,
2. vagina uterina, and
3. the common uterine trunk.

The last named portion may be sometimes absent. The number and mode of origin of the uterine branches varies in the members of the genus and serves as a
specific character. Typically they may be two, four or many. Again, they may arise either dichotomously or simultaneously from the common uterine trunk. The uterine branches nearly fill the body space and ultimately each ends in a receptaculum seminis. The latter is connected with the ovary by means of a fine oviduct. The eggs are small and thick shelled. They are already segmented at the time of deposition.

The male gonoduct is single and unpaired. It consists of:

1. a pyriform ejaculatory duct,
2. a long seminal vesicle, and
3. a single testis.

The ejaculatory duct joins the rectum forming a cloaca. Two spicules make up the accessory male genital apparatus. Generally the left is long and slender while the right is short and stout. In rare cases they may be equal in length or the right one may be slightly larger than the left.

The posterior extremity in the female is generally short and conical. Two lateral phasmids, one on either side, are present, situated behind its middle.
The male caudal extremity is provided with peloderan bursa. At least four pairs of circumcloacal pedunculated papillae always support it. In addition to these a variable number of ventral sessile papillae is also present. Generally these consist of three pre-anal and five pairs of post-anal papillae. Longitudinal ridges or tubercles or rounded prominences are also present on the ventral side.
KEY TO THE INDIAN SPECIES OF THE GENUS PHYSALOPTERA

Parasites of birds of prey ..................... alata.
Parasites of reptiles ......................... 1
Parasites of mammals ......................... 2.

1. The four uterine branches originate by dichotomous branching; post-anal sessile ventral papillae are always in five pairs .... varani.
The four uterine branches originate from the same point; post-anal sessile ventral papillae variable, the minimum number being five pairs and the maximum seven .... paradoxo.

2. Posterior end of the body without prepuce-like cuticular sheath; parasite of mouse ................ musculi.
Posterior end of body with a prepuce-like cuticular sheath; parasites of felidae ......................... 3.

3. Median precloacal papilla of male smaller than the other two .................... masoodi.
Median precloacal papilla of the male larger than the other two ..................... 4.

4. Ventral surface in caudal region in male with longitudinal rows of tubercles in its middle portion ...................... praeputialis.
Ventral surface of caudal region in male with continuous longitudinal ridges only .... brevispliculw
There are only two Indian species of *Physaloptera*, known from the reptiles, viz., *P. varani* and *P. paradoxa*. These two resemble each other so closely that Parona (1917) regarded them as synonyms. Ortlepp (1922) rejected this view and stated that "*P. varani* differs from *P. paradoxa* by its longer oesophagus, longer trunk, mode of origin of the four uteri, and the absence of a denticular ridge on the inner side of each lip."

The present writer, while agreeing with Ortlepp in not recognising the two species in question as synonyms, differs from him in one particular point, namely "the absence of a denticular ridge on the inner side of each lip" in *P. varani*. In the present study the denticles were always found to be present on the inner side of the lips.

Unfortunately, the author was unable to examine any specimen of *P. paradoxa* himself. He has relied mainly upon the accounts given by Ortlepp (1922), Mirza (1935), and Baylis (1939), for his comparisons of the two species.

The mode of origin of the uteri in *P. varani* is definitely dichotomous. In *P. paradoxa*, according to Ortlepp (1922), all the four uteri arise at the
same point by "a double sub-division of the unpaired duct". Mirza (1935) described a similar uterine branching for *P.achari*, which was later regarded by Baylis (1939) as a synonym of *P.paradoxa*. Baylis (1939), however, reports that "in a young specimen...... the branches originated dichotomously". Thus, in spite of this solitary record of dichotomous branching in *P.paradoxa*, the mode of origin of the uterine branches remains the most important character in distinguishing the two species from each other.

The number of post-anal sessile ventral papillae also appears to be variable in *P.paradoxa*. Ortlepp describes five pairs, v.Linstow and Mirza six each, and Monnig seven. Baylis concludes that the number of these papillae in *P.paradoxa* varies from five to seven pairs. On the other hand, in the case of *P.varani* their number is constant and five pairs of post-anal sessile ventral papillae are always present.
**MATERIAL AND METHODS**

*Physaloptera varani* were recovered from *Varanus bengalensis*. These are found almost exclusively in the stomach. Only one more parasite, a Cestode, *Duthersia sp.*, was met within the alimentary canal. *Varanus* is invariably infected with this parasite, the percentage of infection being quite high. On the average about 15 worms were recovered from a single *Varanus* of which nearly 60 per cent were females and the remaining 40 per cent were males.

The fresh material was washed in physiological saline (.85%) and then killed in hot 70 per cent alcohol. The thickness of the cuticle renders them almost opaque. Therefore, for further study they were made transparent. Both glycerine as well as beechwood creosote were used as clearing media. The toto preparations and en face view were mounted in glycerine jelly. Rest were preserved in 70 per cent alcohol.

For the microscopical study series of transverse and longitudinal sections were cut and stained slides prepared in the usual way. Peterunkewitch proved to be quite suitable as a fixative. The stain used was iron alum haematoxylin. Several other stains including
Acid Fuchsin, Phospho-molybdic-acid-haematoxylin and Borax Carmine for particular studies were tried. Silver impregnation was also tried for the study of the nervous system. Of these stains Iron-alum-haematoxylin proved to be the best for the study of the details.

The details of the male and the female reproductive systems were made out by dissections. Spicules in the male were also dissected out. All dissections were done under the dissection microscope.
The worms have a very strong hold into the mucosa of the stomach of the host. Their anterior ends actually penetrate into the mucosal layer and it takes some time to get them detached safely from their holds. Generally they coil up loosely but sometimes they even roll up spirally. They can be kept alive for a few days in physiological saline. During the entire course of the study, involving many dissections of the host to recover the parasites, none of the latter were observed in a state of copulation.

**Female:** Mature females are larger than the males. They are 2.5 to 3.5 cm. in length by about 1 mm. in maximum width. The age of the worm naturally affects its size, particularly the thickness of the body in the gravid females. Sometimes an immature female is practically of the same size as the mature male. The worms are dull white in colour. The body tapers down gradually towards the extremities. The head is typically spiruroid with two large pseudolabia each of which bears two papillae and one amphid. The body is covered with thick cuticle which is striated transversely. On the average the annules are about 70 μ apart and are regularly spaced. Posterior to the
oesophagus and up to near the anal region the striation is rather indistinct but becomes clear again in the tail region, and continues up to the hind end. The mouth is a dorso-ventral slit which directly leads into the oesophagus. The buccal cavity is almost absent. The oesophagus is divisible into two portions: the short anterior muscular and the long posterior glandular region. The muscular part of the oesophagus measures on the average about 430 μ in length by 2.7 μ in width while the glandular part is about 1.67 mm in length by 5.4 μ in width. Posteriorly it leads into the intestine through an oesophago-intestinal valve. The intestine is a straight tube which communicates with a short rectum, the latter opening outside through the anus. The anus is situated on the ventral side about 430 μ from the tip of the tail. The excretory pore is situated about 520 μ from the anterior end of the body. The nerve ring surrounds the muscular part of the oesophagus, about 320 μ from the anterior extremity. The vulva is situated at about one fourth of the body length from the anterior end. It leads into a thick-walled muscular vagina which communicates with the main trunk of the uterus, the latter branching dichotomously into four uterine
branches. Each of these branches is continued into a seminal receptacle which in turn receives the oviduct, the latter being connected with the ovary. Thus there are four ovaries in this worm. Eggs are thick shelled. Segmentation of the eggs start while they are in the uterus. They measure on an average 35 μ long by 25 μ wide.

**Male:** As a rule the males are smaller than the females. They are 1.5 to 2.5 cm. long. In thickness they average about 0.7 mm. The muscular part of the oesophagous measures about 400 μ long and 2 μ wide, while the glandular part is about 1.5 mm. long by 4.9 μ wide. The anal opening is situated about 1 mm. from the posterior tip. The excretory pore lies at a distance of about 505 μ and the nerve ring about 300 μ from the anterior end of the body. The testis is single. It begins at about the middle of the body and proceeds posteriorly parallel to the intestine ultimately leading into a seminal vesicle which is about 3.4 mm. long. At its beginning it is about 170 μ thick. Posteriorly it gradually increases in width reaching the maximum near its posterior part where it is about 400 μ wide. It communicates with the ejaculatory duct which is about 1.5 mm. in length. The latter is the terminal portion of the male gonoduct.
In the cleared, unstained specimens it is the most conspicuous structure and can be distinguished from others by its dark brownish colour. Posteriorly it joins the rectum to form the cloaca. There are two unequal and dissimilar spicules. The left spicule is larger and measures about 3 mm. in length. The right is much shorter and measures only about 258 μ.

The posterior extremity of the male is conspicuous because of the presence of the "bursa". In a worm measuring 2.1 cm. in length it was 1.7 mm. long and .85 mm. broad. The ratio of the length of the bursa to its breadth is about 1:2. Posteriorly the bursa tapers down to a broad point. The cloacal opening is situated at the broadest portion of the bursa. Four pairs of pedunculated papillae are present round the cloaca. Of these, the distance between the first and the second pairs and the third and fourth pairs is more or less the same while that between the second and third is slightly larger. The stalks or the peduncles also vary in length - the variation being very similar to that met with in the four fingers of the human hand. The second one is the largest, the first and third more or less equal, and somewhat smaller, and the fourth is the smallest (Figs. 5,6).

In addition to these pedunculated papillae
there are six pairs and one median sessile papillae. The first pair, together with the single median papillae is pre-cloacal. The second and the third pairs are immediately behind the cloacal orifice. These are situated anterior to the fourth pair of the pedunculated papillae. After a distance, roughly equal to that between the first and the third pairs, is situated the fourth pair followed after a very short distance by the fifth. The sixth and the last pair lies midway between the fifth pair and the posterior end of the tail (Figs. 5,7).

A very large area round the cloacal orifice and enclosing all the four pedunculated papillae and the first three pairs of the sessile papillae together with the median sessile papilla, is covered with small cuticular elevations (Fig. 5).
CUTICLE

The cuticle covers the whole body externally and also extends inwards at the mouth, anus and vulva. The external cuticle is connected intimately with the underlying hypodermis, and though, according to Chitwood and Chitwood (1950), it is a product of the hypodermis, still, the character of its formation is far from certain.

Transverse markings.

As in the case of many other nematodes the cuticle of *Physaloptera varani* is striated (Fig.1), but the striations are neither very pronounced nor uniformly apparent throughout the entire length of the worm. In the adult female worms, the striations begin at a distance of about 350 μ from the anterior tip. On the average, these striations are about 70 μ apart. A short distance before the oesophago-intestinal valve, the striations become less pronounced and gradually they become almost indistinct. Again, a short distance anterior to the anal opening, the striations appear with a definiteness and continue to do so up to the tip of the tail. These striations involve the whole of the cortical layer as well as a part of the matrix layer of the cuticle.
Caudal alae.

As the name suggests these are alae confined to the caudal region of the body. They are further limited to the males only and probably serve as clasping organs during copulation. The bursa or the caudal alae in *Physaloptera varani* can be described as being "peloderan" according to the terminology introduced for their description by Schneider (1866). It denotes that the wide caudal alae in this case meet posterior to the tail (Fig. 5). The caudal alae are made up of only the cortical and the matrix layers of the cuticle and the fiber layers have no part in their formation (Fig. 4).

Cuticular layering.

The cuticle does not take the stain readily and a number of stains were tried to study the cuticular layers. The best differentiation was obtained with 0.5 per cent Acid Fuchsin.

