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SUPERFAMILY CERAMONEMATOIDEA (COBB, 1933) GENERAL MORPHOLOGY

by

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ABSTRACT

The systematics of the superfamily Ceramonematoidea is mainly based on morphological characteristics. A detailed study is made of the most important structures : the general shape, the cuticle and the epidermis, the musculature, the cephalic region, the digestive, nervous, excretory and reproductive systems, and the juvenile stages.

In a previous paper (HASPESLAGH, 1972) some evolutionary trends of the Ceramonematoidea have been shown, and a revision of the systematics has been proposed. The present paper brings a more detailed study of some morphological structures.

GENERAL SHAPE

The body length of adults in the different species of the different families is comprised between ± 400 µm and 2500 µm, without appreciable differences in males and females.

In cylindriform animals the body diameter remains nearly constant all over the body (Pl. I, fig. 1), while in oblong spindleshaped animals it is attenuated in the cephalic and the tail region (HASPESLAGH, 1972, Pl. I, fig. 7) ; generally females are less slender than males, the body diameter being influenced by the development of the oöcytes.

Short specimens often are fixed in a stretched position, while long specimens often curl up. In most males the tail is bent or curved ventrally, always to the right (Pl. I, fig. 1).

Several genera have a distinct annulated outlook due to the very coarse cuticular annules (Pl. I, fig. 1).

CUTICLE

The cuticular structure and its growing complexity is one of the most important morphological characteristics of the group.

The cuticle is always well developed : without the crests the cuticular layers easily take up 1/4-1/5 of the body diameter (Pl. II, fig. 6).

A distinct annulation is due to regular transverse constrictions in the superficial and median cuticular layers.

In *Xenella cephalata* COBB, 1920 the annule width of the ± 2000 annuli reaches only 0.5 µm, but in most species the number of annuli is reduced while their width varies between 5 and 12 µm.

The annule width remains constant all over the body, or varies in different ways as described in HASPESLAGH 1972, p. 238-239 (Pl. I, figs. 4 and 7).

In the anal region often two annuli partially or completely fuse into a clearly broader annulus ; in a *Pselionema* spec. a similar phenomenon has been noticed in the vulvar region.

As far as we could examine the number of annuli on the tail remains constant in juveniles and in adults of the same species, and the excretory pore is situated in the same annulus in juveniles and in adults. So the increase of the total number of annuli in the successive stages is due to an increase of the annuli in mid-body ; in some species growing zones can be distinguished, e.g. in *Cyttaronema* spec. in the region behind the cardia (Pl. I, fig. 5) and in the preanal region, where often duplicating annuli are present.

The long terminal annulus is probably formed by the fusion of several tail annuli ; in some species this process is still visible in adults (Pl. I, fig. 8).

Besides a distinct annulation the cuticle of Ceramonematoidea is characterized by longitudinal crests all over the body, but interrupted between the consecutive annuli. The crests on the annuli have a simple structure, or consist of a rather strong base surmounted by a very thin epicrista (Pl. II, fig. 6 and HASPESLAGH, 1972, fig. 1). Sometimes the crests include small spheric structures, with a refraction-index (or a density) different from that of the surrounding cuticular materials (Pl. I, fig. 7).

Together with the tendency of increasing in width, the structure of the cuticular annuli becomes more complex (HASPESLAGH, 1972, p. 236 and fig. 1).

The median layer of the cuticle has a homogeneous structure (Pl. I, fig. 7), or contains inclusions of a different density and of various shapes. These so-called vacuoles are spread all over the annulus (Pl. I, fig. 5), or are restricted to the area under the longitudinal crests (Pl. I, fig. 4).

