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Postembryonic Development and Reproduction in *Diploscapter coronata* (Nematoda: Rhabditidae)

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Introduction

Diploscapter coronata (Cobb, 1893) Cobb, 1913 has been known for over seven decades, and seven other species of this genus have since been described. However, comparatively little is known about the biology and development of the species of *Diploscapter*. Yokogawa (1936) reported the presence of *D. coronata* in human urinary sediment and Chandler (1938) found the same species in the stomachs of nine human patients with a deficiency of gastric hydrochloric acid. Kämpfe (1962) reported on the effect of desiccation and CO_2 concentration on *D. coronata*, while Wahab (1962) found *D. lycostoma* in the pharyngeal glands of ants and cultured the nematodes on raw potato. Hechler (1967) studied molting in *D. coronata*, and the following is a report on postembryonic development and reproduction in the same species.

Materials and Methods

The nematodes were established and maintained in culture as described by Hechler (1967). To determine the number of molts, newly hatched nematodes were placed individually in a drop of bacterial slime on a coverslip, a drop of agar medium added, and the coverslip inverted over a depression slide and sealed with petroleum jelly. The nematodes were examined every 4 hours until development was complete. For staining to study gonad development and chromosomes, petri dishes in which an abundance of eggs or the larval stages desired was present were flooded with water, the resulting suspension centrifuged, and the supernatant discarded. About 3 ml of Carnoy fixative was poured into the centrifuge tube with agitation to suspend the nematodes. Thirty minutes later the tube was centrifuged, the Carnoy fluid discarded, and the nematodes suspended in a few drops of acetic orcein. After about 12 hours, drops of the suspension of nematodes in the stain were placed on microslides and coverslips were added and sealed. Specimens to be measured were fixed in FAAGO, dehydrated according to the method of Baker, and mounted in glycerine. Measurements for the de Man formulae were made on camera lucida drawings, whereas the genital primordia, stoma, and lips, were measured with an ocular micrometer. In molting specimens the nematode within the exuvium was measured, not the loose cuticle.

Postembryonic Development

Four molts occur during the life cycle of *D. coronata*, all after the first stage larva

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emerges from the egg. All stages feed, and development stops if the nematode is removed from a source of food. The de Man values are similar for each stage, except for a somewhat larger "c" value for the adult. Thus, although the nematodes increase in size, there is little change in body shape except for the comparatively shorter tail in the adult. Development of gonads is uniform throughout the population; nematodes of the same age have gonads at the same stage of development.

FIRST STAGE (Fig. 1A): Dimensions: L = 0.18–0.19 mm; a = 16–19; b = 2.7–3.0; c = 4–5. Genital primordium 4–5 μ long, with its center located at 53–57% of body length from anterior end. Stoma 11 μ long. Lips all rounded, not set off from body or modified as in subsequent stages. Cheilorhabdions form a narrow ring at the anterior end of the stoma. Lateral fields consist of a single ridge which extends from the base of the stoma to the anus. The genital primordium is oval in shape and situated obliquely in the body in ventral view. It contains two large centrally located germinal nuclei which appear lightly stained except for numerous, small, discrete, densely stained particles distributed within them. Two smaller somatic nuclei which stain uniformly are located at the posterior and anterior ends of the genital primordium. The somatic nuclei are appressed to the wall so that they appear crescent shaped in lateral view. Rarely both somatic nuclei occur at the same end of the genital primordium. In the ventral chord, in a single row between the clusters of nuclei at the base of the esophagus and at the anus, there are always 15 nuclei. They stain densely and uniformly with orcein and are always spaced as shown in Figure 1A.

FIRST MOLT: Dimensions: L = 0.19–0.21 mm; a = 13–18; b = 2.9–3.1; c = 4–5. Genital primordium 4–6 μ long at 50–55% of body length from anterior end. The ventral chord nuclei divide during the molt until about 48 are present between the base of the esophagus and the anus, usually in a single row, although occasionally a few overlap each other. There is a gap with no nuclei opposite the genital primordium. The genital primordium changes little in size or shape, but the two somatic nuclei within it become round and less densely stained (Fig. 1B).

