# Observations on the development of juveniles and adults of *Parahadronchus shakili* (Jairajpuri, 1969)

Naseem AHMAD and M. Shamim JAIRAJPURI *

*Section of Nematology, Department of Zoology, Aligarh Muslim University, Aligarh, 202001, India.*

SUMMARY

The buccal cavity of *Parahadronchus shakili* is formed anew during the process of moulting. A total of four moults occur. In the late phase of each moult there are always three dorsal teeth, one of these is cast off along with the old buccal cavity, the second one becomes the functional tooth of the stage to follow, while the third one is the spare tooth of the future stage. The development of the buccal cavity is more pronounced in the adults than in the juveniles. The development of oesophagus and tail in relation to total body length is greater in juveniles than adults. The genital primordium in the first stage juveniles consists of two oval bodies connected by a cellular strand. Each oval body has one germinal nucleus and two somatic nuclei. The cap cell nuclei are derived from the division of the somatic nuclei at the distal and proximal ends of the primordium and do not divide again. The germinal nuclei divide for the first time in the third moult while the somatic nuclei do so in the second moult. The somatic nuclei proliferate in the middle region of each primordium to form the gonoduct. The epidermal nuclei are derived from the somatic nuclei at the opposite ends of the primordia and form the epidermal walls of the testes and ovaries. The vagina is formed by the specialized ventral chord nuclei, whereas the development of spicules and gubernaculum takes place from the spicular primordium in the anal region which is distinguishable in the third stage male juveniles. Sex differentiation occurs in the second stage juveniles when specialized ventral chord nuclei make their appearence in the female juveniles. The development of the genital tract and ovary in various seasons also differed. The frequency of egg production by the anterior ovary was much greater than that by the posterior ovary (2 : 1).

RÉSUMÉ

*Observations sur le développement des juvéniles et des adultes de* Parahadronchus shakili *(Jairajpuri, 1969)*

La cavité buccale de *Parahadronchus shakili* est formée *ab novo* au cours de chacune des quatre mues ; à la dernière phase de la mue trois dents dorsales sont présentes : l'une est rejetée avec l'ancienne cavité buccale, la seconde devient la dent fonctionnelle du stade suivant et la dernière constitue la dent de réserve du stade ultérieur. Le développement de la cavité buccale est plus prononcé chez les adultes que chez les juvéniles. Celui de l'oesophage et de la queue est plus grand, par rapport à la longueur du corps, chez les juvéniles que chez les adultes. Le primordium génital consiste, chez les J1, en deux corps ovales, connectés par une plage cellulaire, et comportant chacun un noyau germinal et deux noyaux somatiques. Les noyaux de la cellule apicale proviennent de la division des noyaux somatiques aux extrêmités distale et proximale du primordium et ne se diviseront plus par la suite. Les noyaux germinaux se divisent pour la première fois à la troisième mue tandis que les noyaux somatiques le font à la seconde mue. Les noyaux somatiques sont le siège de nombreuses divisions pour former le gonoducte. Les noyaux de la gaine des testicules et des ovaires proviennent des noyaux somatiques des extrêmités distale et proximale des primordia. Le v' gin est formé par des noyaux particuliers de la corde ventrale, tandis que le développement des spicules et du gubernaculum s'effectue à partir du primordium spiculaire situé au voisinage de l'anus et distinguable dès le troisième stade juvénile mâle. La différenciation sexuelle a lieu chez les J2 où les noyaux spécialisés de la corde ventrale font leur apparition chez les juvéniles femelles. Le développement du tractus génital et des ovaires peut varier suivant les saisons. La fréquence de production des œufs est plus élevée chez l'ovaire antérieur que chez le postérieur (2/1).

* Present address : Commonwealth Institute of Parasitology, St. Albans, Herts, England.

The dimensions of the body of a nematode species, though important for distinguishing its various life stages, are not sufficient alone because they may be influenced by the environment (Calpham, 1930 ; Bingefors, 1957 ; Van Weerdt, 1958). The gonads and other organs, which either grow or are replaced at each moult, provide reliable criteria for distinguishing various juvenile stages and the adults as was shown by Raski (1950), Van Gundy (1958), Yuksel (1960), Chuang (1962), Coomans and Lima (1965), Yuen (1965), Hirschmann and Triantaphyllou (1967), Roman and Hirschmann (1969), Dasgupta *et al.* (1970), Chin (1977), etc. Mulvey (1961) gave a brief account of the development of buccal cavity and tail of the juveniles and adults of *Anatonchus tridentatus* (De Man, 1876) De Coninck, 1939 ; while Grootaert and Maertens (1976) discussed moulting and the buccal cavity formation in *Mononchus aquaticus* Coetzee, 1968.