The cuticle of *Physaloptera varani* (Figs. 2 and 3) can be divided into six distinct layers as follows:-

1. an external cortical layer,
2. an internal cortical layer,
3. a matrix layer
4. external fiber layer
5. median fiber layer, and
6. internal fiber layer.

The external cortical layer is naturally the outermost and is the most dense of all the cuticular layers. It appears to be a homogeneous dark layer and no structures are seen in it. The next layer dense is the internal cortical layer. It is less than the first. This layer also does not show any structure and seems to be of homogeneous consistency. The third layer is the matrix layer which consists of a spongy mass. It is not very dense and large vacuoles are seen in it. Then follows the three fiber layers conveniently termed as the external, median and the internal fiber layers. The last of this is probably made up of spiral connective tissue.
The nematodes do not possess a true epithelium since the cuticle covers the outermost cellular layer of the nematode body. It has, therefore, been called the hypodermis. It consists of a very thin layer lying in between the cuticula and the somatic musculature of the body. It is to be regarded as a syncytium since no cell boundaries are seen in it. In the posterior region of the body it becomes so thin that it appears to be almost insignificant and it seems as if the musculature is applied directly to the cuticle. In the anterior region in front of the nerve ring, it fills up the space between the oesophagus and the body-wall, but behind the nerve ring it suddenly becomes very thin and is seen as a very thin layer under the cuticle (Fig. 8).

It has four longitudinal thickenings, one dorsal, one ventral and two lateral, protruding internally between the longitudinal muscles in the form of bands and dividing them into four sectors. These bands are known as chords. They are named as dorsal, ventral and lateral chords according to their position. Nuclei are present in the cytoplasm of all the chords. These nuclei belong to the hypodermis and are only found in the chords. No nuclei are seen in the general hypodermal layers. Of these the dorsal and the ventral chords carry the dorsal
and the ventral longitudinal nerves respectively
and the lateral chords in addition to the lateral
nerves also carry the longitudinal excretory vessels.
In Physalloptera varani no sub-median thickenings of
the hypodermis are present.

The lateral chords.

Each lateral chord begins to appear in the
anterior region of the body as undivided thickening
of the hypodermis at a distance of about 50 μ from the
anterior extremity. These run as such for about 150 μ
when the inner lining of the hypodermis begins to grow
inward ultimately dividing the lateral chords, vertically
into two halves (Figs. 10, 11). This division is
maintained throughout the entire length of the chords.
As we proceed posteriorly the size of the chords in-
creases till each of these almost occupies about one
third of the body space. In the posterior region of
the body they gradually decrease in size but continue
right up to the tip of the tail (Fig. 21). These chords
divide the body into two halves one ventral and the
other dorsal.

The neck of the lateral chords, i.e. the place
where they leave the hypodermal layer, is quite narrow
but as they grow inwards they spread out like a fan in the body space (Fig. 8). The cytoplasm of these chords is dense and granular. Generally the nuclei are found in the neck region of the chords, mostly appearing simultaneously in the two halves (Fig. 12). However, they are in no way restricted to this place and are also found scattered in the broad fan like portion (Fig. 8). The nuclei are numerous and no cell constancy seems to be indicated.

The dorsal chord.

It appears practically at the level of the origin of the lateral chords. It also extends right up to the tip of the tail. For a short distance it continues to be quite prominent but gradually it becomes insignificant and remains so almost up to the anus. Behind the anus it again becomes prominent (Fig. 21). Anteriorly very few nuclei are present in it. Their number, however, is increased in the post-anal region (Fig. 9). The dorsal longitudinal nerve runs within it and receives the innervating processes from the somatic muscle cells on its neither side in the dorsal half of the body (Fig. 8).

The ventral chord.

It is diametrically opposite to the dorsal
chord and is situated in the middle of the ventral half of the body. It makes its appearance practically at the same level as does the dorsal chord. Beginning anterior to the nerve ring, it also runs throughout the entire length of the body up to the posterior most extremity of the tail. Just like the dorsal chord its size diminishes in the middle of the body, but, unlike it, it shows modifications in the regions of the excretory pore, the anus and the vulva. These will be dealt with later. It again becomes quite conspicuous in the posterior third of the body and remains so till it reaches the tip of the tail. Only a few nuclei are present in it anterior to the nerve ring but their number increases in the post-anal region (Fig. 9). It carries the ventral longitudinal nerve, and, therefore, like the dorsal chord, it also receives all the innervation processes from the somatic muscle cells on its either side in the ventral half of the body (Fig. 8).
MUSCULATURE

The musculature of the body, in the case of a nematode, is generally divided into two main types: the somatic musculature and the specialised musculature.

Somatic musculature.

Somatic musculature is the general musculature of the body-wall and begins anteriorly on a level with the mouth opening. It is constituted by a single layer of muscle cell which are attached to the underlying hypodermis at their base. These cells lie parallel to each other and are divided into four primary muscle fields due to the presence of the chords. Two of these are sub-dorsal and two sub-ventral. All the cells are almost uniform in height (Fig. 8).

Schneider (1866) was the first to point out that in nematodes the processes of the muscle cells extend to the motor nerves instead of the nerve processes extending to the muscle cells as is the case in other animals. This appears to be true in the present case. Processes always bend in the direction of the dorsal and ventral nerves and never in the direction of the lateral chords. In some cases the processes of the adjacent cells may first anastomose with each other.
(Fig. 8). Posteriorly this tendency appears to be more marked.

In 1860 Schneider proposed the names platymyarian and coelomyarian for the structure of the muscle cells and meromyarian and polymyarian for their number in a particular field. The first division was based on the structure of the fibrillar portion of the individual muscle cell. If it was flat towards the body cavity it was called "platymyarian" and if it was notched it was named as "coelomyarian". The second division was according to the number of cells in a given field. Their arrangement is "meromyarian" if few of them are present in one field, but if they are numerous it is known as "polymyarian". It is also a general coincidence, though there are exceptions, that these nematodes which are platymyarian are also meromyarian and those which are coelomyarian are polymyarian. In *Physaloptera varani*, the musculature is coelomyarian and polymyarian.

**Histology of the somatic muscle cell.**

These cells are made up of two portions: the fibrillar and the sarcoplasmic. On the average these two portions are more or less equal in size throughout the body.
In the fibrillar part, which is in the shape of the letter V or U, the notch varies in depth from a barely perceptible one to one almost reaching the base of the cell (Figs. 14-17). This part is highly muscular and is packed with muscle fibres which are transversely arranged.

The remainder of the cell which faces the general body cavity is constituted by the sarcoplasmic portion. It includes a very large oval nucleus measuring up to 60 μ in diameter, and containing a single, deeply stained nucleolus. The sarcoplasmic portion of these cells gives out processes which join into a common fibre which runs towards the ventral or the dorsal nerves and ultimately joins them. None of these processes, however, goes to the lateral chords.

**Specialised muscles**

Under this head will be described muscles which are apparently of the same origin as the somatic musculature but limited to some particular part of the body such as the oesophagus, the rectum and the bursa in the male.

**Somato-oesophageal muscles**

At a distance of 66 μ from the anterior extremity
of the body are found two pairs of muscles, one in its dorsal and the other in its ventral sector. They start from the general somatic musculature on either side of the dorsal and ventral chords respectively and extend right up to the lumen of the oesophagus. They have an average length of 50 µ and a width of 10 µ (Fig. 13). They enlarge the lumen of the oesophagus by their contraction and thus help in the ingestion of food.

Musculus ani.

This muscle has been described by various authors from different nematodes under different names. Looss (1905) called it "musculi anales" for which, as Magath (1919) pointed out, there is no justification. It is a single muscle and should have a singular name. Magath (1919), therefore, called it "musculus ani". Chitwood (1950), however, names it as "depressor ani".

It is situated between the dorsal wall of the rectum and the dorso-lateral side of the body. From its insertion on the dorsal side of the rectum it spreads out like a fan and assumes a shape which corresponds roughly to the letter H. There is a single, large and spherical nucleus in the centre of this muscle (Figs. 18-20). When it contracts it pulls the gut
down and at the same time straightens the tail. It is because of its characteristic shape and double insertion that it is able to perform this dual function simultaneously.

This muscle is found only in the females. In the males, apparently, its function is taken over by the caudal muscles.

Copulatory muscles.

Transverse muscles are found extending from the ventral sides of the lateral chords to the subventral side of the body in the caudal region of the male. These are confined to the region just anterior to the cloacal opening. Each muscle has a sarcoplasmic region which contains the nucleus (Fig. 21). These muscles, upon contraction, are responsible for the ventral curvature of the body, a persistent difficulty in fixing the tail in a flattened position. During the copulation these muscles bring down the caudal alae around the female's body, thereby affording the male a firmer and stronger grip over the female.
LEGENDS

Plate I

Fig. 1. Anterior end of female from a glycerine cleared toto preparation.

Fig. 2. T.S. through cuticle.

Fig. 3. Same - magnified.

Fig. 4. T.S. through the caudal region of the male.

Fig. 5. Bursa drawn from a glycerine cleared toto preparation.

Fig. 6. The pedunculated papillae.

Fig. 7. The sessile papillae around the cloaca.

Fig. 8. T.S. through the intestinal region of the female.

Fig. 9. Reconstruction of the posterior region of the female from 12 L.S.

Fig. 10. T.S. through very anterior region of the male showing the beginning and formation of the right lateral chord.

Fig. 11. T.S. through very anterior region of the male showing the beginning and formation of the left lateral chord.

Fig. 12. T.S. through the nerve ring.

Fig. 13. T.S. through very anterior region of female.

Figs. 14-17. Individual muscle cells.

Fig. 18. Posterior region of female from a glycerine cleared toto preparation, Lateral view.

Fig. 19. Reconstruction of musculus ani from 8 L.S. through the posterior region of the female.

Fig. 20. T.S. through musculus ani.

Fig. 21. T.S. through the caudal region of the male.
NERVOUS SYSTEM

General plan.

Studies made on the nervous system of nematodes have been very scanty. Whatever work has been done is confined to a few species only. Of these *Ascaris lumbricoides*, *Parascaris equorum* and *Cephalobellous papilliger* are the only worms which have been studied in detail. The work on the nervous system of *Ascaris* has been very extensive and for this we are indebted particularly to Apathy (1894), Deineka (1908) and Goldschmidt (1908-1910). *Ascaris* is one of the highest specialised groups and although its structures present the common fundamental plan of the nemat nervous system they are bound to be specialised and complicated. If some of the less specialised groups are studied on the basis of this monumental work, it would certainly become easier to understand the entire system much more clearly and correctly.

The nervous system of *Physaloptera varani* confirms to the general basic plan of this system in nematodes as a group. There is the usual nerve ring around the oesophagous. It is a little inclined with the dorsal side slightly tilting anteriorly, and is
associated with four ganglia, a dorsal ganglion, a ventral ganglion and a pair of lateral ganglia. Six nerves proceed anteriorly from the region of the nerve ring, four of these go to the labial papillae and the remaining two culminate into the amphids. From the posterior side of the base of each of the cephalic ganglia there starts one longitudinal nerve which runs in a posterior direction embedded in the chord of its side. In the course of the ventral nerve, at the level of the excretory pore, is a small ganglion - the post-ventral ganglion. In the anal region there is one ganglion in the ventral nerve and one ganglion in each of the lateral nerves. The former is called as the anal ganglion while the latter are known as the lumbar ganglia. The arrangement of ganglia and nerves in this region of the body is different in the two sexes. In the male an additional pair of ganglia, the rectal ganglia, develops in the ventral nerve, a little posterior to the anal ganglion. Further each of the pedunculated papillae receives a branch from the lateral nerves. The latter ultimately terminate in the phasmids. The dorsal and the ventral nerves end in the post anal region of the body. The anal ganglion is connected by means of a commissure on each side to the lumbar and rectal ganglia (Figs. 22, 23, 24).
Nerve ring and cephalic ganglia.