SECOND STAGE (Fig. 1C): Dimensions: L = 0.20–0.23 mm; a = 16–20; b = 2.9–3.8; c = 4–5. Genital primordium 7–9 μ long at 52–54% of body length, stoma 11–13 μ long, hamuli 4–5 μ wide. In the second stage the submedian lips, or hamuli, are hook-shaped and sclerotized, and the lateral lips, or laciniae, are thin, oval, with fringed margins, extending anteriorly on either side of the oral aperture as in the adult. The cheilorhabdions and lateral fields are as in the first stage. The genital primordium is slightly larger than in the first stage, with the two terminal nuclei nearly as large as the two central germinal nuclei and of almost the same staining character. No ventral chord nucleus was seen to divide in second stage specimens. However, in a few specimens one, or more rarely two, larger, more lightly stained nuclei were seen in the ventral chord opposite the position of the genital primordium. They usually did not appear until the second molt.

SECOND MOLT: Dimensions: L = 0.25–0.26 mm; a = 15–18; b = 2.8–3.2; c = 4–5. Genital primordium 7–9 μ long at 50–52% of body length. The terminal somatic nuclei in the genital primordium divide once or twice during the molt, to make a total of two large germinal nuclei and four to six smaller somatic nuclei by the time the nematode emerges from the exuvium (Fig. 1D). One or two ventral chord nuclei, larger and lighter in color than the other ventral chord nuclei, are present opposite the genital primordium.

THIRD STAGE (Fig. 1E): Dimensions: L = 0.24–0.32 mm; a = 16–20; b = 2.7–3.9; c = 5–6. Genital primordium 8–15 μ long at 50–54% of body length. Stoma 13–15 μ long, hamuli 5–6 μ wide. Cheilorhabdions and lateral fields as in the first stage. At the beginning of the stage the two central, larger germinal nuclei in the genital primordium are easily distinguished from the smaller somatic nuclei arranged around the periphery. Later both types of nuclei divide, until about 16 nuclei are present. It is then difficult to differentiate the two types of nuclei because they all become similar in size and staining character. As the genital primordium begins to elongate an anterior and a posterior lobe are formed. As the nematode body elongates the small, dark staining ventral chord nuclei become more widely spaced, but none was seen

Figure 1. Stages in the development of *Diploscapter coronata*. A. First stage, lateral view; B. First molt, genital primordium, ventral view; C. Second stage, lateral view; D. Second molt, genital primordium, ventral view; E. Third stage, lateral view; F. Third molt, genital primordium, ventral view; G. Fourth stage, lateral view; H. Fourth molt, genital primordium, ventral view; I. Adult, lateral view.

to divide. The larger, more lightly stained nuclei opposite the genital primordium increase to four by the time the third molt begins.

THIRD MOLT: Dimensions: L = 0.29–0.32 mm; a = 14–18; b = 2.7–3.7; c = 5. Genital primordium 15–36 μ long at 49–53% of body length. The gonad lobes elongate, and by the end of the molt there are seven to nine nuclei in each lobe: one at the terminus, and six to eight nuclei arranged in two rows. The central part of the genital primordium consists of two layers of wedge-shaped cells arranged around the future vaginal opening. Early in the molt there are four large, lightly stained, ventral chord nuclei in a single row opposite the middle of the genital primordium; by the end of the molt six to eight specialized nuclei are present, arranged in two rows (Fig. 1F).

FOURTH STAGE (Fig. 1G): Dimensions: L = 0.32–0.36 mm; a = 16–20; b = 3.4–3.9; c = 5–6. Genital primordium 25–98 μ long, center at 50–55% of body length. Hamuli 6 μ wide, stoma 14–16 μ long. Cheilorhabdions form a narrow ring and lateral fields consist of a single ridge, as in the first stage. The genital primordium elongates considerably until, just before the final molt, the two lobes recurve. At this time there are about 20 germinal cells in each lobe. Proximal to the germ cells in each lobe is a slightly constricted section with four rows of three or four small, densely stained nuclei. This is followed by a less constricted section with four rows of two or three larger, more lightly stained nuclei. The vaginal primordium consists of two rows of five or six dorsal nuclei and two rows of six or seven ventral nuclei. The two ventral rows are farther apart at their centers, surrounding the vaginal opening. The lightly stained ventral chord nuclei increase to about 16, with eight just posterior and eight just anterior to the vaginal primordium. One or two of each group move dorsally within the vaginal opening by the time of the beginning of the fourth molt.