Van Weerdt (1960) studied the development of gonads in *Radopholus similis* (Cobb, 1893) Thorne, 1949 and concluded that the genital primordium of all nematodes has two germinal nuclei irrespective of the number of gonads in the adults. This supported the view of Chitwood and Chitwood (1950). Hirschmann (1962) in *Ditylenchus triformis* Hirschmann & Sasser, 1955 ; Anderson and Darling (1964) in *Ditylenchus destructor* Thorne, 1945 ; Ahmad and Jairajpuri (1979) in *Chiloplacus symmetricus* (Thorne, 1925) Thorne, 1930 have shown that instead of two germinal nuclei there may be only one germinal nucleus in the primordium. Hirschmann (1962) had, however, stated that the number of germinal nuclei in the primordium is independent of number of gonads. Pai (1928) was the first to report and distinguish the germinal nuclei from the somatic ones. He showed that in *Turbatrix aceti* (Müller, 1783) Peters, 1927 the genital primordium in the first stage juvenile consists of two germinal and two somatic nuclei. Usually the sexual difference becomes evident at the third juvenile stage in most species (Van Gundy, 1958 ; Triantaphyllou & Hirschmann, 1960 ; Anderson & Darling, 1964). However, in some nematodes it may become evident even at the second stage as in species of *Heterodera* and *Meloidogyne*. The development of the genital tract and ovary in different seasons of the year was studied by several workers, e.g., Griffin and Darling (1964) ; Flegg (1967) ; Jairajpuri and Bajaj (1978) etc.

In the present work, an attempt has been made to study the development of various organs in *Parahadronchus shakili* (Jairajpuri, 1969) Mulvey, 1978 with special reference to its buccal cavity, oesophagus, gonads, tail etc., and to use these for distinguishing the sexes and the juvenile stages. Observations were made on moulting stages and the development of genital tract and ovary in different seasons.

The observations on the comparative development of the buccal cavity and other organs were based on specimens including moulting stages from a natural population obtained from Bareilly, Uttar Pradesh, India. For the study of development of gonads, live nematodes were stained in 1% acetic orcein and were observed in a drop of dilute stain. In order to study the seasonal development of the genital tract specimens were collected and studied at monthly intervals from July 1977 through June 1978.

## Observations

### Buccal cavity (Fig. 1 A-C)

The buccal cavity was formed anew at each moulting stage and reached its full size before the initiation of the next moult. The comparative measurements of the buccal cavities of the juveniles, moulting stages and the adults are given in Table 1.

As the moulting initiated, the lip region appeared slightly swollen and straight due to the development of the new cuticle underneath it. Later, the old and the new cuticles get clearly separated with a distinct space between (Fig. 1). In the early stages of moulting the walls of the new buccal cavity made their appearance in the form of thin membranous plates just outside the old buccal cavity. The vertical walls of the new buccal cavity were laid down very close to old vertical walls but the gap was a bit wider towards the base. The oblique walls were first almost similar to each other in shape and size, but became differentiated in later stages. The dorsal oblique wall was comparatively shorter than the subventrals. The oblique

Table 1

Comparative measurements of buccal cavities of different stages of *Parahadronchus shakili*

| | *Buccal cavity I* | *Buccal cavity II* | *Buccal cavity III* | *Buccal cavity IV* | *Buccal cavity V* |
|---|---|---|---|---|---|
| First stage juvenile<br>n = 16 | $\overline{X}$ = 23 × 10 µm<br>R = 22-24 × 9-11 µm | | | | |
| First moult<br>n = 5 | $\overline{X}$ = 23 × 10 µm<br>R = 22-25 × 10-11 µm | 30 × 15 µm<br>27-31 × 15-19 µm | | | |
| Second stage juvenile<br>n = 10 | | $\overline{X}$ = 30 × 16 µm<br>R = 29-31 × 14-17 µm | | | |
| Second moult<br>n = 6 | | $\overline{X}$ = 31 × 15 µm<br>R = 28-31 × 14-17 µm | 36 × 19 µm<br>35-37 × 18-23 µm | | |
| Third stage juvenile<br>n = 14 | | | $\overline{X}$ = 37 × 19 µm<br>R = 35-39 × 18-20 µm | | |
| Third moult<br>n = 7 | | | $\overline{X}$ = 36 × 19 µm<br>R = 33-38 × 18-21 µm | 46 × 25 µm<br>40-48 × 23-27 µm | |
| Fourth stage juvenile<br>n = 28 | | | | $\overline{X}$ = 45 × 25 µm<br>R = 41-48 × 22-26 µm | |
| Fourth moult (♀) | | | | R = 46 × 26 µm | 60 × 36 µm |
| Fourth moult (♂♂)<br>n = 2 | | | | $\overline{X}$ = 43 × 25 µm<br>R = 42-44 × 25-26 µm | 55 × 31.5 µm<br>54-56 × 30-33 µm |
| Adults (♀♀)<br>n = 140 | | | | | $\overline{X}$ = 60 × 36 µm<br>R = 50-65 × 32-40 µm |
| Adults (♂♂)<br>n = 62 | | | | | $\overline{X}$ = 55 × 31 µm<br>R = 49-66 × 29-35 µm |