PLATE I

Fig. 1 — *Ceramonema* spec., ♂ : cylindriform shape, coarse cuticular annules, tail bent to the right ;

Fig. 2 — *Pselionema rigidum* CHITWOOD, 1936, ♀ : longitudinal fibers in the cuticle and cells of the epidermis ;

Fig. 3 — *Cyttaronema* spec., ♂ : copulatory muscles in the tail ;

Fig. 4 — *Ceramonemoides chitwoodi* (DE CONINCK, 1942) HASPESLAGH, 1972, ♀ : cuticle at vulvar level ;

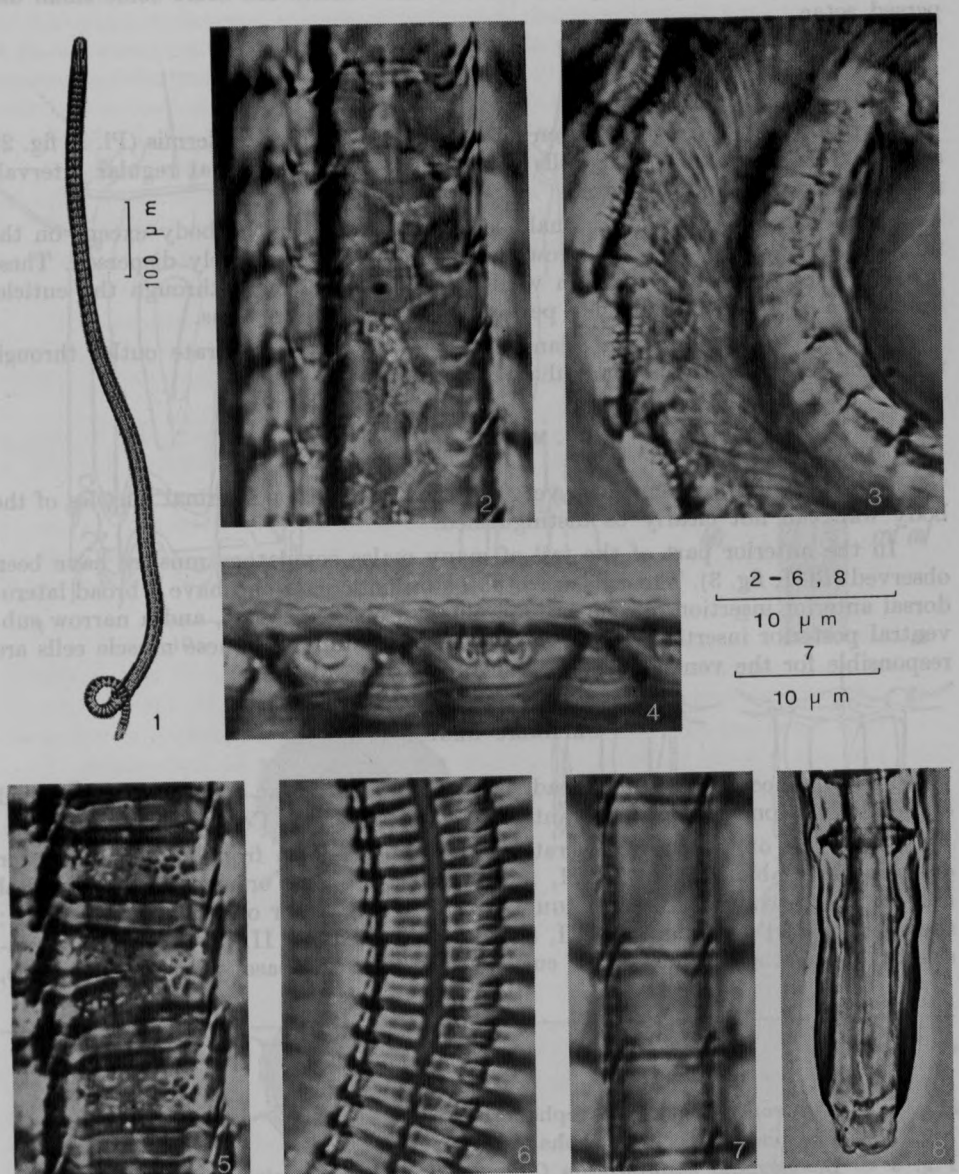
Fig. 5 — *Cyttaronema* spec. : duplicating annulus in the postcephalic region ;

Fig. 6 — *Leptodasynemella albaensis* (WARWICK and PLATT, 1973), ♀ : lateral « field » ;

Fig. 7 — *Pselionema simile* DE CONINCK, 1942, ♂ : broad/narrow annules, light refracting elements in the longitudinal crests ;

Fig. 8 — *Ceramonema attenuatum* COBB, 1920, ♀ : terminal annulus with indication of inclusion of an annule, and obtuse mucron with separate outlet of the three caudal glands.