The circumoesophageal cephalic commissure, popularly known as the "nerve ring", is situated in the posterior part of the muscular portion of the oesophagus, at a distance of about 320 µ from the anterior extremity. It completely encircles the oesophagus which is slightly notched to accommodate it. It is slightly inclined in position with the dorsal side slightly tilting anteriad. On the average, its width is about 60-65 µ. It is composed of fibres and contains a few nerve cells in it (Fig. 12). Four nerves, of which two are sub-dorsal and two are sub-ventral, proceed from it anteriorly to the labial papillae. Another four longitudinal somatic nerves leave it posteriorly to run posteriad, one in each of the hypodermal chords. Associated with the nerve ring are four ganglia, one dorsal, one ventral, and two lateral ganglia (Figs. 1,12,22). There is one more ganglion in the ventral nerve, situated a little behind the nerve ring. This is known as the post-ventral ganglion (Fig. 22).

Dorsal ganglion.

The dorsal ganglion, as its name suggests, is applied to the dorsal side of the nerve ring and lies
anterior to it. It is a comparatively small ganglion made up of 23 nerve cells. These cells are unipolar as well as bipolar and under oil immersion their processes can be studied up to some distance (Figs. 39, 40). This ganglion is in direct connection with the nerve ring (Figs. 22, 25). The dorsal longitudinal nerve starts from the nerve ring just posterior to this ganglion.

**Ventral ganglion.**

The ventral ganglion is comparatively bigger in size and comprises of 40 cells which are very compactly arranged. Here again, the cells are both unipolar and bipolar (Figs. 39, 40). This ganglion is also in direct connection with the nerve ring and is applied anteriorly to its ventral side (Figs. 22, 26). The ventral longitudinal nerve starts from the nerve ring behind this ganglion.

**Post-ventral ganglion.**

At the level of the excretory pore, and in the course of the ventral nerve, is situated another small ganglion, the post ventral ganglion. It consists of about 13 cells which are mostly unipolar (Fig. 39). The number of cells in this ganglion seems to vary in different specimens. In two specimens, 13 cells were
counted, while in another only 11 were found. The ventral nerve bifurcates in the region of the excretory bridge and both the branches thus formed reunite immediately posterior to it. The post-ventral ganglion is situated between these branches (Figs. 22, 23). Goldschmidt (1908-1910) and Magath (1919) also described a similar ganglion in the course of the ventral nerve in *Ascaris* and *Camallanus* respectively.

**Lateral ganglia.**

There are two lateral ganglia situated laterally one on either side of the body (Fig. 22). These have about 25 cells each and are in direct communication with the nerve ring lying mostly posterior to it (Fig. 27). Whereas the dorsal and the ventral ganglia are compact and confined to a small area, the lateral ganglia are rather elongated and occupy considerable space longitudinally on either side of the nerve ring. In fact, some of their cells lie even anterior to the nerve ring. These ganglia are also not so broad as the dorsal and ventral ganglia. The amphidial nerve starts from their anterior end, and posteriorly they give rise to the lateral longitudinal nerves (Figs. 22, 27).
The nerves.

It is customary to divide the nerves in a nematode into two heads viz: the anterior nerves and the somatic nerves. The former are situated anterior to the nerve ring while the latter are found posterior to it.

Anterior nerves.

As has already been mentioned, six nerves are present in the region anterior to the nerve ring. Of these, two are sub-dorsal, two sub-ventral and two lateral. The sub-dorsals leave the dorsal side of the nerve ring and go direct to the two sub-dorsal papillae. Similarly, the two sub-ventrals start from the ventral side of the nerve ring and supply the sub-ventral pair of the papillae. Anteriorly just before reaching the papillae each of these nerves bifurcates, the two branches, however, terminate in the same papilla. Throughout their length these nerves run very close to the oesophagus (Fig. 22).

The two amphidial nerves, which are lateral in position, do not begin, like the papillary nerves, directly from the nerve ring, but start from the lateral ganglia. Anteriorly they innervate the amphids
and run parallel to the papillary nerves (Fig. 22).

Somatic nerves.

The nerves which extend posterior to the nerve ring are collectively known as the somatic nerves. These include a ventral, a dorsal and a pair of lateral nerves which run in the ventral, dorsal and the lateral chords respectively.

Dorsal nerve.

The dorsal nerve begins at the base of the dorsal ganglion from the dorsal side of the nerve ring. It runs throughout the length of the body embedded in the dorsal chord near its inner margin. It receives all the innervating processes from the somatic muscle cells lying on its either side in the dorsal half of the body (Figs. 8, 22). Hence it is to be regarded as a motor nerve. No ganglia were observed in it throughout its entire length. It ends posteriorly in the tail rather insignificantly.

Ventral nerve.

The ventral nerve is situated diametrically opposite to the dorsal nerve in the corresponding
ventral chord. It originates immediately below the ventral ganglion from the ventral aspect of the nerve ring. The ventral nerve bifurcates in the region of the excretory bridge, its two branches go round the post-ventral ganglion and unite posterior to it again forming a single nerve which proceeds backwards, passing to the right of the excretory pore. Occasionally nerve cells are observed during the course of this nerve.

Just like the dorsal nerve, the ventral nerve also receives all the innervating processes from the somatic muscle cells on its either side in the ventral half of the body (Figs. 8, 22). Thus it is also to be regarded as a motor nerve. In the posterior region of the body, beyond the rectum, the ventral nerve is involved in certain ganglionic formations. As these structures are different in the two sexes, they are dealt with separately.

**Lateral nerves.**

One lateral longitudinal nerve is found lodged in each of the lateral chords. It begins directly from the lateral ganglion which is attached to the side of the nerve ring. They run posteriad just like the dorsal nerve. In the region of the rectum these nerves are
also involved in certain ganglionic formations which are described below (Fig. 22).

**Posterior region of female.**

There is a small ganglion associated with the ventral nerve in the region of the rectum. This ganglion is known as the anal ganglion. It consists of 7 cells. One of these cells is multipolar, three bipolar and three unipolar (Figs. 39, 40, 41). Their processes can easily be observed clearly under high magnification. Beyond this ganglion, the ventral nerve continues along its smooth course, passing to the right of the anus, and ultimately ends insignificantly in the posterior region of the tail, (Figs. 23, 29).

In addition to the anal ganglion, two more ganglia are present in this part of the body. These are the lumbar ganglia. They are developed on the lateral nerves in the region of the rectum. These are still smaller each consisting of only 5 cells, all of which are bipolar (Fig. 40). Whereas the anal ganglion is a compact ganglion, the lumbar ganglia are elongated. The lateral nerves continue beyond the lumbar ganglia and ultimately terminate in the phasmids.
Two bipolar nerve cells are present in each of these nerves a little anterior to the phasmds (Figs. 23, 30, 31).

The author could not locate any ano-lumbar commissure connecting the anal ganglion with the lumbar in the female, although it could be observed in the male.

**Posterior region of male.**

The nervous system of the tail region in the male is a little different as compared to that of the female. It is probably due to the increased activity of this region for the reproductive functions.

The anal ganglion in the male is comparatively bigger and much more compact than in the female. It consists of about 10-12 cells, most of which are bipolar (Fig. 40). It is situated in the ventral nerve just behind the union of the reproductive duct with the alimentary canal (Figs. 24, 33).

There are two small ganglia which are situated laterally a little behind the anal ganglion one on either side of the rectum. These are known as the
rectal ganglia. Each of these ganglia is made up of only 4 cells which are bipolar (Fig. 40). Both the ganglia are connected with each other by means of a rectal commissure. Anteriorly they are in communication with the median anal ganglion by means of a pair of ano-rectal commissures (Figs. 24, 34). From here the ventral nerve proceeds backwards to end in the posterior region of the tail.

In addition to the anal and the rectal ganglia two lateral lumbar ganglia are also present. These are similar to those found in the female. They are situated in the lateral nerves slightly posterior to the rectal ganglia. They are larger in size and are more compact than the ganglia of the female and are made up of a comparatively larger number of cells. Each ganglion consists of about 12 cells, most of which are bipolar. A few unipolar cells are also present (Figs. 39, 40). The two lumbar ganglia are connected with each other by means of a transverse lumbar commissure running across the body above the rectum (Fig. 36). They are also connected with the anal ganglion by means of a pair of ano-lumbar commissures (Figs. 24, 35). All these connections together form a kind of ring round the rectum. This ring is not complete in the female as no transverse lumbar commissure
was observed there.

Posterior to the lumbar ganglia the lateral nerves give out branches to the pedunculated papillae of their respective sides, each papilla receiving a single undivided fibre. In this species there are four pedunculated papillae on each side of the tail and therefore the number of the branches given out from each lateral nerve is four. Each of these branches bears a bipolar nerve cell before it enters the pedunculated papilla (Figs. 24, 37). Finally the lateral nerves end in the phasmids. Just as we find in the female, one or two nerve cells are present in their course before they reach the phasmids (Fig. 3).

Phasmids.

Chitwood and Chitwood (1933) divided nematodes into two major divisions known as Phasmidia and Aphasmidia. Their division was based on the presence in the former and absence in the latter of a pair of lateral papillae or "phasmids" found in the tail of the parasitic nematodes. The term owes its origin to Cobb (1923) who, considering their differences from the ordinary sensory papillae met within the group, called them "phasmids", i.e. "ghost-thing".
Very little is known about the phasmids at present. They are found in the tail of the parasitic nematodes and are accredited with some sensory function. Only a pair of these is found on a worm. They are very much like the amphids of the anterior extremity and are more pore-like in nature than papillaeform. They receive their nerve supply from the lateral nerves which terminate in them. Each of the phasmids is further provided with a phasmdial gland (Figs. 32,38).
LEGENDS

Plate II

Fig. 22. Diagrammatic representation of the nervous system in the anterior region of the body.

Fig. 23. Diagrammatic representation of the nervous system in the posterior region of the female.

Fig. 24. Diagrammatic representation of the nervous system in the posterior region of the male.

Fig. 25. Reconstruction of the dorsal ganglion.

Fig. 26. Reconstruction of the ventral ganglion.

Fig. 27. Reconstruction of the lateral ganglion.

Fig. 28. Reconstruction of the post ventral ganglion.

Fig. 29. Reconstruction of the anal ganglion of female.

Fig. 30. Reconstruction of the lumbar ganglion of female.

Fig. 31. L.S. through the phasmod of female.

Fig. 32. L.S. through phasmodial gland of female.

Fig. 33. Reconstruction of the anal ganglion of male.

Fig. 34. Reconstruction of the rectal ganglion of male.

Fig. 35. Reconstruction of the lumbar ganglion of male.

Fig. 36. T.S. through the lumbar commissure.

Fig. 37. T.S. through the pedunculated papillae.

Fig. 38. T.S. through the phasmodial gland of male.

Fig. 39. Unipolar nerve cells.

Fig. 40. Bipolar nerve cells.

Fig. 41. Multipolar nerve cells.
EXCRETORY SYSTEM

The history of the study of the excretory system of nematodes is very interesting. For a long time the function of the structures that we now know as being excretory could not be settled. Attempts were made to assign them circulatory functions. They even have been regarded as salivary glands. Again, at times, these structures were studied as such without making an attempt to ascribe any function to them.

Bojanus (1817), working with *Parascaris equorum*, was the first to discover a pair of vessels in the lateral chords. In the anterior region of the body these vessels were joined with each other through the formation of a bridge. He thought them to be the blood vessels. Cloquet (1824) too observed the lateral vessels together with the bridge. He also thought them to be circulatory. Mehlis (1831) seeing a gland opening near the head in *Contracaecum spiculigerum* considered it to be a salivary gland. He also found such glands opening at the mouth in strongylids and regarded them to be salivary glands. Schneider (1860) found these glands to be excretory. In 1841 von Siebold also noted the presence of paired lateral canals with
their ventral opening but did not assign any function to these structures.