$\overline{X}$ = Mean R = Range

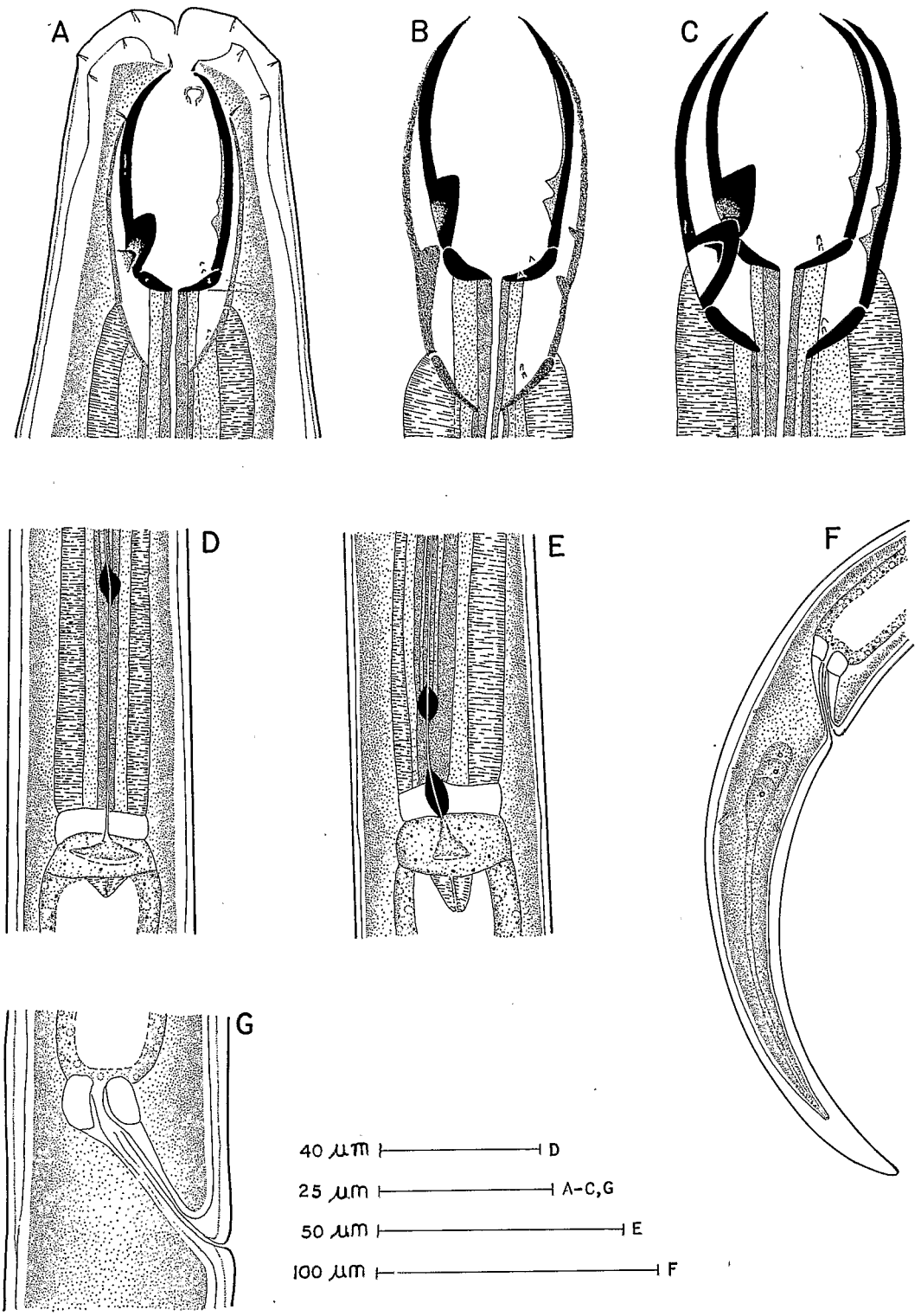


Fig. 1. A-C : Development of buccal cavity ; D : Oesophago-intestinal junction without tubercles ; E : Oesophago-intestinal junction with newly formed tubercles while the older ones are migrating upwards ; F : Abnormal tail (third moulting stage) ; G : Anal region (Fourth moulting stage).

subventral walls increased mainly in length. During each juvenile stage the dorsal tooth appeared hollow with a spare tooth near its base. With the increase in the size of buccal cavity the dorsal tooth moved towards the base of the buccal cavity and finally attached itself to the new vertical wall (Fig. 1 A & B). The spare tooth, which first appeared like a small conical piece, came into existence (Fig. 1 C). Thus in the later phase of each moult there might be three dorsal teeth. The first of these was the tooth of the previous juvenile stage which was in the process of being cast off along with the old buccal cavity, the second one was the functional tooth of that particular stage, and the third one the new spare tooth which would become the functional tooth of the future stage (Fig. 2). The dorsal tooth was hollow in young adults but afterwards became solid. The subventral teeth and the foramina developed in the later phase of each moulting stage. The subventral teeth were not present in the first stage juveniles, but in other stages they were always present.

A comparative study of the buccal cavity showed that it gradually increased in size from the first stage juvenile to the adult, but it developed more markedly in the adults than in the juveniles. The development in the first and second stages was minimal, it was much more pronounced in the adult females than the males. The distance of dorsal tooth from base of buccal cavity when calculated as a percentage in relation to the length of the buccal cavity was found to be comparatively greater in the adults than in the juveniles. Among juveniles, it was maximal in the first stage and minimal in the fourth stage. In the second and third stage juveniles it was the same.

### Oesophagus

At the time of formation of the new buccal cavity a new oesophageal lining and new set of tubercles were also formed, while the old ones were pulled anteriad (Fig. 1 E). At the beginning of each moult, the oesophago-intestinal junction became flattened. Sometimes, the development of new tubercles took place quite late while the old tubercles had already migrated upwards and it appeared as if the oesophago-intestinal junction was of non-tuberculate type (Fig. 1 D). The oesophageal length in relation to body length was comparatively greater in the juveniles than the adults. Among the juveniles, it was maximum for the first stage but was same for the third and fourth stages.