PLATE I



In or near the basal layer sometimes longitudinal fibers are visible in the middle of the annular fields ; they probably contribute in keeping together the consecutive annuli (Pl. I, fig. 2).

In a few species the reinforced parts of the median layer are partly interrupted in the annules along the « lateral fields » of the postcephalic region (Pl. I, fig. 6).

On the tail of most males there are two rows of setae in subventral or latero-

ventral position ; exceptionally the tail of some females too bears some small dispersed setae.

EPIDERMIS

Large cells have regularly been observed in the lateral epidermis (Pl. I, fig. 2), and often groups of 3-4 small cells with a very large nucleus at regular intervals in the dorsal and ventral chord.

In numerous species very small pores occur all over the body except on the tail, situated in four sublateral rows although sometimes widely dispersed. These pores probably are in connection with epidermal gland cells through the cuticle, but it is not excluded that they perform also sensory functions.

Each of the three caudal glandcells probably has a separate outlet through the mucron of the terminal annulus (Pl. I, fig. 8).

MUSCULATURE

Because of the presence of a very thick cuticle the longitudinal muscles of the body wall can not clearly be distinguished.

In the anterior part of the tail of many males copulatory muscles have been observed (Pl. I, fig. 3). The cells are situated on both sides and have a broad laterodorsal anterior insertion on one tail annulus, an oblique course, and a narrow subventral posterior insertion on the second next tail annulus. These muscle cells are responsible for the ventral bend or curving of the tail.

CEPHALIC REGION

The presence of a distinct head- or cephalic capsule at the very anterior end of the body is one of the important characteristics of the Ceramonematoidea.

The shape of the capsule is rather variable : open in front (Pl. II, fig. 5) or enclosing the labial region (Pl. II, figs. 1 and 2) ; short- or elongated cylindrical (Pl. II, fig. 2), conical (HASPESLAGH 1972, Pl. II, fig. 2) or of a transitional form ; the anterior part is rounded (Pl. II, fig. 2) or flattened (Pl. II, fig. 5), or has a transitional form, it sometimes is less cuticularized than the basal part of the capsule,

