Morphology and Biology of the Genus *Plectus* (Nematoda: Plectidae)*

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The genus *Plectus* Bastian, 1865 is one of the nematode groups of fundamental importance in the present classification of the Adenophorea (v. Linst., 1905), Chitwood, 1958. Because of the key position of this genus a study with emphasis on histologic morphology and biology was undertaken.

The species of *Plectus* are bacterial feeders and are among the so-called "free-living" nematodes. Nielsen (1948) reports that *Plectus* comprises approximately 68% of the nematodes found in moss and only 10% of those found in soil. Species of this genus have been collected from the Arctic to the Antarctic, and are reported from all major areas of the world, from sea level to over 14,000 feet above sea level.

I am particularly indebted to Dr. M. W. Allen for his encouragement, advice and interest throughout the progress of this paper. Appreciation is extended to Dr. B. G. Chitwood for his advice, and to Dr. W. Nicholas for the advice on the culturing of nematodes.

MATERIALS AND METHODS

Histologic studies were made, for the most part, with females of *Plectus parietimus*. Specimens of P, parietimus used for serial sectioning were killed by gentle heat and then fixed in $2\frac{1}{2}\%$ formalin for at least 24 hours. The processes of dehydration and dealcoholization were carried out in a depression slide. Xylene was employed to accomplish dealcoholization.

Chitwood and Chitwood's 1930 procedure for embedding was followed. Sections were microtomed at 5 microns. Pantin's (1948) procedure for regressive iron hematoxylin staining was used. Sections were stained with Baker and Jordan's (1953) modification of Heidenhain's (1896) iron hematoxylin. A 2-½% ferric alum solution was employed as a mordant and saturated solution of Pieric acid in 95% ethyl alcohol as a destain.

MORPHOLOGY

All specimens of the genus *Plectus* examined have six lips. There are interspecific differences in lip structure including size, shape, amalgamation and distinction from the general cephalic region.

Chitwood and Chitwood (1950) reported 12 papillae on the lips of *Plectus* in two circles, one external and one internal. I was able to see only six papillae, one medianly located on each lip (Fig. 1, A).

Four cephalic setae were present on all specimens of the species examined, two dorso-lateral and two ventro-lateral (Fig. 1, B). The flexibility of the cephalic setae is easily seen in living specimens and their innervations are visible in both totomounts and stained sections. Setae most commonly are located two or three annules behind the lips.

The amphids of *Plectus* have been described in the literature as unispiral or as shepherd crooks, apparently because the refraction of light through the amphidial pouch and tube creates this impression. The external form of the amphid is either a complete oval or a circle, depending on the species observed. The amphidial pouch is larger than its external opening (Fig. 1, C); it narrows rapidly at the posterior margin of the external opening into the amphidial tube. This tube is not symmetrically located but is shifted

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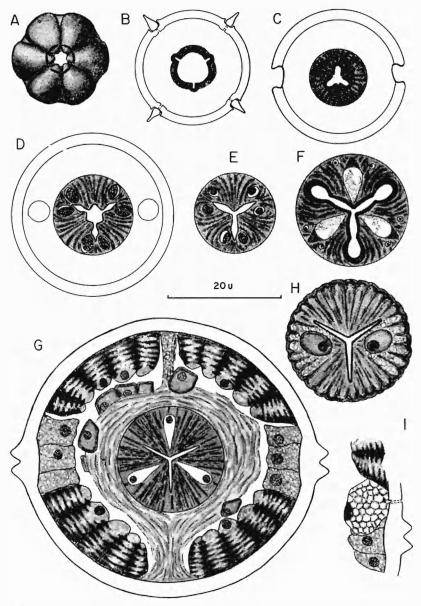


Fig. 1. Plectus parietinus female (all of equal magnification). A. Lip region, B. Prostom, C. Meso-metastom and amphidial pouches, D. Junction of stoma with esophagus, E. Fore-part of esophagus (corpus), simple triradiate lumen, F. Corpus of esophagus, lumen with radial tubuli, G. Cross section at level of nerve ring and "hemizonid," H. Anterior portion of posterior bulb, I. Hypodermal gland.

dorsally. The amphidial tube continues at the same diameter posteriorly to the sensilla pouch. The sensilla pouches are located in the region just posterior to the stoma (Fig. 1, D). Nerves leading from the sensilla pouches could not be followed. It is my opinion that the two subdorsal gland cells near the excretory or renette cell are the amphidial glands (Fig. 4, A and B, 1 and 2).