The "circulatory" hypothesis reached its climax when Blanchard (1847) described the large nucleus in the wall of the lateral vessel of *Ascaris lumbricoides* as a "heart". He also asserted the presence of another pair of vessels just under the cuticle.

Schneider (1858, 1860, 1863, 1866) critically examined and put together all the available information and different interpretations regarding these structures. He showed that Blanchard was mistaken in both of his conclusions. Firstly, his "heart" was simply a large nucleus in the vessel wall, and, secondly, there was no second pair of vessels besides the one in the lateral chords which after forming a bridge opened to the outside by a single median ventral pore. As a general statement he said that all "more" and "polymyarian" nematodes have got lateral vessels which are usually absent in "holomyarian" nematodes, an exception being made, in the latter case, for *Anguina tritici*. In 1866, for the first time, he pointed out that this system of vessels is to be regarded as
excretory, being responsible for the excretion of the chemical waste products of the nematid metabolism. Bastian (1866) verified most of Schneider's observations and made special mention about the absence of vibratile cilia in the lateral vessels of nematodes. He thought that these vessels were not respiratory but excretory in function. Both Bastian (l.c.) and Cobb (1890) considered that the excretory system in nematodes originates from a single cell. Golowin (1902) differed from these authors and concluded that the terminal excretory duct and the excretory sinus originates separately. Goldschmidt (1906) in his description of the excretory system in *Ascaris* substantiated Golowin. Mueller (1929) after an extensive study of *Ascaris lumbricoides* and *Paraascaris equorum* came to the conclusion that this system was not excretory in function. Chitwood (1938) examined the fluid coming out of the excretory pore in pig ascarids. He claimed that 0.02 per cent of urea was present in it. He was, however, doubtful as to whether this urea was the excretory waste of the *Ascaris* itself, and also thought of the possibility that it could have been derived from the host. However, it was established that this system does eliminate urea from the nematid body, no matter whether it is obtained from the host or is a normal excretory
product of nematodes. Since then the excretory role of these structures in nematodes is, more or less, firmly established. Attempts have been made to divide the whole group in four main and fundamental types as follows:-

1. the oxyuroid or simple H-shaped system. It is found in oxyuroids, some ascaridoids, and some times in the Spirurina.

2. the rhabditoid system. It is a combination of H-type with two sub-ventral glands. It is found in rhabditids and strongyloids.

3. the ascarid or the inverted U-shaped system. It is met with in ascaridids, many spirurids and also in some free-living forms.

4. the asymmetric system, known only in Anisakinae and Tylenchoidea.

Basir (1949) studied in detail the excretory system of Physaloptera varani. In Physaloptera varani the excretory system is that of the ascaridid or the inverted U-type. The canals lie in the two lateral chords in a V- or U-shaped area formed at the union of the two halves of the chords towards the body cavity. This is a thick granular portion devoid of any nuclei (Fig. 47). The canals, throughout their course, lie within the chords as can easily be seen since the inner
margin of the chords is always found between them and the body cavity. The canals begin as blind tubes in the posterior third of the body and run within the lateral chords in an anterior direction up to a point about 570 μ from the anterior tip of the body. At this place the lateral chords extend towards the ventral chord where they anastomose with each other forming a sort of bridge. The lateral vessels are also carried along with these chords and join ventrally to form a sinus. From this sinus is given out a short terminal duct, which after describing an outward turn come to the exterior on the ventral side at a distance of about 520 μ from the anterior end of body (Figs. 43, 45).

The histological composition of the lateral canals is far from certain. They appear to be formed by two layers, the inner of which very much resembles the cuticle. It is to be noted that many authors believe it to be derived from the external cuticle. But it is to be remembered that the canals are blind posteriorly and open only through a very minute pore anteriorly and, under these circumstances, the invasion of cuticle through the minute excretory pore may not be easily explained. The layers are perfectly uniform throughout their entire length. No nuclei were observed in them.
Situated in the middle of the bridge in the region of the sinus is a large nucleus, almost round in shape and measuring 9 µ in diameter (Fig. 42). The bridge, no doubt, encircles the oesophagus ventrally but the intervening distance is about 200 µ and, apparently there seems to be no histological connection between the two. Such histological connections are indispensable if oesophagus is to be accredited with some excretory function. In the present case, therefore, it seems that it has nothing to do with excretion.

The terminal excretory duct or the excretory vesicle opens to the exterior on the ventral side at a distance of 522 µ from the anterior end of the body (Figs. 43, 46). A nucleus is seen just on the top of the duct and medial to it (Fig. 44). It is the nucleus of the carrying cell of the excretory vesicle.

This cell proves to be the sole and major objection in the acceptance of the general conception of the unicellular origin of the excretory system in nematodes. The fact that Cobb and other advocates of this idea not only fail to account for it but also do not, apparently, acknowledge its existence, is worthy of note. Basir (1949), working with Physaloptera varani, also mentioned these two cells, and concluded "The excretory system in this case appears to be developed
from two cells originally, forming two separate structures, one cell forming the terminal excretory duct and the other giving rise to the sinus which gives out the lateral excretory ducts. The terminal excretory duct joins the sinus to complete the system." The present author is in full agreement with this view and does not think that the excretory system in nematodes is unicellular in origin, but is derived from two cells: one of the sinus and the other of the terminal excretory duct.
DIGESTIVE SYSTEM

The digestive system in *Physaloptera varani* is well developed and shows the usual components of the nematid digestive system. It begins with a dorso-ventral oral opening which is enclosed by two fleshy lateral lips. The mouth is continued into the oesophagus through a very short and reduced stoma. The oesophagus is divisible into two regions: a short anterior muscular portion and a long posterior glandular part. It communicates with the intestine through a conspicuous oesophago-intestinal valve. The intestine is a long, straight tube which opens posteriorly into the rectum through an intestino-rectal valve. In the females the rectum opens to the exterior by a ventrally situated anus while in the males the reproductive duct unites with it to form a cloaca which ultimately opens to the exterior on the ventral side as the common ano-genital aperture.

Cephalic structures.

In an en face view (Fig. 48) two massive, fleshy and unlobed pseudolabia are observed. They are lateral in position. Each of these bears a large pointed median tooth towards its inner external margin, one
small lateral tooth on each side and seven denticles between the median and each of the lateral teeth. Thus the number of the lateral teeth on each lip is two and the number of the denticles is fourteen. Each lip bears two double papillae on its external surface, one of which is sub-dorsal and the other sub-ventral in position. Each of these papillae is believed to have been formed by the fusion of the originally dorso-dorsal and latero-dorsal papillae in the case of the sub-dorsal, and ventro-ventral and latero-ventral papillae in the case of the sub-ventral. This fact is also borne out by the nerve supply to these papillae. The papillary nerves supplying each of these papillae divide into two branches at the time of entering them, both of these branches innervating the same papilla. In addition to these papillae each lip also bears an amphid which is lateral in position and externally appears like an aperture.

**Stoma.**

The universal condition of a reduced stoma in the family **Physalopteridae** is no exception here. It is greatly reduced, the oesophageal tissue almost reaching the very base of the pseudolabia. Moreover, it is because of this condition that the oesophageal
lumen at its commencement is not triradiate but is dorso-ventral.

**Oesophagus.**

The detailed study of the oesophagus of *Spirurina* has more or less been neglected. The oesophageal glands of some members of this group have been studied by Looss (1896), Jagerskiold (1897), Magath (1919) and Hsu (1933). Basir (1948) has, however, given a detailed account of the histological anatomy of the oesophagus of *Physaloptera varani*, the species under study.

The oesophagus is a cylindrical tube which is narrow at the beginning and which gradually becomes wider posteriorly. It begins just after the very short stoma, as a dorso-ventrally flattened slit at a distance of about 48 μ from the anterior extremity (Fig. 49). Immediately after its commencement, the median slit gives forth a branch on the right side in the middle of the lateral sector. This branch ultimately forms the right sub-dorsal ray of the oesophageal lumen. It attains its full length at about 90 μ from the anterior tip from where the oesophagus assumes
its characteristic nemat appearance with a triradiate lumen (Figs. 50, 54). Normally one arm of the tri-radiate lumen always points towards the ventral side, the remaining two being sub-dorsal. The ends of the lumen taper to a point and there is absolutely no indication of the presence of any cylindrical tubes in any region. The lumen is lined by a cuticular lining which is in continuation with the external cuticle of the body. In a transverse section it appears to be quite thick, measuring about 1 μ in thickness (Fig. 54). The external covering of the oesophagous, tunica propria, is comparatively thin and it appears to be semi-cuticular in nature. The lumen continues to be triradiate throughout the length of the oesophagous till just before the formation of the oesophago-intestinal valve where it again becomes laterally compressed (Fig. 57). The length of the oesophagous varies with the age of the worm. On the average, it is about 7.5 per cent of the total body length.

The oesophagous can roughly be divided into two portions: a short anterior muscular region followed by a long posterior glandular part. These two regions of the oesophagous can easily be differentiated from each other. A slight constriction is seen posteriorly in
the muscular region of the oesophagus. This is to accommodate the nerve ring rather than to demarcate the two portions of the oesophagus (Fig. 55). The short muscular portion of the oesophagus consists solely of the muscles. As has already been stated the relative measurements of the various parts of the oesophagus are dependent upon the age of the worm. In a worm, 2.7 cm. long, the anterior muscular portion measures 430 μ. It terminates just behind the nerve ring.

The rest of the oesophagus consists of the glandular part which measures 1.67 mm. in a worm 2.7 cm. long. The ratio between the two portions of the oesophagus will thus be about 1:3.9. The glandular oesophagus consists of the radial muscles and the glandular protoplasm. It is certainly much wider than the muscular region and the oesophageal glands and the innumerable gland and the radial muscle nuclei are lodged in it. Although these two divisions of the oesophagus certainly differ histologically from each other still they are to be regarded as two regions of one and the same structure because:-

(1) Both have a continuous external covering.

(2) In both the inside lumen together with its lining is continuous.
(3) The protoplasmic contents of both these regions are also continuous.

(4) No valve is present between them.

The radial muscles in the glandular part of the oesophagus are dispersed. The marginal muscles are not found here, their work being taken over by the radial muscles themselves.

**Oesophageal glands.**

Three oesophageal glands are present, one dorsal and two sub-ventral. These appear at the anterior margin of the glandular portion of the oesophagus. They open directly into the lumen of the oesophagus by means of ducts. These terminal ducts are lined by a thick cuticle which is a continuation of the cuticula of the oesophageal lumen. All these glands are multi-nucleate. It is interesting to note that the opening of these glands is not a constant feature. In one female all the three glands open simultaneously at a distance of about 522 μ from the anterior extremity (Fig. 43). In other males and females the glands do not open simultaneously. The opening of the dorsal gland is a few micra anterior to the openings of the sub-ventrals. However, in all such cases where the
glands do not open simultaneously their openings are never far removed from each other and are situated only a short distance posterior to the anterior margin of the glandular portion of the oesophagus. It is also to be noted that Looss (1896) and Jagerskiold (1897) have also reported the glandular openings in this genus as being placed more or less at the same level. Basir (1948) describing the gland orifices in *Physaloptera varani* observed that "Sections of a younger specimen show that the openings of the sub-ventral glands are about 65 μ posterior to the orifice of the dorsal gland but in fully mature specimens they seem to migrate anteriorly so that the openings of all the glands come to be situated at more or less the same level".