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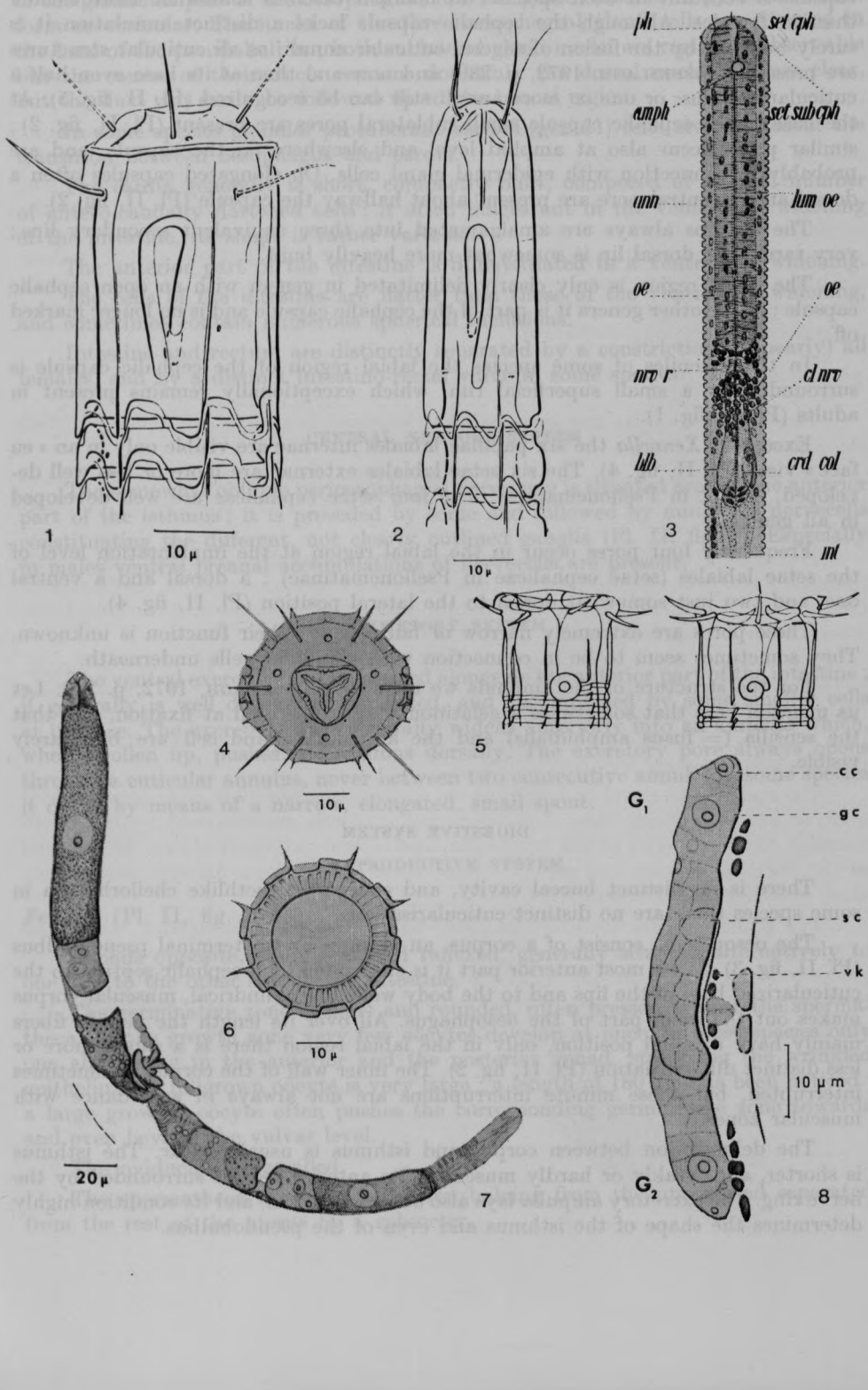
PLATE II

Fig. 1 — *Cyttaronema* spec. ♀ : cephalic region ;
Fig. 2 — *Pselionema* spec. ♂ : cephalic region ;
Fig. 3 — *Dasynemella sexalineatum* COBB, 1920, juv. : anterior body end with oesophagus (after COBB) ;
Fig. 4 — *Cyttaronema* spec. : « en face » view ;
Fig. 5 — *Metadasynemoides latus* (GERLACH, 1957) HASPESLAGH, 1972 : cephalic region ♀ and ♂ (after GERLACH) ;
Fig. 6 — *Cyttaronema* spec. : cuticular annule in front view ;
Fig. 7 — *Cyttaronema* spec., ♀ : gonads ;
Fig. 8 — *Cyttaronema* spec., fourth juvenile stage ♀ : genital primordium, cc : capcell, gc : germinative cell with large nucleus, sc : epithelial cell, vk : nucleus in the ventral chord.

PLATE II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sc
vk
10 µm
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8

in other species the labial region bears an inner reinforcement. The shape of the capsule is constant in each species ; in males it often is somewhat more slender than in females. Although the cephalic capsule lacks a distinct annulation it is surely built up by the fusion of several cuticular annuli, as all cuticular structures are present (HASPESLAGH, 1972, p. 239) and now and then at its base even half a cuticular annulus, or one or more annuli still can be recognized (Pl. II, fig. 5). At the base of the cephalic capsule small sublateral pores are present (Pl. II, fig. 2) ; similar pores occur also at amphid level and elsewhere on the capsule, and are probably in connection with epidermal gland cells. On elongated capsules often a dorsal and a ventral pore are present about halfway the capsule (Pl. II, fig. 2).