Cervical papillae (deirids) have been reported on *P. sambesii* by Andrássy (1958). They are present on all *Plectus* and located in or near the lateral longitudinal alae at the level of or just posterior to the nerve ring. They are also found to be present on the closely related genera *Anaplectus* and *Wilsonema*. *Plectus annulatus* has a single longitudinal ala with the cervical papilla dorsal to the ala. The cervical papillae are set into definite sockets and are innervated. The nerves could not be followed in either totomounts or stained sections. Chitwood and Chitwood (1950) state that in *Ascaris* each deirid is innervated by a branch of the nerve trunk which connects the medial externo-lateral ganglia with the nerve ring.

The external cuticle of *Plectus* species is marked by transverse striae which begin at the base of the lips and usually end approximately five annules anterior to the spinneret.

Lateral longitudinal alae occur as well defined ridges in the male and female. There are two alae on each side of the body in all known species except *P. annulatus* as noted above.

On longitudinal sections stained with Heidenhain's hematoxylin, transverse string are evident in the trough between the non-striated longitudinal alae.

Males of *Plectus* do not have caudal alae. Preanal supplementary structures may or may not be present on *Plectus* males. Preanal supplementary structures when present consist of either preanal tubuli or a single preanal seta. The preanal tubuli are not always cuticularized or associated with glands. In some species a large sensory seta, short, but broad at its base, lies just anterior to the cloacal opening.

The body setae are not rigidly fixed but flexible. All have nerve connections and are set into sockets. Placement of setae on the body is variable. Usually there are three pairs of caudal setae on the female tail. The anterior pair are subdorsal, the next pair subventral and the most posterior pair subdorsal. The caudal setae of the male differ in appearance and number from those found on the female tail. On those males observed there were seven, eight or nine pairs of setae, the number depending upon the species. The caudal setae of males resemble the preanal setae. The males of some species also possess caudal papillae.

The hypodermis forms four chords, one dorsal, two lateral, and one ventral. The chords contain discrete cells, whose number varies from species to species.

Anteriorly the dorsal hypodermal chord of *P. parietinus* has a single row of nuclei. Posterior to the esophagus it is non-nucleated. The ventral chord contains a single row of cells and nuclei which persist throughout its length. The ventral chord contains the ventral nerve cord. Lateral hypodermal chords are composed of three rows of cells, two sublateral and one lateral (Fig. 1,G). The nuclei of the three rows are of equal size, and each cell is uni-nucleate. Near the tail region the lateral chords diminish in size but remain clearly defined to the middle of the tail. The thin non-nucleated portion of the hypodermis surrounds the body between the cuticle and the muscle sectors.

Hypodermal glands were not observed in all species of *Plectus*. In *P. parietinus* they are unicellular and occur sublaterally. Their number varies from specimen to specimen. The gland cells lie in the lateral chords, near the sublateral rows of cells, and open through sublateral pores in the cuticle (Fig. 1, I). Hypodermal glands begin in the esophageal region and continue posteriorly into the tail.

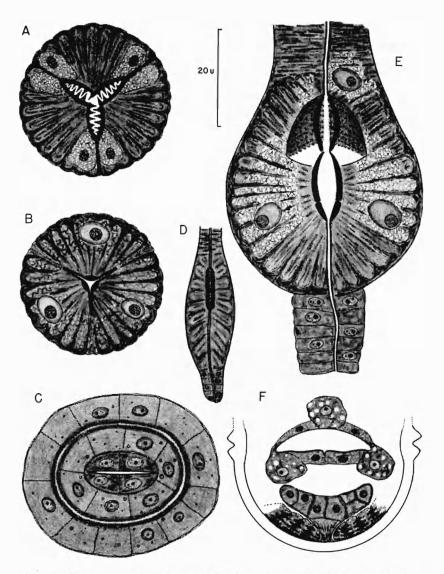


Fig. 2. Plectus parietinus female (all of equal magnification). A. Triradiate denticulated valve of posterior bulb, B. Posterior bulb at level of three posterior esophageal gland nuclei, C. Esophago-intestinal valve and intestine, D. Posterior bulb, first larva from egg, E. Posterior bulb, adult, F. Section through rectum and pre-anal ganglion.