### Gonads

*First stage juvenile* (Fig. 3 A)

The genital primordia in the first stage juvenile consisted of two oval bodies connected by a cellular strand, lying at about 61% from the anterior end of body. These anterior and posterior primordia gave rise to the anterior and posterior gonads respectively. Each oval body contained a single large centrally located spherical nucleus and two somatic nuclei. The two types of nuclei could be differentiated from each other by their taking up the stain differently. The germinal nuclei appeared coarsely granular with a few dark areas, while the somatic nuclei stained darkly. The nuclei of the ventral chord which showed a granular pattern, numbered about 23 from middle of primordia to base of oesophagus. Total length of primordia varied from 30-33 µm. During the first moult no obvious changes occurred in the primordia.

*Second stage juvenile* (Fig. 3 B and 4 A)

During this stage the number of germinal and somatic nuclei remained same but the length of the primordia increased to 42 µm. In some juveniles two or three oval nuclei that stained darker than the ventral chord nuclei were also present near the posterior end of the primordia. These were the specialized ventral chord nuclei, supposed to be derived from the ventral chord nuclei (Hirschmann, 1962). These nuclei were present only in those juveniles that were to develop into females. Thus male and female juveniles could be distinguished during the second stage. The number of ventral chord nuclei from base of oesophagus to the primordia varied from 33-36. During the second moult (second stage moulting into third stage) the germinal nucleus did not divide, but the somatic nuclei divided giving rise to four to six nuclei,

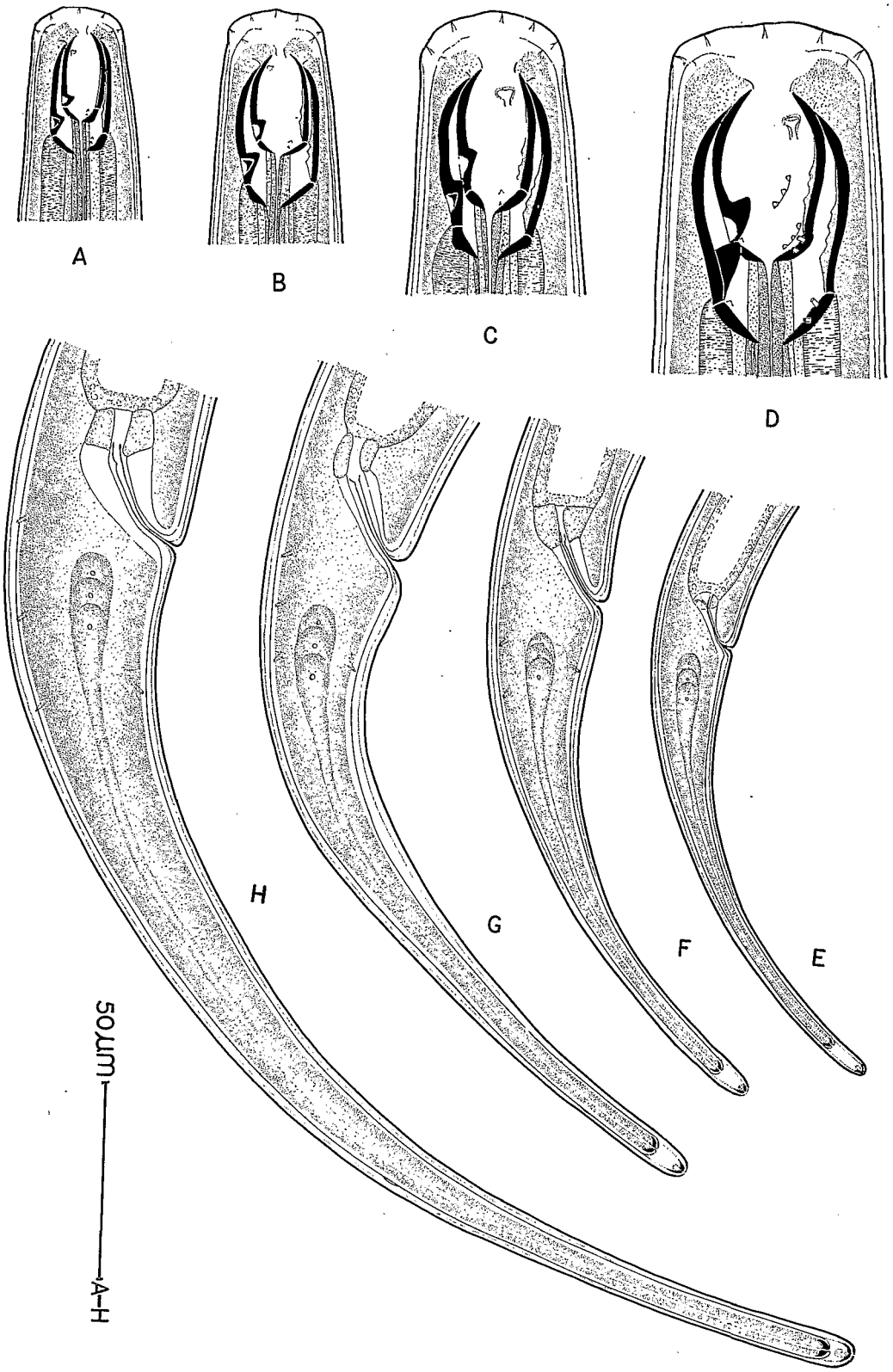


Fig. 2. A-D : Head ends of first, second, third and fourth moulting stages, respectively ; E-H : Tails of first, second, third and fourth moulting stages, respectively.