The glandular ramifications are numerous. A longitudinal duct runs in each gland. The former, during its course, gives out diverticulae on its sides. Both the longitudinal duct and its diverticulae appear to be devoid of any cuticular lining. The gland nuclei are numerous, as many as fifteen being counted in a single cross-section. They are found in a much larger number in the posterior region of the glandular part of the oesophagus. These nuclei are rather small in size and have a uniform shape. Each of these contains a spherical black-staining nucleolus in the centre.
The significance of these glands is far from certain. However, their position, and openings into the lumen of the oesophagus would no doubt suggest some digestive function. Chitwood (1950) and several other workers are of the same opinion.

Nuclear distribution.

Looss (1896) first observed a nuclear or cell constancy in the nemic oesophagus with reference to the marginal, radial and the gland nuclei. Since then a number of other workers have confirmed his observations.

In the present case only six marginal nuclei were observed lying in two groups of three each. These are confined to the anterior muscular region of the oesophagus. In the glandular part no marginal nuclei were found as there are no marginal muscles in this region. Their place is taken up by the radial muscles which are widely dispersed. The first set of the marginal nuclei is found at a distance of about 110 μ from the anterior end of the body. This is followed by three groups of the radial nuclei, each consisting of three nuclei. These, in turn, are followed by the second and the last set of the marginal nuclei. In the younger specimens, however, only two sets of the radial
nuclei are found between the two sets of the marginals. This account agrees with the observations of Basir (1948).

The radial nuclei are numerous and are found throughout the whole length of the oesophagus. They are present in two groups: one of three and the other of six. The latter are situated on either side of the tips of the radii while the former are inter-radial in position (Fig. 52). The former are considerably bigger in size than the latter. These nuclei possess a big black-staining nucleolus in the centre.

There are only six nerve cells forming two groups of three each. The nerve cells are inter-radial in position (Fig. 53). Between these two groups of nerve cells is situated another group of three radial nuclei. All the nerve cells are found in the vicinity of the oesophageal gland openings. The cells contain a round nucleus and a deeply staining spherical nucleolus (Fig. 53). In the younger specimens, however, the first set of the nerve cells is found at the posterior margin of the muscular region of the oesophagus. Basir (1948) counted only five nerve cells in Physaloptera varani. His first set consisted of two cells only. In the present study, however, six cells were always observed, the two sets consisting of three cells each.
The presence of only a few nerve cells may be due to the absence of a valved oesophageal bulb which necessitates a complicated oesophago-sympathetic nervous system as is found in some other groups of nematodes.

As already stated above the gland nuclei are numerous and are found scattered throughout the glandular portion of the oesophagous.

### Table I.

<table>
<thead>
<tr>
<th>R.S.V.</th>
<th>D</th>
<th>L.S.V.</th>
</tr>
</thead>
<tbody>
<tr>
<td>r 3</td>
<td>r 1</td>
<td>r 2</td>
</tr>
<tr>
<td>r 6</td>
<td>r 4</td>
<td>r 5</td>
</tr>
<tr>
<td>r 9</td>
<td>r 7</td>
<td>r 8</td>
</tr>
<tr>
<td>r 12</td>
<td>r 10</td>
<td>r 11</td>
</tr>
<tr>
<td>N 3</td>
<td>N 1</td>
<td>N 2</td>
</tr>
<tr>
<td>r 15</td>
<td>r 13</td>
<td>r 14</td>
</tr>
<tr>
<td>N 6</td>
<td>N 4</td>
<td>N 5</td>
</tr>
<tr>
<td>r 18</td>
<td>r 16</td>
<td>r 17</td>
</tr>
<tr>
<td>r 21</td>
<td>r 19</td>
<td>r 20</td>
</tr>
<tr>
<td>r</td>
<td>r</td>
<td>r</td>
</tr>
<tr>
<td>r</td>
<td>r</td>
<td>r</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Oesophago-intestinal valve.

Most of the nematodes possess a valve at the junction of the oesophagus with the intestine. Many of the authors have designated it as an "oesophageal valve", while others, notably Looss (1905, 1911) believe it to be an intestinal valve. In the present case, however, it has been found that it is definitely formed by the oesophageal tissue. Chitwood (1931) proposed the term "oesophago-intestinal valve" for this organ. He (1950) further remarked that "strictly speaking the oesophago-intestinal valve is a part of the oesophagus". Magath (1919), working with Camallanus americanus, also comes to the same conclusion. In the species under study the valve presents a more or less triangular outline. It is about 90 μ in length (Fig. 59).

Just before the formation of the valve the sub-dorsal rays of the triradiate lumen of the oesophagus begin to shorten progressively till they merge with the ventral ray, leaving the lumen as a dorso-ventrally compressed slit (Figs. 56, 57). This place is to be regarded as the starting point of the oesophago-intestinal valve. Along with this change in the shape of the lumen, there is a gradual increase
in the radial musculature of the oesophagus and a gradual decrease in the glandular tissue which even in this region contains numerous nuclei (Fig. 57). Gradually the glandular tissue disappears altogether leaving behind only the oesophageal musculature, which is rather quite massive as would be expected if the valve is to be accredited with its usual function (Fig. 57). With the complete disappearance of the glandular tissue the oesophageal valve is completely enclosed within the intestinal epithelium (Fig. 58). This region of the valve is full of radial muscles. The valve as a whole contains two pairs of radial nuclei. This observation also agrees with the findings of Basir (l.c.).

**Intestine.**

The part of the alimentary tract lying between the oesophagus and the rectum is known as the intestine or the mesenteron. It is more or less a simple, straight tube lying generally towards the ventral side of the body. Due to the enormous growth of the reproductive organs in the female it has to accommodate itself in the body-cavity according to the space available. Morphologically it does not vary to any considerable extent throughout its entire length.
The wall of the intestine consists of a single row of epithelial cells. Externally these cells are covered by a layer termed the "basal lamella". Internally they bear a "bacillary layer" which in turn is followed by a "sub-bacillary layer". Each cell has, towards its base, a single large nucleus (Fig. 60).

(1) The bacillary layer.

It appears to be made up of very fine "rods" or "cilia" which sometimes appear as being quite distinct from each other while at others they present a more or less compact arrangement. On the average the width of this layer is about 5 µ, i.e., about one fourth of the rest of the cell. In some preparations, especially of the more posterior region of the intestine, free "rods" were also seen (Fig. 61).

The significance and the structure of the bacillary layer is far from certain. It has been called as "stäbchensaum" to designate the "rod like structure" on the inner surface of the intestinal cells. Its possible function is doubtful. Three possibilities have been out forward:

(1) It is composed of very minute tubes which are excretory or help in resorption.

(ii) It is a protective secretive product.
(iii) It represents degenerate or amalgamated cilia.

There appears nothing to support the first suggestion. The second view has also been dispensed with by Chitwood (1950) on the grounds that this layer does not develop according to the protective needs of the nemic intestine. For instance in nematodes like *Rhabditis* and *Trichuris* which hold to a liquid or a semi-liquid diet and where, apparently, there is no need for protection, this layer is well developed while in nematodes like *Metoncholaimus* which utilize a solid diet and where, apparently, the intestine would require some protection against the coarse food this layer is absent altogether. However, the assumption, put forward by Hetherington (1923), that the nemic intestine once possessed cilia which have now undergone modification, helps us to a certain extent in understanding the structure of this layer.

(2) The sub-bacillary layer.

Immediately below the bacillary layer is a second layer which is named as the sub-bacillary layer. This layer is comparatively much thinner than the outer bacillary layer and also stains comparatively more deeply with the iron-haematoxylin. It resembles the
bacillary layer in having similar "rod-like" structures (Fig. 61). The significance of these structures is also not clear.

(3) The intestinal epithelial cells.

The intestine in this case is "myrioctus", i.e. it has a very large number of cells. All these cells are similar to each other throughout the length of the intestine. No specialization or modification is seen with regard to these cells anywhere in the intestine. However, all of these cells are not of uniform size, and it is due to this inequality in their size that the lumen of the intestine is thrown into irregular folds (Fig. 60). Each cell has a large spherical nucleus measuring about 4 μ in diameter and containing a central large nucleolus which stains deeply. The nuclei are situated at the base of the cells almost at the same level in all of them (Figs. 61, 62).

(4) The basal lamella.

Covering the intestinal cells externally is a darkish, homogeneous layer known as the basal lamella. It is, on the average, 3 μ wide. This layer does not
show any division into cells and appears to be syncytial. The epithelial cells seem to be attached to it internally. The layer can in no way be regarded as a differentiation of the outer surfaces of the epithelial cells. It appears to be a quite distinct and separate layer. There can be little doubt that it acts as a protective sheath for the intestine (Figs. 61, 62).

**Posterior gut.**

The last portion of the alimentary tract that lies beyond the intestine is known as the posterior gut. In nematodes it comprises of four distinct structures: (1) intestino-rectal valve, (2) rectum, (3) cloaca and (4) the so-called rectal glands. In the females the reproductive system has no connection with the alimentary canal except for one solitary example of the genus *Rondonia* Travassos, 1920 (Attractidae). In the males, however, the reproductive system always communicates with the rectum to form a cloaca and opens to the outside through a common ano-genital aperture.

(1) **Intestino-rectal valve.**

Just as the oesophagus forms an oesophago-intestinal valve at the place where it opens into the intestine, in the same way the intestine also forms an
intestino-rectal valve at the place where it communicates with the rectum. It is a simple structure and is formed by the extension of the terminal portion of the intestine which narrows and projects into the lumen of the rectum in the form of a valve. The intestine becomes swollen just before the formation of this valve and at this place its epithelial cells are much smaller and very compactly arranged. The number of these cells is thus greatly increased. The regular arrangement of the nuclei is also disturbed at this place (Fig. 63).

The action of the valve is controlled by a sphincter muscle which encircles it completely. This muscle also gives out extensions to the general somatic musculature of the body (Fig. 64). It is by this muscle that the intestino-rectal valve is closed during defaecation, preventing the re-entry of the waste products into the intestine. The entire process of defaecation is not accomplished by this muscle alone. The musculus ani, an H-shaped uninucleate rectal muscle, which is situated on the dorsal side of the rectum (Figs. 18, 20), plays a much greater part in it. It performs this function in two phases. First it elevates the dorsal wall of the rectum thus helping to draw the waste products from the intestine into the rectal cavity, and then it opens the anus for defaecation by pulling its posterior lip.
The rectum is a more or less flattened tube formed of a cuticular layer which is a continuation of the external cuticula of the body. However, in the formation of the rectal cuticula only the outer two layers of the external cuticula, i.e. the cortex and the matrix layers, take part. The fiber layers stop at the anal opening and do not continue into the rectal cuticula. The cuticular striations of the external cuticula are also absent here and the lining is smooth and straight (Fig. 63). Posteriorly the rectum terminates into a transverse slit-like opening, the anue, which is situated on the ventral side. The cuticula of the edges of the anal slit is slightly raised to form the anal lips. In a worm measuring 2.7 cm. in length, the rectum is 310 μ long and 90 μ wide at its beginning gradually narrowing down towards the anal opening which is only 10 μ wide.

3) The cloaca.

As has already been mentioned, the cloaca is formed only in the males. The vas deferens joins the rectum just posterior to the intestino-rectal valve from the ventral side. Certain structures of the male
reproductive system such as the spicules which are associated with it will be described under the reproductive system. The cloaca terminates posteriorly into a ventrally situated cloacal orifice which is about 30 \( \mu \) wide. The muscles responsible for the opening of the orifice have already been described.

(4) The rectal glands.