In males and females of *Plectus* there are three caudal glands arranged in tandem which discharge their contents through a cuticularized spinneret. They are just posterior to the rectum or the cloaca.

The somatic musculature of *Plectus* is meromyarian. Each muscle cell is semi-coelomyarian (Fig. 3). Near the vulva there are 32 muscle cells. The exact number of cells in either the extreme exterior or posterior region of the body could not be determined. The nuclei of the muscle cells are large and are seen throughout the length of the animal.

The generic name *Plectus* was derived by Bastian from the odd loopings of the cuticularized excretory duct (Fig. 4, A) which opens ventrally just posterior to the region of the nerve ring. The lining of the duct is continuous with the external cuticle. Epithelial tissue surrounds the duct throughout its course, but nuclei were not associated with duct tissue. The excretory duct extends posteriorly to the excretory gland. It makes two loops after entering the gland, one on each side of the esophagus. The majority of the loopings are within the gland tissue (Fig. 4, A and B). The excretory gland is ventral, dorso-ventrally flattened, and extends laterally almost to the hypodermal chords. Its nucleus is large and centrally located. The long cuticularized terminal excretory duct is reminiscent of the Secernentea, as typified by the Rhabditids.

There are at least four coelomocytes in the body of *P. parietinus*; two are at the level of and subventral to the excretory gland (Fig. 4, A and B, 3). One and sometimes two occur halfway between the base of the esophagus and the anterior extremity of the reproductive system; if two, they are subventral, and if one, either ventral or subventral. The most posterior coelomocyte is located dorsal to the caudal glands.

The stomodeum of *Plectus* is divisible into three regions: stoma, esophagus, and esophago-intestinal valve.

The oral opening, which is immediately followed by the stoma, is formed by the joining of the lips and interlabial areas (Fig. 1, A). The stoma proper is divisible into three sections: cheilostom, prostom and meso-metastom. The cheilostom is hexagonal in cross section and heavily cuticularized. The six cheilorhabdions comprising the cheilostom are connected to the prorhabdions by a thin cuticular membrane (Fig. 1, A). The prostom is sub-circular in cross section. Short radial arms project into the body cavity from the two subdorsal areas, and the ventral region (Fig. 1, B).

The meso-metastom is distinctly narrower in diameter than the prostom, the radial arms are elongated, and the inter-radial areas are strongly convoluted (Fig. 1, C). Posteriorly the lumen of the meso-metastom decreases in size until it finally merges with the lumen of the esophagus (Fig. 1, D).

The esophagus is divided: corpus, isthmus, and posterior bulb. Posterior to the stoma the esophagus is muscular and has a simple triradiate lumen (Fig. 1, E). The first of the marginal nuclei appear in this region (Fig. 1, D.). There are six pairs of marginal (epithelial) nuclei in the corpus. Six pairs of radial (muscle) nuclei also occur in the corpus. The dorsal esophageal gland opens in the anterior region of the corpus. Posterior to the orifice of the dorsal esophageal gland, the radial arms of the humen are modified distally by tubuli (Fig. 1, F). The major portion of the corpus is characterized by these radial tubuli.

The isthmus begins just anterior to the nerve ring. It is characterized by the complete absence of nuclei and a trivadiate lumen without radial tubuli. In the isthmus each radial arm is strengthened by longitudinal ridges persisting to the region of the posterior bulb. Muscle fiber attachments are concentrated at, and below, these ridges (Fig. 1, G).

The isthmus swells gradually to the heavily muscled posterior bulb. The triradiate lumen persists in the anterior portion of the posterior bulb but there are no longitudinal ridges on the radial arms (Fig. 1, H). The lumen expands just anterior to the triradiate denticulated valve. This valve is very conspicuous, and on its inner surface it bears several rows of denticle-like thickenings (Fig. 2, A and E).