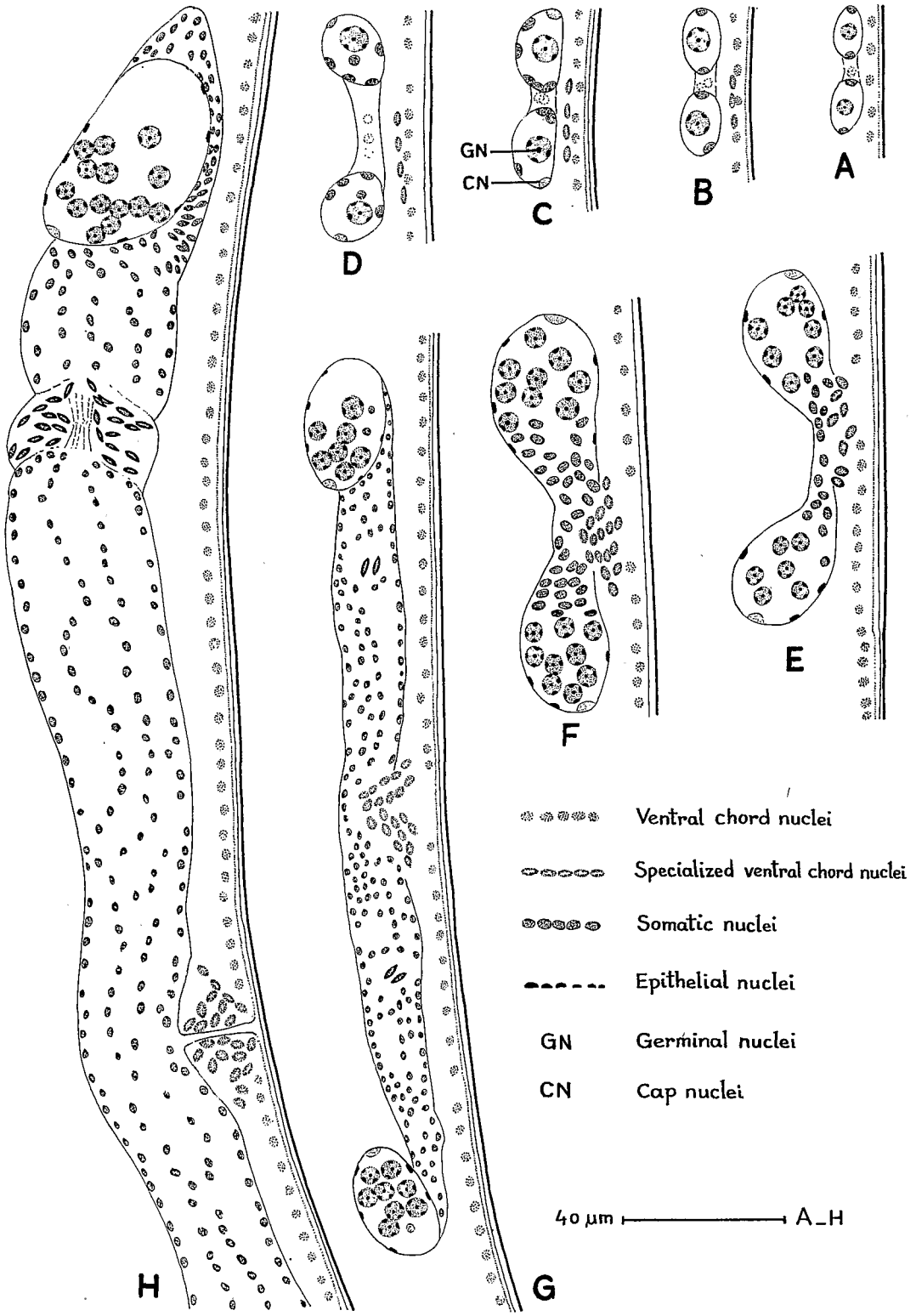


Fig. 3. Development of female reproductive system. A : First stage juvenile ; B : Second stage juvenile ; C : Second moulting stage ; D : Third stage juvenile ; E : Third moulting Stage ; F : Fourth stage juvenile ; G : Early fourth moulting stage ; H : Late fourth moulting stage.