In the entire nemat morphology there is no point more controversial than the significance and the function of the so-called rectal glands. These are found in the form of three or sometimes six cells around the posterior end of the intestine. Walter (1856) was probably the first to observe them in *Cosmoserca trispinosa* (= *Oxyuris ornata*). They are of common occurrence in parasitic nematodes and come under the observation of almost every worker but, in spite of this, not much is known about them. They have usually been called as the rectal glands and as such a secretive function has been ascribed to them. On the other hand, Looss (1905), Magath (1919) and a few others regarded them as simple cells connected with the rectal sphincter. According to these authors they are not glandular in nature.
In the present case three cells were observed round the posterior end of the intestine. One of these is dorsal and the other two sub-ventral in position (Fig. 64). They are about 20 μ in diameter. Each of these cells has a spherical nucleus in which there is a distinct, deeply-stained spherical central nucleolus. These cells could not be found to be connected in any way with the lumen of the intestine. In a transverse section they appear to be rather in intimate contact with the rectal sphincter (Fig. 64).

These so-called glands are absent in the entire Aphasmidia with the possible exception of Enoplus communis. In Phasmidia they are usually present except in Tylenchoidea, Dracunculus and Dirofilaria. In all cases the outlet openings should be indispensible if these cells are to be accredited with any glandular function. So far only Chitwood (1930, 1931, 1933) has reported to have observed such orifices in Habditis, Heterakis, Macracis, Cephallobelus and Hystignathus. Baker (1936) has confirmed this observation in Heterakis.

In view of these observations it is very difficult to ascribe any definite function to these cells. In the present case on outlet openings were observed.
Therefore they cannot be regarded as functional gland cells. Their close association with the sphincter muscle would, on the other hand, suggest that they might be a component part of the sphincter itself. But because these cells open into the rectum in some forms it might be possible that they represent gland cells which are functional in lower groups of Phasmdia and have lost this function in the higher groups where they are represented by non-functional cells only. Nothing, however, can be said with certainty. There is no doubt that some light would be shed on these disputed points with more extensive embryological and physiological studies of these cells.
Fig. 42. T.S. through excretory bridge.
Fig. 43. T.S. through excretory pore.
Fig. 44. T.S. through excretory duct cell.
Fig. 45. L.S. through anterior portion of female.
Fig. 46. L.S. through excretory pore.
Fig. 47. T.S. through lateral chord showing the excretory canal.
Fig. 48. En face view.
Fig. 49. T.S. through anterior region of the female just at the beginning of triradiation of the oesophageal lumen.
Fig. 50. T.S. just posterior to Fig. 49.
Fig. 51. T.S. through the muscular region of oesophagous showing the marginal nuclei.
Fig. 52. T.S. through the glandular region of the oesophagous.
Fig. 53. T.S. through the muscular region of the oesophagous.
Fig. 54. Same.
Fig. 55. L.S. through the anterior portion of the female.
Fig. 56. T.S. passing through the beginning of the oesophago-intestinal valve.
Fig. 57. T.S. through oesophago-intestinal valve.
Fig. 58. T.S. immediately posterior to the oesophago-intestinal valve.
Fig. 59. Oesophago-intestinal valve drawn from a toto-preparation.
Fig. 60. T.S. through the intestine.
Fig. 61. A portion of the same magnified.
Fig. 62. L.S. through the intestine.
Fig. 63. L.S. through the posterior region of the female.
Fig. 64. T.S. through the intestine.
The vulva is situated at about one-fourth of the body length from the anterior end. It is more or less a rounded aperture, situated on a slight elevation. It leads into a posteriorly directed ovijector which comprises the vagina vera and the vagina uterina. The ovijector narrows down posteriorly and ultimately communicates with the uterus which after a short distance divides into two branches. Each of these branches again sub-divide into two. The mode of branching of the uterus is, therefore, dichotomous. These uterine branches run in a posterior direction and each of them ultimately opens into a seminal receptacle. During their course they are coiled upon themselves. The seminal receptacle communicates with an S-shaped oviduct which in turn is connected to the ovary. The ovaries also show a little coiling (Figs. 66, 79).

According to Seurat's classification (1913-1920), the species under discussion would fall in the opliosto-delphous group, i.e. all the uterine branches are directed posteriorly and run parallel to each other. Ortlepp (1922) placed it in his tetradelphys group because of the presence of only four uterine branches.
There are four ovaries in *Physaloptera varani*. All of these lie in the last quarter of the body, one pair lying slightly posterior to the other pair. Each ovary is connected to the uterus through an S-shaped oviduct. The distal ends of the ovaries are blind and are directed anteriorly. Each ovary is divisible into two regions, one, the germinal zone lying distally followed by a proximal growth zone, which in turn is connected to the oviduct. The ovary as a whole is covered over by a single epithelial layer. This layer is quite thick and comprises of a single layer of epithelial cells.

**Germinal zone.**

Starting from the distal end, the germinal zone runs in a posterior direction for about half of its length, then bends upon itself, forms a loop and runs anteriorly till it meets the growth zone (Fig. 65). This zone forms about half the total length of the ovary. It is about 2.7 mm. long and has a maximum width of 50 u. It contains an unorganised mass of germ cells (Fig. 69). These cells are spherical in shape and measure about 5 u each in diameter. Each of these cells contains a large
nucleus with a distinct nucleolus in the centre. The cell boundaries are clearly visible and the region is definitely cellular and not syncytial as reported in some other instances. The epithelial covering in this region is very thin. The blind end of the ovary is covered by a prominent cap cell (Fig. 67). The nature of the cap cell is open to question. Musso (1930) and some other workers regard it as an undifferentiated germinal stem cell, while others, including Chitwood (1950), believe it to be an epithelial cell. In the present study it has been definitely observed that this cell lies within the epithelial layer covering the germinal zone of the ovary and has no connection or relation whatsoever with the germ cord. Therefore it is regarded as a purely epithelial structure which has nothing to do with the germ cord.

Growth zone.

The proximal part of the germinal zone continues into the growth zone which also runs anteriorly. This is the region where the oogonia grow and increase in size. This zone has a length of about 1.95 mm. and is 65 to 75 μ in width (Fig. 65). The growing cells fill the entire cavity enclosed by the peritoneal layer of this region and are arranged in a characteristic fashion.
The oogonia appear like the spokes of a wheel joined together at the centre by their apices where they appear to form a rachis like structure (Fig. 70). The rachis or germ chord here is not very prominent and distinct as has been described in other cases, nevertheless there can be no doubt about its presence. In a single transverse section eleven or twelve oogonia are present. They are conical in shape with their apices directed inwards and bases outwards. Each of these contains a big nucleus measuring about 5 μ in diameter and containing a very prominent and deeply staining spherical nucleolous in the centre (Fig. 70).

Oviduct.

The proximal end of the ovary opens into the oviduct which bends twice to assume the shape of the letter S. Before it joins the uterus it suddenly expands to form a receptaculum seminis. The wall of the oviduct consists of two definite layers, an outer membranous layer and an inner epithelial layer. The membranous layer has been described in certain cases as a layer of circular muscle fibers but no such fibers were observed in the present case. The inner epithelial layer appears to be in continuation with the epithelial layer covering the ovary. The epithelial cells in this
region are, however, much higher as compared to the cells in the ovary (Figs. 71,74). Rauther (1918) has described the presence of a sphincter muscle at the junction of the ovary and the oviduct in Macracis. No such muscle was found in the present study.

The oviduct is divisible into two distinct regions. The first is the oviduct proper which is in the form of a simple S-shaped tube of uniform width connected to the ovary on the one hand and on the other is continued into the second region of the oviduct which is in the form of a wide sac-like structure, the receptaculum seminis (Figs. 71,72). The first part is about 700 \( \mu \) long and 30 \( \mu \) in width. The receptaculum seminis measures 400-500 \( \mu \) in length and from 130-230 \( \mu \) in diameter. Here the epithelial cells become still higher forming prominent projections which are clearly visible in its lumen (Figs. 73,76). Anteriorly the seminal receptacle narrows down to a diameter of about 20 \( \mu \) and opens into the uterus.

**Uterus.**

The uterus is the most conspicuous part of the entire female reproductive system and almost fills in the whole of the body cavity behind the vulva. All the
four oviducts open into their respective uteri which run in an anterior direction along with the intestine. The uterine branches are more or less uniform in diameter and are somewhat coiled. Their length, however, varies slightly, one pair being slightly longer than the other. The uterine branches join in pairs to give rise to two branches each of about 100 μ in length which ultimately unite to form the common uterine trunk (Figs. 66, 67). The latter is a short tube about 500 μ long and 40 μ wide (Fig. 80). The uterine wall is composed of simple epithelial cells. The four uteri occupy most of the available space in the body cavity (Fig. 79).

The uterine branches are literally filled with eggs which are oval in shape and measure, on the average, about 35 μ in length and 25 μ in width. Each of these contains a big conspicuous nucleus measuring about 17 μ and having a deeply staining large nucleolus (Fig. 79).

Vagina.

The uterus communicates with the outside through a muscular tube which has been called as the "ovijector" by Seurat (1912, 1920). It is divisible into two portions, the vagina vera and the vagina uterina.
Vagina uterina.

Anteriorly the uterus opens into the vagina uterina. It is a spindle shaped tube with a diameter of about 35 μ at its beginning, 160 μ in the middle and about 30 μ near its end. The total length of the vagina uterina is about 1.5 mm. In its natural condition in the body it lies rather in a slanting position (Figs. 82, 84). The wall of the vagina uterina is composed of two distinct layers; an outer muscular layer consisting of circular muscle fibres and an internal epithelial layer which seems to be a continuation of the epithelial layer of the uterus (Fig. 84).

Vagina vera.

The terminal portion of the vagina is known as the vagina vera. It is internally lined with a cuticular layer which appears to be continuous with the external cuticula. The musculature in the outer muscular layer is very massive, the layer being about 10 μ thick. At the junction of the vagina vera with the vagina uterina the musculature almost closes the passage between the two. Here also there is an epithelial layer below the muscular layer but the cells of this layer are comparatively few and not very high. The vagina vera also lies in a slanting position almost up to the region of the
vulva where it suddenly bends in a ventral direction to open to the outside. At the place where the vagina vera bends ventrally towards the vulva, it is completely encircled by a sphincter muscle (Fig. 85). The sphincter is about 4.5 \( \mu \) wide. Apart from this sphincter, strands of muscle fibres also run from the somatic musculature to the vagina vera. In the wall of the vagina vera near its opening into the vulva, five cells were observed. These are situated just close to the vulvar opening. Four of these cells are in pairs of two each, and the fifth cell lies medial to them. Each of these is about 5 \( \mu \) in diameter and has a distinct eccentric nucleus (Fig. 86).

The vulva in the present case is non-protuberant and rather inconspicuous. It is situated predominantly in the anterior half of the body at about the junction of its first and second quarter. Its opening is almost circular in outline and is about 100 \( \mu \) wide. The vulvar lips are hardly represented and are very poorly developed (Fig. 85).
Fig. 65. Complete ovary drawn from a dissection.
Fig. 66. Diagrammatic scheme of the female reproductive system.
Fig. 67. The cap cell.
Fig. 68. T.S. through seminal receptacle.
Fig. 69. T.S. through germinal zone of ovary.
Fig. 70. T.S. through growth zone of ovary.
Figs. 71 & 72. Seminal receptacle, oviduct and a portion of the growth zone of the ovary and uterine branch.
Fig. 73. T.S. through seminal receptacle.
Fig. 74. T.S. through oviduct.
Fig. 75. Surface view epithelium in the growth zone of the ovary.
Fig. 76. L.S. through seminal receptacle.
Fig. 77. T.S. through the uterus exactly at the point of branching.
Fig. 78. Cells forming the vaginal wall.
Fig. 79. T.S. through the uterine branches.
Fig. 80. T.S. through uterus just before the uterine branching.
Fig. 81. Uterus and uterine branches drawn from a toto-preparation.
Fig. 82. Vagina uterina drawn from a toto-preparation.
Fig. 83. T.S. through vagina vera.
Fig. 84. T.S. through vagina uterina.
Fig. 85. Same magnified.
Fig. 86. T.S. through vagina vera just posterior to vulva.
MALE REPRODUCTIVE SYSTEM

In the female the reproductive system begins in the posterior region of the body and proceeds anteriorly to open ultimately at the vulva which is situated at the anterior half of the body. In the male, on the contrary, the reverse is true. The reproductive organs begin in the anterior region and run posteriorly by the side of the gut with which they ultimately unite to form a cloaca and open near the posterior end of the body through the cloacal aperture.