There are 12 marginal, 12 radial, and five esophageal gland nuclei in the posterior bulb. According to Chitwood and Chitwood (1950) the order Chromadorida is characterized by the presence of three esophageal gland nuclei. However five esophageal gland nuclei have been seen in the genus *Plectus* in hematoxylin stained serial sections, a variety of totomounts, living specimens (with and without vital stains), formalin fixed specimens, and glycerine mounts. The esophageal gland nuclei are at two levels in the esophagus: two anterior to the denticulated valve (Fig. 1, H) and three

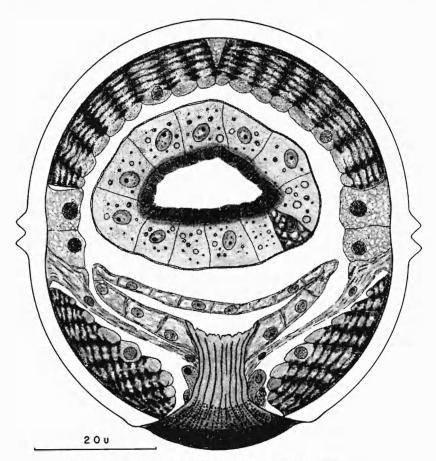


Fig. 3. Section through vulva and vagina, Plectus parietinus.

posterior to the valve (Fig. 2, B). The two anteriorly located nuclei are subventral. One of the three posterior nuclei is dorsal, and two are subventral. The orifices of the subventral glands are at the level of the nerve ring, and the orifice of the dorsal esophageal gland is near the base of the stoma. The lumen of the esophagus in the region of the three posterior glands is augmented between the radial arms by a thickening of the cuticular lining (Fig. 2, E).

Immediately behind the posterior esophageal gland nuclei the bulb tapers rapidly to the esophago-intestinal valve (Fig. 2, C and E). The cuticularly lined lumen in this region of the esophagus is triradiate without special modifications. The valve is dorso-ventrally flattened and composed of approximately 12 cells, and it invaginates the intestine.

The stomadeal nervous system consists of three longitudinal nerves, one dorsal and two subventral. The main nerves are contained in the esophageal sinuses, which run longitudinally in the three radial sectors of the esophagus (Fig. 1, F and G). According to Chitwood and Chitwood (1950) the stomodeal nervous system in Ascaris is connected to the central nervous system by the subventral stomodeal nerves; these enter into the esophagus at its beginning. This could not be confirmed for Plectus; it is assumed that the construction is the same or similar.

Morphologically the mesenteron of *Plectus* is polycytous and heterocytous. It is bounded by a thin membrane, the basal lamella. The cells of the mesenteron are uni-nucleate, columnar, and possess a bacillary layer (Fig. 3). A section parallel to the basal lamella shows the cells to be generally hexagonal.

The mesenteron is not divided into distinct regions. However, some histologic variations occur in the bacillary layer, stored food, and the shape of the lumen. Anteriorly and posteriorly the bacillary layer is low (Fig. 2, C): being higher in the remainder of the intestine (Fig. 3). The lumen is at first rather tubular; then, in the main region of the intestine highly irregular, and becoming triradiate just prior to the rectum. Stored food products and inclusion granules also diminish in the posterior region.

The mesenteron is heterocytous and two kinds of cells are present. The majority of cells probably function in absorption. The second kind are fewer in number and are found randomly throughout the mesenteron. These cells probably function as secretory cells. These cells and the nucleolus were more receptive to Heidenhain's hematoxylin than the cells presumed to be absorbers. Morphologically secretory cells are more vacuolated, and have fewer cell inclusions (Fig. 3). Absorbing cells and their nuclei stained lightly with hematoxylin (Fig. 3).

Between the mesenteron and the proctodeum there is an uninucleate sphincter muscle with a laterally placed nucleus.

The proctodeum in *Plectus* is the rectum. It is dorsoventrally flattened at the rectal-intestinal junction. The cuticle of the ventral wall is thicker than that of the dorsal surface which is curved and there is a visible fold in the cuticle along the lateral margins (Fig. 2, F). The ventral wall is somewhat flattened and has a median groove down its entire length (Fig. 2, F). It sweeps up at the lateral margins. The rectum is supplied with discrete epithelial cells which surround it to its posterior end.

There are three cells in addition to epithelial cells located at the anterior end of the rectum, one dorsal and two subventral. It is the author's opinion that these cells are rectal glands. Rectal glands are a rarity among the Adenophorea but have been suspected before (Chitwood and Chitwood, 1950). These glands are at least three times the size of other rectal epithelial cells. Their nuclei are larger, and the endoplasm appears more vacuolated and stains a deeper blue with hematoxylin than that of associated cells (Fig. 2, F). The dorsal gland orifice appears to be in the dorsal wall of the rectum. The orifices for the subventral glands appear to be at the junction of the ventral and dorsal walls of the rectum.