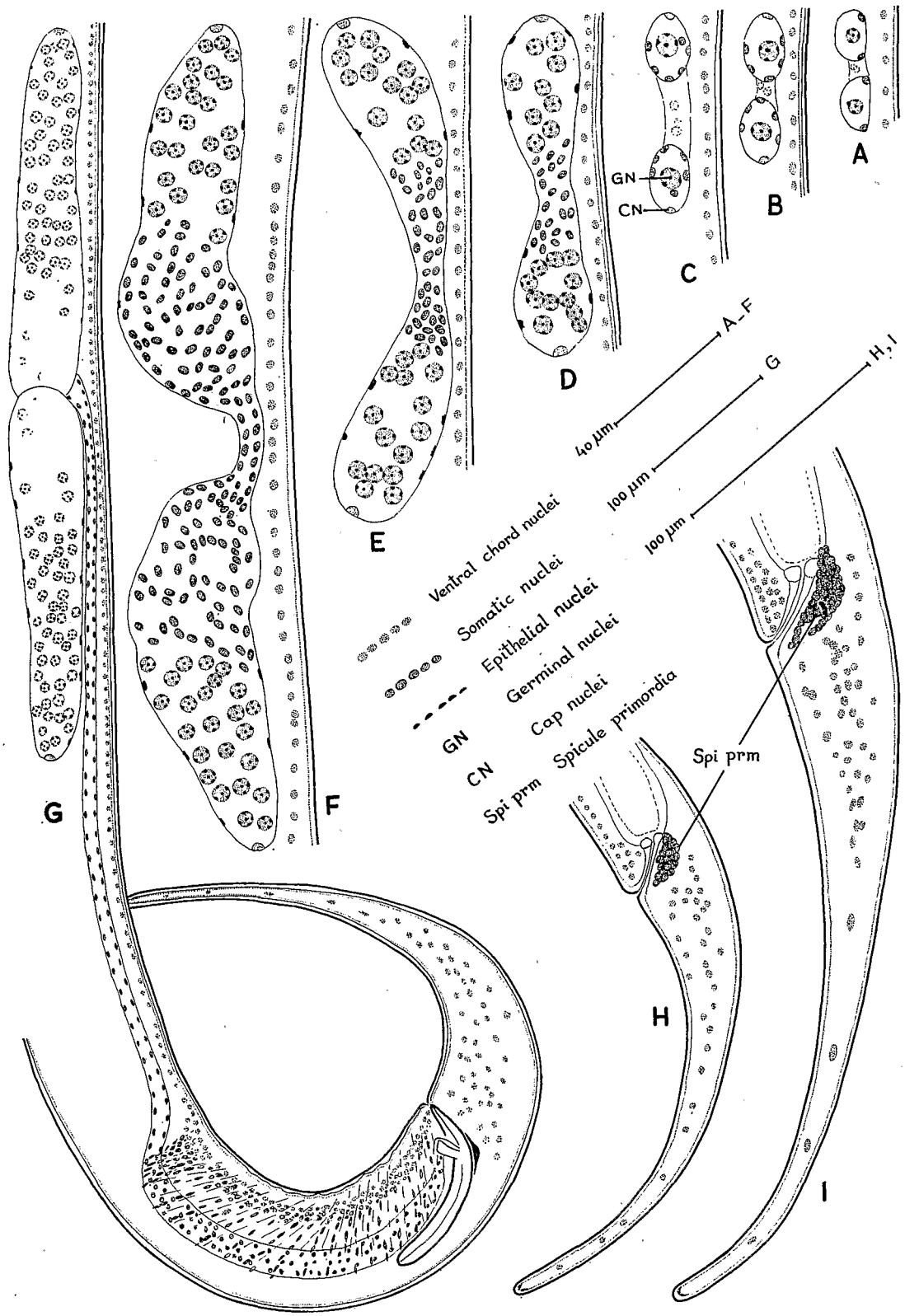


Fig. 4. Development of male reproductive system. A : Second stage juvenile ; B : Second moulting stage ; C : Third stage juvenile ; D : Third moulting stage ; E & F : Fourth stage juvenile ; G : Fourth moulting stage ; H : Third stage male tail ; I : Fourth stage male tail.

one of which became the cap nucleus at the distal end and the other at the proximal end of the anterior and posterior primordium respectively (Fig. 3 C & 4 B). These two cap nuclei did not divide any further during gonad development. The remaining somatic nuclei formed the gonoduct and the epithelial layer of the ovaries and testes during the future course of development of the females and males respectively. The number of ventral chord nuclei remained the same as in the second stage. The specialized ventral chord nuclei were four in number (Fig. 3 C).

*Third stage juvenile* (Fig. 3 D and 4 G)

During the third stage the genital primordia enlarged further, measuring approximately 62 µm, with seven nuclei in each primordium (one germinal and six somatic). The somatic nuclei were positioned as follows : one anterior, one posterior, two dorsal, one ventral and one adjacent to the germinal nucleus. In male juveniles, a small compact mass of dark staining nuclei appeared in the anal region. This mass represented the primordia of the future spicules and gubernaculum (Fig. 4 H). The multiplication of the ventral chord nuclei also took place ; these nuclei numbered 54, spreading from the middle of the primordia to base of oesophagus.

At the time of the third moulting the primordia further developed and enlarged in both sexes. The somatic nuclei proliferated further and their number increased in the middle region of the primordia. The most marked developmental change was the repeated division of germinal nucleus in each primordium, which had remained undivided so far, resulting in six to eight germinal nuclei in females (Fig. 3 E) and nine to eleven in males (Fig. 4 D). At the end of this moult, besides the cap nucleus, three or four small, darkly stained epidermal nuclei were present in each primordium. The number of ventral chord nuclei from base of oesophagus to middle of primordia averaged 136. In females, the number of specialized ventral chord nuclei doubled and these apparently became grouped in fours. In males, the spicular and gubernacular primordia enlarged further by repeated multiplication.

*Fourth stage juvenile* (Fig. 3 F and 4 E & F) :

During this stage there was considerable elongation of the developing gonads. Though both of the primordia were equally developed in the early stage, their further development in females was asymmetrical. The anterior primordium grew more quickly than the posterior one. The germinal nuclei at the end ranged from 11-25 in males and nine or ten in females. The somatic nuclei proliferated further and arranged themselves irregularly along the longitudinal axis of body. The specialized ventral chord nuclei now numbered sixteen in the vaginal area with their more inward migration. In males, the spicular and gubernacular primordia advanced further (Fig. 4 I).