The six lips always are amalgamated into three equivalent secondary lips ; very rarely the dorsal lip is somewhat more heavily built.

The labial region is only clearly delimitated in genera with an open cephalic capsule ; in the other genera it is part of the cephalic capsule and is no longer marked off.

In the juveniles of some species the labial region of the cephalic capsule is surrounded by a small superficial rim, which exceptionally remains present in adults (Pl. II, fig. 1).

Except in *Xennella* the six papillae labiales internae are visible only in an « en face » view (Pl. II, fig. 4). The six setae labiales externae are more or less well developed, except in Pselionematinae. The four setae cephalicae are well developed in all genera.

Frequently four pores occur in the labial region at the implantation level of the setae labiales (setae cephalicae in Pselionematinae) : a dorsal and a ventral one, and two just somewhat dorsal to the lateral position (Pl. II, fig. 4).

These pores are extremely narrow or fairly wide ; their function is unknown. They sometimes seem to be in connection with glandular cells underneath.

For the structure of the amphids we refer to HASPESLAGH, 1972, p. 240. Let us mention here that sometimes a gelatinous bar is liberated at fixation, and that the sensilla (= fusus amphidialis) and the amphidial gland cell are but rarely visible.

DIGESTIVE SYSTEM

There is no distinct buccal cavity, and except for teethlike cheilorhabdia in some species there are no distinct cuticularisations.

The oesophagus consist of a corpus, an isthmus and a terminal pseudobulbus (Pl. II, fig. 3). At its most anterior part it is suspended by a cephalic septum to the cuticularized base of the lips and to the body wall. The cylindrical, muscular corpus makes out the main part of the oesophagus. All over its length the muscle fibers mainly have a radial position, only in the labial region there is a short, more or less distinct differentiation (Pl. II, fig. 2). The inner wall of the corpus is sometimes interrupted, but these minute interruptions are not always in accordance with muscular zones.

The delimitation between corpus and isthmus is usually clear. The isthmus is shorter, and weakly or hardly muscular. Its anterior part is surrounded by the nerve ring. The excretory ampulla lays also at isthmus level, and its condition highly determines the shape of the isthmus and even of the pseudobulbus.

The terminal widening of the oesophagus, the pseudobulbus, mainly consists of the glandular part of the oesophagus ; it is elongated, sacciform, pyriform, bulbiform or vesicular. The nuclei of the three oesophageal gland cells are situated in the base of the pseudobulbus ; both sublateral gland nuclei are regularly observable but the course of their ducts remains doubtful ; the dorsal nucleus is less clear, but the duct can easily be followed up to the buccal region.

In some species globular protuberant cardial (gland?) cells are situated at the transition between oesophagus and cardia.

The cardia generally is short, compactly built, composed of a small number of antero-caudally flattened cells ; it often bulges out in the ventricular widening of the intestine, its shape is rather variable.

The anterior part of the intestine is differentiated in a ventricular widening.

The cells of the intestine are flatter than those of the ventricular widening, and sometimes contain numerous spherical inclusions.

Intestine and rectum are distinctly separated by a constriction in (nearly) all females, and by a distinct intestino-rectal valve in some species.

CENTRAL NERVOUS SYSTEM

The somewhat oblique perioesophagial nerve ring is situated around the anterior part of the isthmus ; it is preceded by some and followed by numerous nervecells constituating the different, not clearly outlined ganglia (Pl. II, fig. 3). Especially in males ventral preanal accumulations of nervecells are present.

EXCRETORY SYSTEM

The ventral excretory cell is situated alongside the anterior part of the intestine ; it generally is well developed, elongated, and accompanied by some smaller cells at its base. The excretory duct generally widens anteriorly into an ampulla which, when swollen up, pushes the isthmus dorsally. The excretory pore always opens through a cuticular annulus, never between two consecutive annuli ; in some species it opens by means of a narrow, elongated, small spout.

REPRODUCTIVE SYSTEM

Females (Pl. II, fig. 7)

Gonads opposite, equivalent and reflexed, generally situated alternatively to one and to the other side of the intestine.