The depressor ani muscle is of the usual "H" shape. This cell has posterior and anterior projections; the latter are attached on the rectum.

The female of *Plectus* has simple telogonic gonads with didelphic amphidelphic arrangement (Fig. 5, A). The reflexure occurs at the junction of

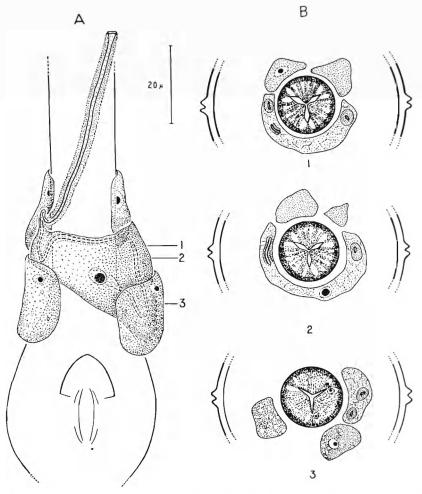


Fig. 4. Plectus parietimus (illustrations of equal magnification). A. Totomount illustration of exerctory system and associated glands and coelomocytes, B. Crosssections through exerctory system: 1 and 2 subdorsal amphidial glands and exerctory cell; 3 subventral coelomocytes and exerctory cell.

the ovary and the oviduct; and the ovaries are reflexed in such a manner that the anterior ovary is on the right and the posterior ovary on the left side of the body. Both ovaries are pyriform, the germinal zone being at the narrow distal extremity and the growth zone at the broad proximal end. The oviduct is approximately one-fourth the length of the entire reproductive system and is followed by the uterus and vagina.

The ovary is covered by a thin synytial epithelium. There are no discrete cap cells at the distal end of the ovaries. The oogonia are at first regularly arranged with one cell terminal. As the oogonia develop the regularity is upset, and no particular plan can be discerned. Near the proximal end of the ovary a regular arrangement again prevails and the oocytes are placed alternately; this condition persists until an egg is developed. It then occupies the entire proximal end of the ovary. At the distal end of the oviduct there appears to be a network of muscle.

The syncytial epithelium terminates at the junction of the ovary with the oviduct. The oviduct consists of discrete, uni-nucleate, columnar epithelial cells. The cells are closely appressed and a lumen is not easily discerned unless an egg is passing through.

The uterus is distinguished by its increased diameter and by the tall columnar epithelial cells forming its wall. The proximal end of the uterus is distinguished by the lower height of the epithelial cells.

The vagina is supplied with squamous epithelium continuous with the epithelium of the body wall. The euticle of the vagina is marked by striae and punctations. These markings do not cover the entire surface of the vagina but are concentrated near the vulva (Fig. 3).

There are four dilator vulval muscles, two anterior and two posterior. Each muscle contains four cells which are attached to the base of the vagina. From the vagina the muscles run obliquely, anteriorly and posteriorly respectively, to the lateral chords (Fig. 3).

The scarcity of males in the genus *Plectus* has made it impractical to study the reproductive system histologically. For this reason only the gross morphology can be discussed.

Males of *Ptectus* have a reproductive system of the generalized type found in free-living nematodes (Fig. 5, B). Two testes (diorchic) are present and opposed.

The testes are covered with a syncytial epithelium like that covering the ovaries. The remainder of the reproductive system is covered with discrete epithelial cells which vary in size and arrangement according to the various regions they constitute (Fig. 5, B.).

In various species it was observed that the spicules are not symmetrical either in size or shape. The gubernaculum remained constant in appearance in any one species. The intestine runs between the head (manubrium) end of the spicules and joins into the cloaca near the distal end of the spicules.

The origin for the retractor muscles is in the region of the lateral chords. The insertion of the retractor spicule muscle is in the manubrial sinus on the latero-proximal surface. There are dorsal and ventral protractor muscles which are attached to the proximal end of the spicule. The ventral protractor muscle runs to the subventral body wall. The dorsal protractor muscle, however, appears to be inserted to the posteriorly directed dorsal process of the gubernaculum. The gubernaculum itself is supplied with muscles which run from the dorsal process to the ventral body wall. In addition to the