During the fourth moult the gonads developed considerably. In the early stages those of the female juveniles consisted of reflexed ovaries connected to a long genital duct with a large number of somatic nuclei arranged in irregular manner. The sphincter which differentiated the genital duct into oviduct and uterus appeared as a small structure with spindle-shaped nuclei and poorly developed cuticular linings. The uteri consisted of a larger number of somatic nuclei while the oviduct had fewer nuclei. In the vaginal area there were 20-24 specialized ventral chord nuclei arranged in a somewhat circular manner with space between. With the completion of this moulting, the cuticular linings of the vagina were formed (Fig. 3 G & H). In adult females the size as well as the number of germinal nuclei (oogonia) increased.

In male juveniles the gonads differentiated into testes and gonoduct. The somatic nuclei proliferated and were arranged along the gonoduct. In the anterior part of the gonoduct *(vas deferens)* these nuclei were arranged in two rows while in the posterior region *(ejaculatory duct)* their arrangement was irregular. The germinal nuclei in the testes also underwent further division. Spicules appeared as faint refractory lines during the earlier stages of the moult but became gradually thickened. Simultaneously with the formation of spicules, the gubernaculum and the lateral accessory pieces were also formed. The copulatory muscles also developed along with the formation of spicules, but development of the ventromedian supplements began rather late. From cloaca to the

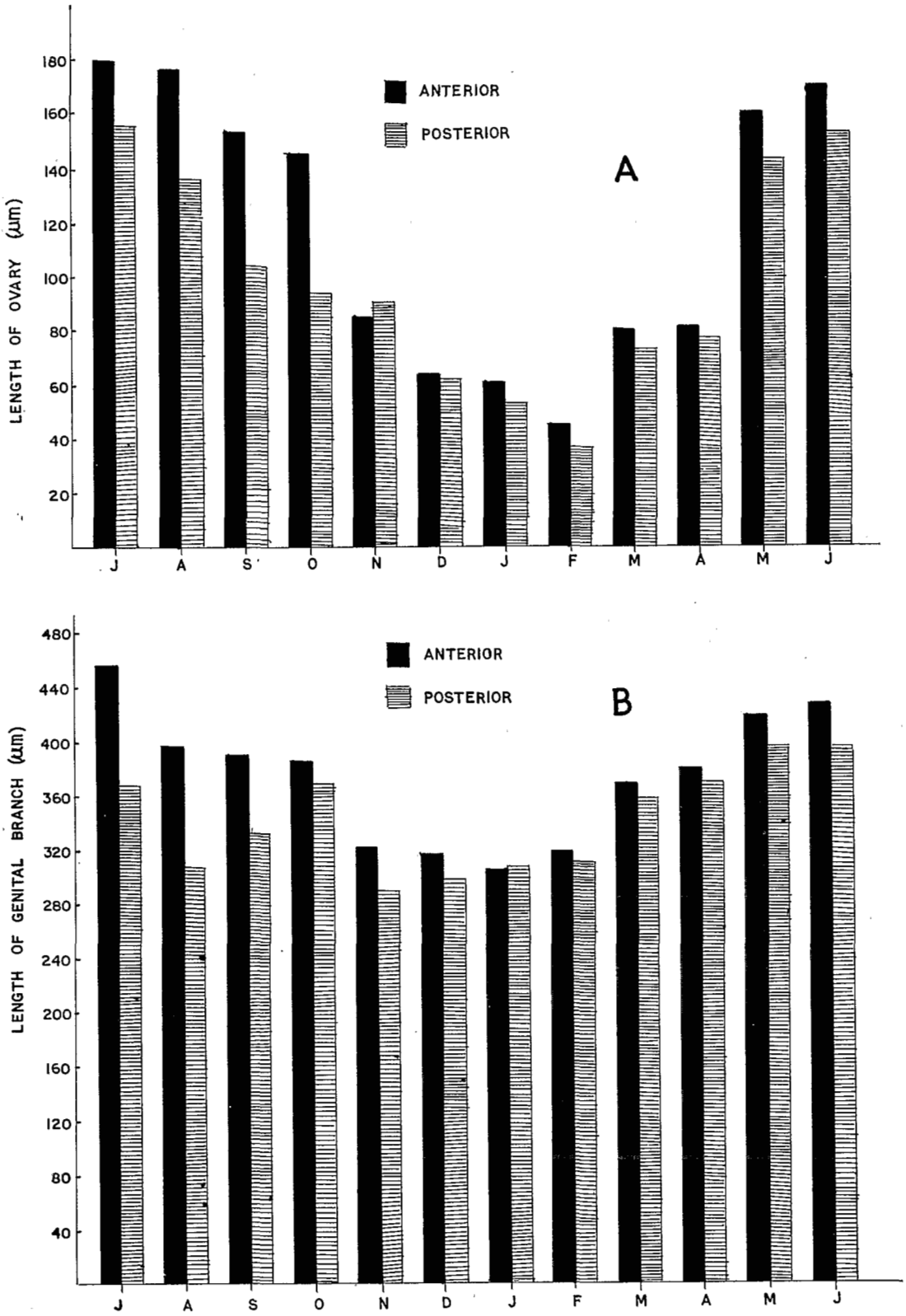


Fig. 5. A : Lengths of ovary in different months ; B : Lengths of genital tract in different months.

anterior region of the ejaculatory duct where the accessory copulatory muscles originated a large number of nuclei running ventrodorsally could also be distinguished. The nuclei close to the ventral chord nuclei were difficult to distinguish but the other type of nuclei stained comparatively darker and were more or less spindle-shaped. Moreover, in the region where the accessory copulatory muscles originated, there was accumulation of these nuclei in a triangular area (Fig. 4 G). In adults, the number of all types of nuclei increased.