The germinative zone is short and rounded, often pressed against the spermatheca. In the growth zone very few oöcytes develop at once, in most species only one alternating in the anterior and the posterior gonad, stretching the wrinkled epithelium. A fullgrown oöcyte is very large : a length of 180 µm has been noticed ; a large growing oöcyte often pushes the corresponding germinative zone towards and even beyond the vulvar level.

The oviduct is thinwalled.

The spermatheca is thinwalled, often bulging from the uterus and separated from the rest of the uterus by a sphincter.

The shell gland (= tricolumella, quadricolumella, crustaformeria) often has large swollen cells, even when no oöcytes are ripening in the corresponding gonad. A fertilized egg is thinwalled and stretches the uterus. Each uterus is in connection with the vagina.

The vagina is generally surrounded by a strong sphincter ; sometimes vaginal glands are present near the uterine wall.

The vulva consist of a transverse slit, situated between two consecutive annuli ; only in one *Pselionema* spec. the vulva is situated in the middle of a large, double vulvar annulus. In *Pselionema rigidum* CHITWOOD, 1936 an egg with a developing embryo was still attached to the vulva by eggmembranes. There is a cuticular reinforcement around the vulvar slit ; it is limited to both the vulvar annuli in species with broad cuticular annuli, but in species with narrow annuli, several annuli partly fuse together and build up a broad lipstructure. In *Metadasynemella macrophalla* DE CONINCK, 1942 a vulvar apron (epiptygma) is constituted, probably by concrescence of zygapophysae.

Males (Pl. III)

Two testes, opposite and stretched, the posterior is always less developed than the anterior.

The germinative zone is short and is immediately followed by a zone of differentiation. Immediately after formation spermatozoa often lay piled up in the form of a stack, but further they lay more disorderly.

The wall of the gonoduct often is granular (possibly indicating a glandular function), the granules are smaller than the nuclei of spermatids or spermatozoa. Often there is a short, fine dotted zone at about the junction of both gonoducts, where the vas deferens starts.

The wall of the vas deferens contains many gland cells all over its length, having a different outlook (different function?) in the consecutive zones. Three (very) coarsely granulated glandcells (= ejaculatory glands?) situated in the distal part of the vas deferens in the cloacal region often grow out far anteriorly, sometimes nearly reaching the testes.

The spicula are equal in length, more or less ventrally bent ; the capitulum is more or less cylindrical, the calamus (corpus) is chiefly cuticularized ventrally and dorsally, the distal part of the lamina has also lateral cuticularisations. The spicula of the different species and genera all are built on the same pattern, and seldom show good specific characteristics.