FOURTH MOLT: Dimensions: L = 0.41–0.42 mm; a = 14–17; b = 3.7–3.9; c = 4–6. Genital primordium 98–110 μ long, center at 50–52% of body length. During the final molt the gonad lobes increase in length and width and the germinal cells divide until there are about 30 in each lobe, arranged in three or four rows in the widest part (Fig. 1H). At the junction of ovary and uterus the small densely stained nuclei are arranged around the periphery of a round to ovate structure which becomes considerably expanded in the adult. Proximal to this structure the tubular form of the uterus becomes apparent. The vaginal nuclei originating within the gonad become smaller and more densely stained than they were in the fourth stage and most of them are grouped on either side of the flattened vagina, with a very few located dorsally. During the molt the remaining specialized ventral chord nuclei move within the vaginal tube. They are similar in size and staining character to the lateral nuclei, but located centrally and ventrally.

ADULT (Fig. 1I): Dimensions: L = 0.46–0.54 (0.50)* mm; a = 16–20 (17.7); b = 3.8–5.1 (4.5); c = 6–8 (6.6); V = 45–54 (50)%. Stoma 20 μ long, hamuli 8–9 μ wide. Head framework consists of two bowed sclerotized pieces, one dorsal and one ventral, surrounding the stoma at their centers and extending anteriorly and laterally at each end. Cheilorhabdions forming a shallow inverted funnel at the anterior end of the stoma. Lateral fields composed of two ridges between the base of the stoma and the anus. Excretory pore opposite median bulb, hemizonid anterior and contiguous to it. Nerve ring just behind middle of isthmus. Amphids located just posterior to laciniae. Papillae in center of laciniae easily seen. Papillae on submedian lips, seen on only two favorable en face views, located lateral to the centers of the hamuli. Phasmids about 15 μ posterior to anus, small and inconspicuous. Gonads recurved at ends, each lobe 105–170 μ long, germ cells four to five to a cross section at widest part of ovary. Wall of ovary thin and seems to be anucleate. An oval, hyaline structure with about 14 small, densely stained nuclei spaced around its periphery is present at the junction of ovary and uterus (Fig. 2C). This would probably function as a spermatheca in the presence of spermatozoa. Proximal part of gonad with thick, convoluted walls containing nuclei which are larger and stained lighter in color than those in the oval structure. Vulva a crosswise slit. Both anterior and posterior to the vagina about 10 densely stained nuclei of ventral chord origin are located centrally and ventrally, while on either side of the vagina are a posterior and anterior group of about nine similar nuclei originating from the gonad.

* Value in parentheses is the mean.

There are about 56 ventral chord nuclei arranged in a single row between the base of the esophagus and the anus, excluding those involved in the structure of the vagina.

Reproduction

Although mitotic divisions occur throughout the distal half of the ovary, it is very difficult to identify and count individual chromosomes in the dividing nuclei. In cells which are not dividing the nuclei contain many small discrete particles which stain deeply with orcein. In the proximal part of the ovary the deep staining particles disappear and the nuclei appear lighter in color than the surrounding cytoplasm. Prophase of meiosis becomes evident when the cell reaches the proximal end of the ovary. At that time the nucleolus and two long, double, twisted strands appear in the nucleus (Fig. 2A). Before the oocyte passes into the uterus the nucleolus disappears (Fig. 2B). The chromatin then begins to contract to deeply staining rods which appear double (Fig. 2C), and meanwhile the oocyte moves into the uterus. The rods continue to contract until they are of the shape shown in Figure 2D and they separate completely. There is no pairing of the chromosomes, either side by side or end to end. One maturation division occurs, usually near the middle of the long axis of the egg, and one polar body is formed which remains visible until the end of the second or third cleavage division. Both the polar body and the egg nucleus contain two rods (Figs. 2D, 2E). No second meiotic division takes place. The egg nucleus moves to the center of the egg and the two rods elongate and become double (Fig. 2F). The first cleavage division occurs either before or after the egg is laid. At the cleavage metaphase two double strands of chromatin are present and at telophase two short chromosomes can be seen at each pole (Fig. 2G). They elongate again before the next cleavage (Fig. 2H). The phenomenon of chromosome diminution was not detected as late as the eight cell stage. Subsequent nuclei were so small that the chromosomes were difficult to see.