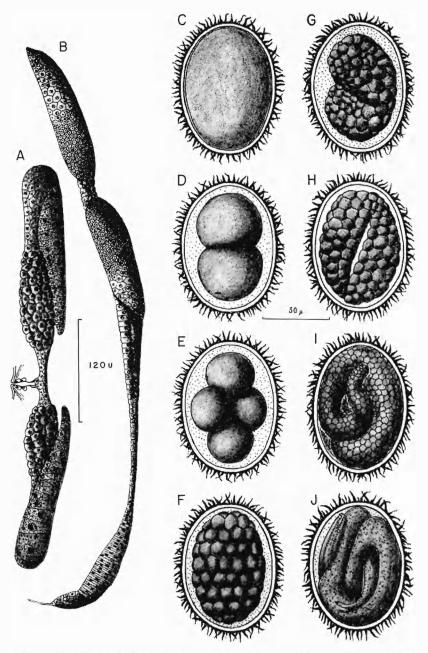


Fig. 5. Plectus parietinus. A. Female reproductive system, B. Male reproductive system, C. Single-celled egg, D. Two-celled egg stage, E. Four-celled egg stage, F. Gastrula, G. Embryo, beginning larval formation, H. Embryo in "tadpole" stage, I. Embryo pre-larval stage, J. Fully-formed larva just prior to hatching.

muscles of the spicules and gubenaculum, the male tail contains many accessory oblique muscles. These are attached to the lateral chord region and ventral body wall and are posteriorly directed.

Various components of the nervous system have already been discussed: setae innervations, cervical papillae and the stomodeal nervous system.

The main structure of the central nervous system is the circum-esophageal commissure, nerve ring, which is located around the isthmus just posterior to the corpus.

A structure is seen in totomount specimens which appears to be the same as the "Hemizonid" reported by J. B. Goodey, (1951) and described and identified by him in 1959. Stained sections show this "Hemizonid" to be that region where the circum-esophageal commissure extends to the ventral nerve cord in the ventral hypodermal chord, (Fig. 1, G). The totomount impression is created by the combination of the ventral extension from the nerve ring (ventro-lateral commissures) and the beginning of the ventral nerve cord.

The ventral nerve cord can be easily followed. Five major ganglia are recognized along the course of this cord. The first, the retrovesicular ganglion, occurs just posterior to the excretory cell, and anterior to the posterior bulb. A second is located just anterior to the vulva. The ventral cord proceeds posteriorly from this latter ganglia passing to the right of the vagina. Posterior to it there is a third ganglion. Two more ganglia are located in the posterior region of the body, one anterior (Fig. 2, F) and one posterior to the rectum. In addition to the major ganglia, minor ganglia occur along the ventral nerve cord and probably serve to innervate the somatic muscles.

BIOLOGY

MATERIALS AND METHODS: Cultures of *Plectus parietinus* were reared on Asparagine-mannitol agar (Thornton, 1922). The culture technique was modified and suggested by W. Nicholas (personal communication). A soil suspension was prepared by placing a teaspoon of soil in one liter of water, mixing well by shaking and then allowing it to stand a few minutes. From the suspension 0.2 ml. was pipetted off and placed on the agar plate (20 cc. of 2% agar in a four-inch petri dish). Plates were left at room temperature for three days in order to give the bacteria time to become established.

Experiments were conducted at 40°F, 50-55°F, 70°F and at a variable 70°F (room temperature), to determine the temperature most favorable to population increase. The temperature of 50-55°F proved to be the best of those tested, and subsequently cultures were kept at this temperature. Subculturing insured a continual supply of adults and eggs.

According to Nielson (1949) a major factor contributing to the death of eggs and larvae appears to be oxygen deficiency caused by rapid bacterial growth. This problem was minimized by constructing plastic frame well slides. The internal well measurements were 20 mm. \times 20 mm. \times 1 mm. deep. Agar was poured into the well slightly higher than the well depth. This allowed a free exchange of oxygen when a coverslip was placed over the well. Only the amount of bacteria transferred with eggs or adults from the stock culture was used to inoculate the slide. The slides were kept in petri dishes with moist filter paper. With this method eggs could be observed with the high dry objective of a compound microscope and in some instances even the oil immersion lens could be used.

Information concerning the life cycle of *Plectus parietinus* is derived from the experiments carried out at 50-55°F using these plastic frame well slides.

Discussion: As with most free-living genera of nematodes, there is no special complexity of the female reproductive system. This is correlated with the slow production of eggs and also with the relatively few eggs produced at one time. Seldom are more than two fully developed eggs found in the uterus of *Plectus*, and when two are present, normally one egg is the product of the anterior ovary and the other the product of the posterior ovary. However, there are exceptional cases where several eggs are retained in the uterus.