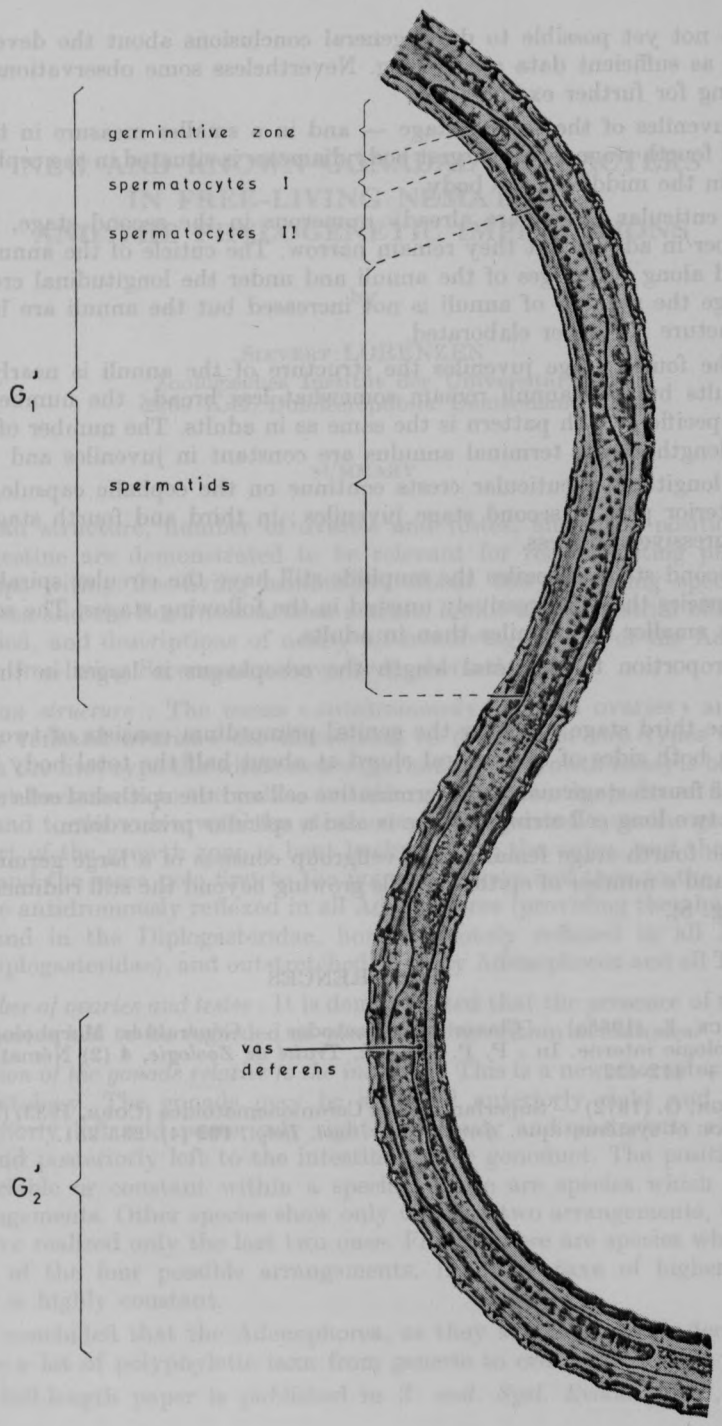
The gubernaculum generally is about half as long as the spicula. It consists of a single or double, heavily cuticularized median piece, and two rather long lateral pieces (wings), which distally form the gliding grooves for the spicula.

In most species the protractor of the gubernaculum is well developed ; the whole copulatory musculature is only exceptionally to be observed.

PLATE III

Cyttaronema spec., ♂ : gonads.

PLATE III


germinative zone
spermatocytes I
spermatocytes II
G1
spermatids
vas
deferens
G2

JUVENILE STAGES

It is not yet possible to draw general conclusions about the development in juveniles as sufficient data are lacking. Nevertheless some observations are worth mentioning for further examination.

In juveniles of the second stage — and in a smaller measure in those of the third and fourth stage — the largest body diameter is situated in the cephalic region, and not in the middle of the body.

The cuticular annuli are already numerous in the second stage, 60-80 % of the number in adults, but they remain narrow. The cuticle of the annuli is mostly developed along the ridges of the annuli and under the longitudinal crests. In the third stage the number of annuli is not increased but the annuli are broader and their structure is further elaborated.

In the fourth stage juveniles the structure of the annuli is nearly the same as in adults but the annuli remain somewhat less broad ; the number of annuli and the specific growth pattern is the same as in adults. The number of tail annuli and the length of the terminal annulus are constant in juveniles and adults.

The longitudinal cuticular crests continue on the cephalic capsule, nearly up to its anterior part in second stage juveniles ; in third and fourth stage juveniles they progressively regress.

In second stage juveniles the amphids still have the circular spiral structure ; in most species they progressively unwind in the following stages. The setae remain somewhat smaller in juveniles than in adults.

In proportion to the total length the oesophagus is larger in the youngest stages.

In the third stage juveniles the genital primordium consists of two small cell-groups on both sides of the ventral chord at about half the total body length.

In the fourth stage males the germinative cell and the epithelial cells are dividing and form two long cell strings ; there is also a spicular primordium.

In the fourth stage females each cellgroup consists of a large germinative cell, a capcell and a number of epithelial cells growing beyond the still rudimental vagina (Pl. II, fig. 8).

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