No sperm cells are present within the body of females and, among several hundred thousand females seen during this investigation, only three males were found. These males were treated with Carnoy-orcein. They were so old that meiosis was no longer proceeding in their testes, although spermatozoa were present. Therefore, nothing was learned about the process of spermatogenesis.

Discussion

Hirschmann (1962) reported that in *Ditylenchus triformis* the ventral chord nuclei, whose descendents will eventually form the lining of the vagina, can be identified in young second stage females because they are larger and less deeply stained than the other ventral chord nuclei. Similar nuclei could also be detected in a few second stage *D. coronata* females, and they were always present by the second molt. Most of the nuclear divisions in the ventral chord occur during the first molt in *D. coronata*, at the time the nuclei increase from a constant number of 15 to about 48. Possibly the specialized nuclei arise at this time and differentiate by the time of the second molt.

During the first stage the epithelial nuclei in the genital primordium are smaller and more uniformly stained than the germinal nuclei and the two types of nuclei are easily distinguished. As development of the nematodes progresses, the two types of nuclei become increasingly similar in size, shape, and staining characteristics. During the third stage they could not be differentiated. By the third molt it is again possible to recognize some of the somatic nuclei because of their location within the developing genital primordium, but the nature of each nucleus is not absolutely clear until late in the fourth stage. Therefore, it was not possible to determine the contribution of each of the early somatic nuclei to the final structure of the gonads or to determine whether the terminal cell of each lobe was of somatic or germinal origin. Since in hundreds of stained females the terminal nucleus was never seen to divide, it is probably somatic.

All four molts occur after the nematode emerges from the egg. As noted by Thomas (1965) for *Acrobeles complexus*, the lip region of the first stage is of a different form in *D. coronata* than in subsequent stages, with the lips all rounded rather than being modified to hamuli and laciniae. This change was noted previously by Hechler (1967), as well as the change in the stoma during the final molt, when the adult cheilostom becomes wider and