The usual time between the appearance of the eggs in the uterus and egglaying is three days. Normally eggs are laid in the single cell stage (Fig. 5, C). The cleavages of the egg are holoblastic and spiral. The first cleavage of the single cell is transverse; two distinct cells are formed (Fig. 5, D). The second cleavage is longitudinal, both the anterior and posterior cell dividing (Fig. 5, E). Twenty-four hours after the single cell egg is laid it has developed to an eight-celled form; 48 hours following this latter stage the egg has developed to a mature gastrula (Fig. 5, F). During the next 24 hours the embryo begins larval formation (Fig. 5, G).

Forty-eight hours after the first signs of larval formation, the embryo has lengthened considerably and is in the "tadpole" stage (Fig. 5, H). From this stage onward the embryo can be observed to move about within the egg shell. Lengthening of the "tadpole" continues until, at the end of ten days, the embryo is distinctly in the pre-larva form (Fig. 5, I). Fourteen days after egg formation the larva is fully developed (Fig. 5, J). Hatching occurs two to four days later.

It was not determined with certainty whether or not the larva molts once before hatching. When the larva first leaves the egg it differs morphologically from the adult in the form of the posterior bulb of the esophagus. In the first larva the posterior bulb is only slightly swollen, and the valvular apparatus consists of three denticulated longitudinal plates (Fig. 2, D). The expanded valve characteristic of all other larval stages and the adults of *Plectus parietinus* is absent (Fig. 2, E). For this reason it is believed that the first molt does not take place within the egg. The first apparent molt takes place approximately seven days after hatching and the posterior bulb and valve of this stage is like the adult.

Development from egg to adult female requires approximately 45-55 days at 50-55°F, and 60 days until eggs are again laid. Nielsen (1949), working with two species of *Plectus*, reported for one 20-25 days at 20-22°C and approximately 20 days for the other species at 15-16°C.

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The Development and Morphological Variation of Philophthalmus gralli Mathis and Leger, 1910 with a Comparison of Species of Philophthalmus Looss, 1899*

HILDA LEI CHING**

Looss (1899) created the genus Philophthalmus for P. palpebrarum, a nonspinous trematode with a very large pharynx, found in the eyes of birds in Egypt. Braun (1902) emended the generic diagnosis to include Distantant lucipetus Rudolphi, 1819 which has a spiny cuticle and a pharynx smaller than the oral sucker. Braun also described P. lacrymosus from Larus maculipennis from Brazil. Looss (1907) described P. nocturnus from birds in Egypt. Mathis and Leger (1910) described but did not include a figure for P. gralli from poultry in Tonkin. Sugimoto (1928) redescribed P. gralli from chickens and named P. anatinus from ducks in Formosa. To date, 21 species have been described from domestic and wild birds. One species, P. lacrymosus, has also been reported from man (Markovic, 1939) and Dissanaike and Bilimoria (1958) described Philophthalmus sp. from a man in Ceylon. Fisher and West (1958) found Philophthalmus sp. in the belted kingfisher and green heron in Indiana. At least four specific descriptions are based on single specimens: P. indicus, P. nyrocae, P. occulare, and P. problematicus. P. skrjabini was described from immature specimens.

Members of the genus are found in the eyes of vertebrates except for P. coturnicola and P. skrjabini located in the small intestine and P. offlexorius in the oral cavity of birds. Skrjabin (1947) named sub-genera of Philophthalmus on the basis of types of vitellaria but these are not recognized by Yamaguti (1958).

Fisher and West (1958), West and Fisher (1959), and Alicata and Noda (1959, 1960) described the life cycles of two unspecified members of the genus Philophthalmus, Both are similar to the life histories of species in a closely related genus, Parorchis aritus Linton, 1914 and P. acanthus var. australis Angel, 1954 determined by Stunkard and Cable (1932) and Angel (1954), respectively. The sexually-mature worms of these two genera have, in their uteri, eggs containing oculate miracidia in which mother rediae are already developed. The cercariae which are derived from daughter rediae are of the megalurous type with spiny cuticles, well-developed digestive tract, and tail with invaginated tip. They encyst readily on objects to form metacercariae which are infective upon ingestion by the vertebrate hosts. However, Alicata

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