The entire reproductive system, apparently, looks like a single tube divided into different specific regions. To begin with there is a single testis which is continued, after a sharp constriction, into a long and broad seminal vesicle. The last and the most conspicuous structure in unstained but cleared specimens is the dark brown "ductus ejaculatorious". It is exactly of the shape of a carrot beginning at the end of the seminal vesicle as a broad, glandular duct, which gradually tapers down and ultimately joins the proctodaeum, a short distance after the intestino-rectal valve, to form a cloaca. Two "ejaculatory glands" are present at the posterior extremity (Fig. 87). Also associated with the male reproductory organs are two very unequal spicules which are to be considered merely as being accessory organs associated
with the male genital apparatus.

Testis.

The testis begins at about the middle of the body and proceeds parallel to the intestine. It is a more or less straight tube which usually does not show any coiling during its course. Like the ovary it is also divisible into two regions: an anterior germinal zone followed by a growth zone.

Germinal zone.

The first half of the testis forms the germinal zone. It is about 1.8 mm. long and about 50 μ wide near its beginning. It gradually increases in width and attains a diameter of about 100 μ, near its end. It is in the form of a tube composed of a single layer of the epithelial cells. Distally it ends blindly and proximally it is continuous with the growth zone of the testis. It contains the primary germ cells which are spherical in outline and are compactly packed in it. On the average each of these cells measures about 1 - 1.5 μ in diameter and possesses a clearly staining spherical nucleolus in the centre (Fig. 38).

Growth zone.

It is continuous with the preceding germinal zone.
of the testis and measures about 1.6 mm. in length. At its beginning it is 100 μ wide gradually becoming wider till about its middle where it attains its maximum width of about 170 μ. Henceforth it gradually narrows down measuring only about 90 μ near its posterior extremity. There is nothing particular to divide or separate it from the preceding germinal zone and, as a matter of fact, the latter passes rather inconspicuously into it. The covering epithelial layer of this region is continuous with that of the germinal zone. However, this layer here is comparatively slightly thicker (Figs. 90, 91).

The tube is full of spermatozoa. These are only of one type and measure from 2 to 2.5 μ in diameter having a spherical nucleus in the centre.

**Seminal vesicle.**

After a sharp constriction the testis is continued posteriorly into the seminal vesicle. The latter is a sac-like structure which is 3.4 mm. long. It is about 170 μ wide at its beginning but gradually increases to about 400 μ posteriorly, again narrowing down to about 200 μ near its end (Fig. 93). The wall of the seminal vesicle is in direct contact with that of the testis and, as a matter of fact, the seminal vesicle is itself a dilated portion of the male gonoduct serving as a temporary store house for the still maturing sperms.
passed out by the testis. The thickness of its wall is about 2.2 μ (Fig. 98).

The seminal vesicle has a very characteristic structure. It appears to be divided into a number of "chambers" by transverse septa which can also be observed in whole mounts (Fig. 94). These "chambers" are from 20 to 25 μ wide, their width, apparently, depending upon the number of sperms contained in each one of them. At their middle the thickness of their walls is from 8 to 12 μ. The spherical sperms inside them are on the average 2 μ in diameter (Figs. 95,97).

*DUCTUS EJACULATORIOUS.*

This is the terminal portion of the male gonoduct and measures 1.5 mm. in length. At its anterior end, immediately following the seminal vesicle, it is 180 μ wide and after a distance of 250 μ it attains its maximum width of about 280 μ. Henceforth it gradually tapers down till at its posterior extremity, where it joins the rectum, it measures only 30 μ (Fig. 101). In the glycerine cleared, unstained specimens it is most conspicuous and is easily distinguished from other structures by its dark brownish colour. Roughly it corresponds to the shape of a carrot.
The junction of the ejaculatory duct with the seminal vesicle is guarded by a well developed triangular valve (Figs. 96,99). This valve is 190 μ long and 120 μ broad at its base. Near its apex or free end it narrows down to a width of only 40 μ. The ejaculatory duct is lined by a thick wall measuring about 5 μ in width. The glandular region which is so characteristic of the phasmidians, is also present here. The epithelial cells are high. The nuclei are many and arranged along the margins of the cells and measure about 2 μ in diameter each possessing a single, well stained nucleolus in the centre (Figs. 96,100,106).

At the posterior end of the ductus ejaculatorius there is a pair of bilaterally symmetrical pouches which have been designated by some authors as ejaculatory glands. These are much shorter in height as compared with those described in Rhabditids. Along the dorsal side of the duct, median to the two "ejaculatory glands" are seen epithelial cells which are associated with certain definite and very fine cilia-like processes (Fig. 102). Chitwood (1931) also described such processes and considered them to be possibly homologous with cilia. Much earlier Cobb (1883) working with the ascaridids and later Rauther (1918) working on trichuroids described "hair like processes" from the epithelial cells of the vas deferens. None of these, however, claims any vibratile movements for them.
for them. These structures are very similar to those met within the nemic intestine cells. Although no direct relationship between the two is claimed, the apparent similarity and likeness in their external appearance might be significant.

**Spicules.**

There are two unequal and dissimilar spicules. The left is approximately ten times as long as the right one. The right spicule is provided with a sharp hook at its distal extremity. The left spicule has no such structure.

**Left spicule.**

The left spicule, the larger of the two, is 3 mm. long. At its head it measures 60 μ in diameter and immediately below it 50 μ. It is almost cylindrical in shape and narrows rather suddenly near its distal end in a blunt point. (Fig. 104). On its ventral side it has got a longitudinal groove which is present almost throughout its entire length. The groove is 8 to 10 μ wide (Fig. 105).

**Right spicule.**

The right spicule is comparatively much shorter and
measures only 258 μ in length. At its head it is only 9 μ wide, becoming 30 μ immediately below it. Then it gradually increases in size till about the middle of its length it reaches the maximum. Here it is 50 μ wide. Henceforth it tapers down to a width of only 15 μ. At a distance of about 200 μ from the head it describes a sharp turn and forms a characteristic hook. The hook is 55 μ long and at its proximal end 15 μ wide. It gradually tapers down to end in a blunt point (Figs. 107, 108).

In a transverse section the spicules appear to consist of two distinct cuticular layers, the inner of which stains comparatively more deeply. Internally they are filled up by what Magath (1919) has very aptly called the "granular pulp". Each of the spicules is separately enclosed in a muscular "spicular sheath" or the "musculi exsертores spiculorum" (Figs. 108, 107). The muscles of this sheath are responsible for the movements of the spicules during copulation.

Functions of the spicules.

Although the presence of either one or two spicules is a universal feature throughout the nematode group yet, there is little, if any, agreement as to the real nature
of their functions and significance. The popular conception that these serve as intromittent organs during the coaculation still seems to exercise a hold in spite of the fact that Schneider as early as 1866 pointed out that the spicules are never hollow and as such generally the sperms can not flow "through" them. It is to be noted here that the spicules are never in direct connection with the ejaculatory duct. Thus the spicules can not be regarded as true intromittent organs in the orthodox sense of the word. The spermatozoa do not flow through them and there are very few chances of their conveyance by them in any other way. For the letter two possibilities have been put forward. Looss (1905) and zur Strassen (1907) believed that by a close approximation of the two flanged spicules as found in Ancylostoma and Philometra, some sort of tube is formed through which the sperms flow. It would be difficult to explain with this theory the cases having only one spicule, which is the general condition in Trichuroidea, Dioctophymatoidea, Oxyuridae and Theleostomatidae. Later workers including Mueller (1925), Baylis (1929) and Reuther (1930) thought that the sperms might be passing down along the ventral groove in either of the spicules, i.e., in Baylis' words "(spicules) act as 'gutters' along which the sperm is guided". Others including Butschli (1872), Leuret (1920) and Chitwood and Chitwood (1933)
thought that the spicules serve as the organs for location and excitation. Thus Chitwood and Chitwood (1933) commenting upon the functions of the spicules say, "the spicule can be considered as only an auxiliary sexual organ, the principal function of which is in locating the vulva, stimulating the female and preventing closure of the vulva". Of all these Baylis (1929) appears to be the nearest to the truth when he says, "their (spicules) chief function is probably that of 'holdfasts' during copulation, or instruments for expanding the vagina of the female" and that they "act as 'gutters' along which the sperm is guided".

For cases with unequal spicules Seurat (1920) put forward a rather interesting and at the same time, apparently, quite plausible theory. According to him the smaller, hooked spicule keeps the vulva open and the larger grooved one penetrates into the vagina and along it the sperms find their way into the vagina. Considering the structure of the spicules in the present case this theory appears to be correct. The right spicule which is short and bears a strong hook would easily keep apart the vulvar lips to allow a free passage of the larger left spicule. The latter by virtue of its length would be better able to penetrate into the long and tubular vagina and its groove would easily serve as a
'gutter' or guide for the sperms. It is important to note that the small, hooked right spicule which, according to this theory, plays no part in the transmission of the sperms has no groove at all while the larger one is provided with a groove. As the latter has to move in and out of the vagina smoothly, it also does not possess any hooks which if present would prove an obstacle in its movement.

The relative sizes of the spicules, though often regarded as a specific character, are not always so. Chitwood and Chitwood (1951) mentioned a marked dissimilarity in the spicular morphology in *Dirofilaria immitis* from muskrat. They found besides the normal type, "a specimen in which the left spicule blade was degenerate and another in which the left spicule was absent ...... in a single muskrat." On similar basis they expressed doubt about the "numerous species of filarids being described at the present time, and differentiated entirely or wholly on diversity of spicular form". The present writer is, therefore, in accord with Mirza (1935) who "does not attach much importance to the size of spicules in differentiating a species, for, it has been determined that the spicules in different individuals of the same species vary in size".
LEGENDS

Plate V

Fig. 87. Diagrammatic scheme of male reproductive system.
Fig. 88. T.S. testis germinal zone.
Fig. 89. Growth zone of testis drawn from a dissection.
Fig. 90. T.S. growth zone of testis.
Fig. 91. A portion of the same magnified.
Fig. 92. T.S. passing through the region between testis and the seminal vesicle.
Fig. 93. Seminal vesicle drawn from a dissection.
Fig. 94. A portion of the same magnified.
Fig. 95. L.S. through seminal vesicle.
Fig. 96. L.S. through the junction of the seminal vesicle and the ejaculatory duct.
Fig. 97. T.S. through seminal vesicle.
Fig. 98. A portion of the same magnified.
Fig. 99. T.S. through the anterior region of the ejaculatory duct.
Fig. 100. T.S. through the middle region of the ejaculatory duct.
Fig. 101. Ejaculatory duct drawn from a dissection.
Fig. 102. L.S. through the ejaculatory glands.
Fig. 103. Head of the left spicule.
Fig. 104. Left spicule.
Fig. 105. T.S. through the left spicule.
Fig. 106. T.S. through the posterior region of the ejaculatory duct.
Fig. 107. Right spicule.
Fig. 108. T.S. through the right spicule.
Fig. 109. T.S. through the caudal region of the male passing through the spicular canals.
Fig. 110. Same magnified.
LIFE-CYCLE STUDIES

It is surprising to find that very little work has been done to investigate the life-cycle of members of the genus Physaloptera. That a group having more than a hundred species and established over a century ago has been neglected in this respect is difficult to understand. It is, however, encouraging to note that now this long neglected problem is being taken up and efforts have been made to discover the life-cycle of members of this group by Alicata (1937) and Hobmaier (1941).