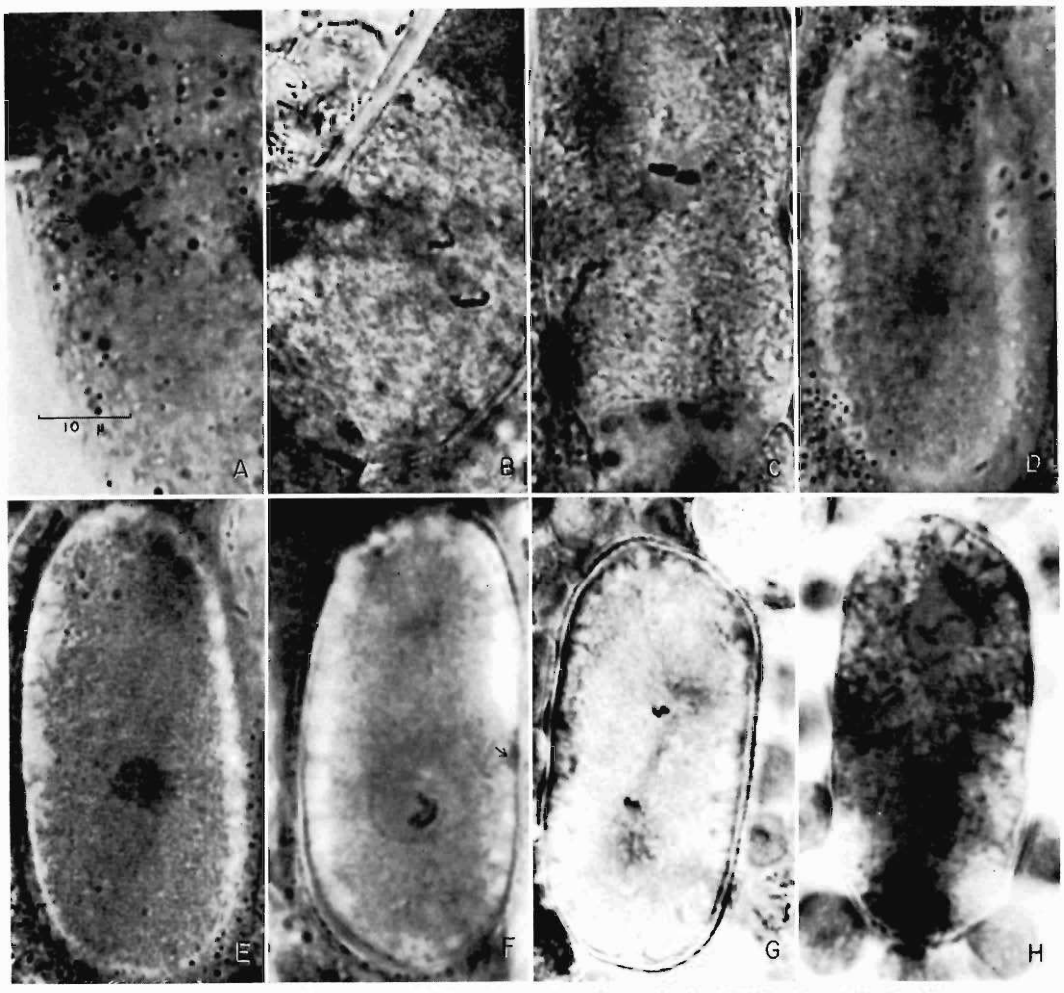

Figure 2. A. Prophase I showing nucleolus (arrow) and two dyads; B. Prophase I after disappearance of nucleolus; C. Late prophase I; D. Telophase I showing polar nucleus; E. Egg nucleus, same egg as shown in Figure D; F. Prophase of first cleavage, nucleus migrating to center of egg, polar body (arrow) at side; G. Telophase of first cleavage; H. Prophase of second cleavage.

funnel-shaped. In addition there is an increase from one to two ridges in the lateral fields at the final molt.

Yuen (1965) stated that in *Helicotylenchus vulgaris* the principal growth of the gonads occurs during the molts whereas there is little change in them between molts. In *D. coronata* the gonad changed little from hatching through the second molt. However, beginning early in the third stage dividing nuclei could be seen in the genital primordium throughout the further development of the gonad. Growth seems to proceed at the same rate during the larval stages as during the molts.

During maturation of the egg in *D. coronata* doubling of the chromatin could be seen during prophase, with two dyad groups in the nucleus by metaphase. These groups could never be resolved as tetrads. Pairing of the two dyad groups, either side by side or end to end, was not observed; although occasionally the groups seemed to lie side by side at metaphase it was

probably coincidental since this behavior was not consistent. After the first maturation division the inner nucleus was found at the center of the egg, with two doubled chromosomes, and only two chromosomes were found in each telophase nucleus of the first cleavage. It is therefore concluded that there is a somatic number of two unpaired chromosomes in this isolate of *D. coronata*. No second maturation division was detected, the chromosomes did not pair before meiosis, and no sperm cells were seen within the females. Hence this isolate reproduces by mitotic parthenogenesis, as reported by Triantaphyllou (1962, 1963, 1966) for *Meloidogyne javanica, M. arenaria*, and some populations of *M. hapla*.

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Helicometra antarcticae sp. nov. from Antarctic Coastal Fishes[1]

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Introduction

The following species ascribed to the genus *Helicometra* Odhner, 1902 may be added to the list of Manter (1954), subsequent taxonomic changes are indicated: *H. torta* Linton, 1910 (Siddiqi and Cable, 1960 synonymized *H. pretiosa* Bravo-Hollis and Manter, 1957 with this concept); *H. plovmornini* Isaychikov, 1928; *H. equilata* (Manter, 1933) Siddiqi and Cable, 1960; *H. markwitschi* Pogoreltzeva, 1954; *H. insolita* Polyanski, 1955; *H. pteroisi* (Gupta, 1956) Fischthal and Kuntz, 1965; *H. boseli* Nagaty, 1956; *H. dochmosorchis* Manter and Pritchard, 1960; *H. marmotatae* Nagaty and Abdel Aal, 1962; *H. nasae* Nagaty and Abdel Aal, 1962; *H. indica* Agrawal, 1964; *H. rectisaccus* (Fischthal and Kuntz, 1964); *H. borëoensis* Fischthal and Kuntz, 1965 bringing the total number of species to 22 including species described in this paper and acceptance of synonymy suggested.

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