*Development of genital tract* (Fig. 5)

The length of ovaries as well as the total length of the genital tract were much greater in the breeding season (March to October) than during the non-breeding season. The length of both ovaries reached a maximum in July. Thereafter, their length decreased gradually till October. From November to February (non-breeding season) there was a sharp reduction in the length of the anterior ovary to about one-fourth of its maximum in February. From March onwards, there was continuous increase in length till July. The pattern for posterior ovary was almost the same except that the reduction was about one-fifth of its maximum length. The length of the anterior ovary was greater than the posterior one in all months (Fig. 5 A). Apart from this, the hind part of the ovaries appeared brownish in colour during the breeding season due to the presence of ripe oocytes which had granular cytoplasm. During the non-breeding season (November-February) the ovaries appeared colourless and contained oocytes with non-granular cytoplasm.

The changes in length of the anterior genital tract through the months closely paralleled those of the anterior ovary. The posterior genital tract followed a slightly different pattern. Its minimum length was reached in November. From December to June it gradually increased in length but later growth was irregular. The length was almost same in the months of July, October and April. Throughout the year the anterior genital tract was always longer than the posterior one except in January when the two were almost equal (Fig. 4 B). Immediately before the beginning of the breeding season the intestinal region showed changes similar to those described for some species of *Xiphinema* (Griffin & Darling, 1964 ; Jairajpuri & Bajaj, 1978).

A large number of gravid females (382) were observed either live or dead and were grouped in three categories : those having *i*) eggs in the anterior uterus, *ii*) eggs in the posterior uterus, and *iii*) eggs in both uteri. The frequency of the first category was 58% while that of the other two was 21%. From these data it can be inferred that there was only 21% chance of both ovaries producing eggs simultaneously, otherwise only one of the two ovaries produced an egg at a time. Upon counting the number of eggs in each branch separately, it was also noted that the frequency of egg development by the anterior branch was much higher (65%) than that of the posterior branch (35%). This shows that the anterior ovary is much more active in egg production than the posterior one.

Tail (Fig. 2 E-H)

With the formation of new cuticle in the anterior region, the new cuticle of the tail and lumen of rectum was also laid down simultaneously (Fig. 1 G). The tail length in relation to body length followed a similar pattern to that of the oesophagus, but in males the ratio c was smaller than in females. The anal body-width in relation to tail length (c′) on the average was more in the males than juveniles, but in the females it was the reverse. Among juveniles, the abw/tail length ratio (c′) was at its maximum in the first stage and minimum in the fourth stage.

## Discussion

The above observations show that the formation of new cuticle precedes the formation of the buccal cavity ; the new cuticle is fully formed before the old cuticle is cast off. At the same time, the spare tooth of the previous stage also becomes fully developed and a new spare tooth is formed at the base of the functional tooth. These observations agree with those of Grootaert and Maertens (1976) on *Mononchus aquaticus*. The last phase of moult-

ing commences with the separation of old and new cuticle by large spaces. First, the rupture of the old cuticle takes place at the anterior end. The buccal cavity is ejected along with the old oesophageal linings and tubercles. Later, the old cuticle of the tail and rectum becomes loose and soon the juveniles escape from the exuvium. The other parts which are formed anew are spinneret, amphids, denticles, foramina etc. During the entire development there are four moulting stages (Fig. 2). The size of the buccal cavity in different developmental stages shows that the least development takes place in the first and second stages. This might be due to the shorter durations of these stages. Further, the development of oesophagus and tail (in relation to body length) shows that their development is comparatively greater in juveniles than adults.

The primordia in the first stage consist of two oval bodies, each with one germinal nucleus and two somatic nuclei. The somatic nuclei divide for the first time in the second stage while the germinal nuclei divide in the third moulting stage. As shown by earlier workers (Maupas, 1899 ; Pai, 1928 ; Hirschmann, 1962 etc.) the cap nucleus is derived from the somatic nuclei and does not divide later but remains a part of the ovaries or testes. The sexes become differentiated at the second juvenile stage because of the presence of specialized ventral chord nuclei in the females and spicular and gubernacular primordia in the third and fourth stages in the male juveniles. This situation is similar to that reported for *Ditylenchus triformis* (Hirschmann, 1962). The development of the gonads in the last stage is comparatively more in the male juveniles than in the females. Moreover, the two gonads are almost equally developed in the male juveniles, whereas in the females one of them grows more quickly than the other. These observations agree with those of Coomans and Lima (1965) on *Anatonchus amiciae*. The nuclei of the sphincter are also probably derived from the somatic nuclei. The vagina is formed by specialized ventral chord nuclei. The measurements show that the size of the genital primordia, like that of the buccal cavity, does not overlap in different juvenile stages.

The changes in the genital tract during the breeding and non-breeding seasons agree fully with those described by Jairajpuri and Bajaj (1978) for *Xiphinema basiri* and partially with Flegg (1967) for *Xiphinema vuittenezi*.

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