Cram (1932) was the first to identify Physaloptera larvae encysted in the breast and leg muscles of bob white quail and ruffed grouse. Mirza (1934) reported encysted Physaloptera larvae in the body cavity of the Indian squirrel, Sciuris palmarum. It is not known, however, whether the squirrel serves as a natural intermediate host or it was an accidental infection. Boughton (1937) confirmed the observations of Cram. It is to be noted that all these descriptions are from the definitive host and none from the intermediate host. Alicata (1937) did pioneer work in this field. He worked with P. turgida Rud. which parasitises the opposum Didelphis virginiana. He was able to infect the German cockroach, Blatella germanica, with the eggs of P. turgida and trace the development up to the third stage larva. According to him, the first and
the second stage larvae are found free in the body cavity of the cockroach. The third stage larvae were found after about a month, encysted in the tissues surrounding the body cavity. The larvae were coiled loosely within the cyst. According to Alicata "encysted third stage larvae were found to be enclosed in a thin brownish chitinous-like substance, probably representing a deposit derived from the tissue of the cockroach. This would probably present a defense reaction to a foreign invader ....... These deposits appear first usually at the anterior and the posterior extremities of the larva, and gradually spread until the larva is enclosed within a tube formed by these deposits. Eventually the larva is killed and becomes completely chitinized." This would mean, according to Basir (1948) that "B. germanica can serve as an intermediate host for P. turgida but is probably not the natural intermediate host." This is amply borne out by the fact that when the infective larvae were fed to a dog, cat, rabbit, guinea pig, rat and chick the results after a month were all negative for any physalopteran infection.

Hobmaier (1914) carried on the good work started by Alicata and was successful in infecting B. germanica with the eggs of P. maxillaris Molin up to the infective stage. He described briefly and figured the first and the third stage larvae. The time taken for the development up to the third stage was from 4-6 weeks. He further stated
that "one or more larvae may be found enclosed in colourless cysts according to the severity of the infection. Some of the cysts may show a golden brownish colour similar to that of the cuticle of the cockroach, with or without destruction of the enclosed larva." Hobmaier also could not complete the development in the definitive host and wrote "no parasites were found on examination 6 weeks after having fed infected cockroaches to cats, dogs and guinea pigs." Therefore, here again it appears that whereas B. germanica may be infected experimentally with the eggs of P. maxillaris in all probability it does not serve as the natural intermediate host.

Basir (1948) for the first time described a Physaloptera larva from the earwig, Labidura repara Pallas. He records only two larvae which "were found free and unencysted in the body cavity" of the insect. The great importance of this discovery lies in the fact that this is the first record of natural infection of Physaloptera in a possible intermediate host.

Since the writer began his experiments on the life-cycle of P. varani, Schell (1950) has published his results on the life-cycle of P. hispida Schell, a parasite of cotton rat. He was able to develop the
Physalopteran eggs in ground beetles, European earwigs, and German cockroaches. Petri and Ameel (1950) were also successful in infecting the field crickets (*Gryllus assimilis*), flour beetles (*Tribolium confusum*) and ground beetles (*Harpalus* spp.) with *P. rara*.

During the course of the present studies, a number of insects were exposed to *Physaloptera varani* infection. These were cockroaches, earwigs, field crickets and beetles. Cockroaches were kept in small cages and pieces of crumpled paper were placed in them to serve as hiding places. Dry sugar was the only food given. This arrangement requires a minimum of care and provides satisfactory conditions for parasitic experiments. The earwigs, *Labidura* spp. were kept in small glass jars in which sand was placed up to a height of one and a half inches and small stones were placed in them to serve as hiding places. They were fed on potatoes. The field crickets and the beetles were kept in small glass jars which were placed in an incubator adjusted at the temperature of 33 degrees centigrade.

The eggs of *Physaloptera varani* are already embryonated when laid. These were pasted on very small pieces of potatoes and on crystals of sugar. The insects were then allowed to feed upon them.
Care had been taken to dissect out a fair number of all the four insects to make sure that there was no natural infection of Physaloptera in them.

After two weeks, five cockroaches, five earwigs, four crickets and six beetles were dissected but no larvae were found, all the results being negative for Physaloptera infection. Again at the end of four weeks after infection all the remaining insects were examined. Only the earwigs were found to contain encysted third stage larvae of Physaloptera. All the five earwigs were infected. The minimum number of larvae being two and the maximum seven. The cysts were attached to the upper portion of the intestine. They were of pale white colour and the larvae were loosely coiled inside. Unlike the earlier reports by other workers none of the cysts showed any colouration. The average length of the larva was about 2.00 mm.

The third stage larva of Physaloptera can easily be distinguished from similar stages of other nematodes by the characteristic formations of their head parts. As in adult Physaloptera these are already triangular in outline. The delicate structure of the two lips with teeth and papillae are already discernable.
Unfortunately the life-cycle could not be carried on in the definitive host because infection-free varanii were not available at the time.

Previous records show that although Alicata and Hobmaier have been successful in developing the Physalopteran eggs in the German cockroach, *Blatella germanica*, they were not able to complete the life-cycle by using these experimentally infected cockroaches as the intermediate host. The author, however, could not develop the eggs of *Physaloptera varani* in the Indian cockroaches. Moreover it is also thought that they cannot serve as the natural intermediate host since the percentage of infection in the definitive host is so high that it warrants the intermediate host to be one of the stable items of its diet. It is doubtful if cockroaches can be so easily available to *Varanus*. Schell (1950), after successfully infecting ground beetles, earwigs and German cockroaches concluded that "it is not likely that the German cockroach functions as intermediate host under natural conditions, but earwigs and ground beetles might very well serve as possible intermediate hosts for *Physaloptera* in the natural environment of the cotton rat." Successful infection of earwigs by Schell (l.c.) Petri and Ameel (l.c.)
and Basir's (l.c.) record of natural Physalopteran infection in earwigs would strongly suggest that they might serve as a natural intermediate host for *P. varani* in the normal environment of *varanus*.
KEY TO LETTERING OF FIGURES

a       anus.
a g     anal ganglion.
a lu com ano-lumbar commissure.
am    amphid.
am n    amphidial nerve.
b    bursa.
ba l    basal lamella.
b l    bacillary layer.
camus    caudal muscles.
ch d    dorsal chord.
ch ll    left lateral chord.
ch lr    right lateral chord.
ch v    ventral chord.
c l    cloaca.
cor    cortex.
c u    cuticle.
de    denticles.
d g    dorsal ganglion.
d n    dorsal nerve.
ce    epithelial cells.
ce n    nucleus of the epithelial cell.
ed    ejaculatory duct.
ed gl    ejaculatory gland.
ed gir glandular portion of the ejaculatory duct.
ed mus muscular portion of the ejaculatory duct.
ed n    nucleus of the wall of the ejaculatory duct.
es v valve between the seminal vesicle and the ejaculatory duct.
es esophagous.
es gl d oesophageal gland duct.
es gl glandular oesophagous.
es gl o oesophageal gland opening.
es l v oesophago-intestinal valve.
es l oesophageal lumen.
es mus oesophageal muscles.
es musr muscular oesophagous.
es n c oesophageal nerve cell.
et external tooth.
ex b excretory bridge.
ex b c excretory bridge cell.
ex c excretory canal.
ex cor external cortical layer.
ex d c excretory duct cell.
ex fr external fiber layer.
ex p excretory pore.
ex s excretory sinus.
fibr fibrillar portion of muscle cell.
fr fiber layer.
g c germ cell.
gl nu gland nucleus.
in cor internal cortical layer.
in fr internal fiber layer.
int intestine.
Int c
intestinal cell.

int sph
intestinal sphincter.

lrv
intestino-rectal valve.

la
labium.

lg
lateral ganglion.

ln
lateral nerve.

lu com
lumbar commissure.

lug
lumbar ganglion.

zax
matrix layer.

ze fr
median fiber layer.

m nu
marginal nucleus.

mus a
musculus ani.

mus c pr
processes of muscle cells.

nc
nerve cell.

nc d g
nerve cell of dorsal ganglion.

nc l g
nerve cell of lateral ganglion.

nc v g
nerve cell of ventral ganglion.

nr
nerve ring.

nrc
cell of the nerve ring.

nu
nucleus.

nu ch d
nucleus of the dorsal chord.

nu ch l
nucleus of the lateral chord.

nu ch v
nucleus of the ventral chord.

nu es
oesophageal nucleus.

nu int c
nucleus of the intestinal cell.

nu mus a
nucleus of musculus ani.

nu mus c
nucleus of muscle cell.
o  ova.
ov  ovary.
ov d  oviduct.
ov ge z  germinal zone of the ovary.
ov gr z  growth zone of the ovary.
p  papillae.
ph  phasmid.
ph gl  phasmidial gland.
p n  papillary nerve.
p p  pedunculated papillae.
p p n  nerve to pedunculated papillae.
p s  sessile papillae.
p v g  post-ventral ganglion.
ra  rachis.
r com  rectal commissure.
re  rectum.
re gl  rectal gland.
r g  rectal ganglion.
r nu  radial nucleus.
s  sperm.
sar  sarcoplasm.
sb l  sub-bacillary layer.
s o mus  somatic musculature.
s o mus c  somatic muscle cell.
sp  spicule.
sp c  spicular canal.
<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>sp gr</td>
<td>spicular groove.</td>
</tr>
<tr>
<td>sp l</td>
<td>left spicule.</td>
</tr>
<tr>
<td>sp m</td>
<td>spicular muscles.</td>
</tr>
<tr>
<td>sp r</td>
<td>right spicule.</td>
</tr>
<tr>
<td>s r</td>
<td>seminal receptacle.</td>
</tr>
<tr>
<td>s v</td>
<td>seminal vesicle.</td>
</tr>
<tr>
<td>s v c</td>
<td>nucleus in the wall of the seminal vesicle.</td>
</tr>
<tr>
<td>s v ch</td>
<td>&quot;chambers&quot; in the seminal vesicle.</td>
</tr>
<tr>
<td>t</td>
<td>testis.</td>
</tr>
<tr>
<td>t ge z</td>
<td>germinal zone of the testis.</td>
</tr>
<tr>
<td>t gr z</td>
<td>growth zone of the testis.</td>
</tr>
<tr>
<td>u</td>
<td>uterus (common trunk).</td>
</tr>
<tr>
<td>ut b</td>
<td>uterine branch.</td>
</tr>
<tr>
<td>ut b I</td>
<td>first uterine branching.</td>
</tr>
<tr>
<td>ut b II</td>
<td>second uterine branching.</td>
</tr>
<tr>
<td>vag</td>
<td>vagina.</td>
</tr>
<tr>
<td>vag sph</td>
<td>vaginal sphincter.</td>
</tr>
<tr>
<td>vag u</td>
<td>vagina uterina.</td>
</tr>
<tr>
<td>vag v</td>
<td>vagina vera.</td>
</tr>
<tr>
<td>v g</td>
<td>ventral ganglion.</td>
</tr>
<tr>
<td>v n</td>
<td>ventral nerve.</td>
</tr>
<tr>
<td>vu</td>
<td>vulva.</td>
</tr>
</tbody>
</table>
REFERENCES


38. YORK AND MAPLESTONE. The nematode parasites of Vertebrate J. & A. Churchill 7 Great Marlborough Street, London 1926.