

THE RHIGONEMATIDA (NEMATODA) OF DIPLOPODS : reclassification and its cladistic representation

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SUMMARY. Morphological variation in the Rhigonematida (Nematoda) is reviewed with the aim of identifying evolutionary trends to construct a reclassification. The order is divided into two superfamilies, namely the Rhigonematoidea and the Ransomnematoidea, and a cladistic representation of the generic relationships is given for each. The Rhigonematoidea includes the Rhigonematidae with *Rhigonema*, *Xustrostoma*, *Obainia* and *Glomerinema*, and the Ichthycephalidae with *Ichthyocephalus*, *Paraichthyocephalus* and *Ichthyocephaloides*. The Ransomnematoidea includes the Ransomnematidae with *Ransomnema*, the Hethidae with *Heth*, and the Carnoyidae with *Carnoya*, *Rondonema*, *Urucua*, *Raonema*, *Clementeia*, *Brumplaemilius* and *Waerebekeia*. Geographical and host distributions are reviewed and it is suggested that *Rhigonema* may be a paraphyletic group including primitive members of several different lineages.

Les Rhigonematida (Nematoda) de Diplopodes : reclassification et schéma cladistique.

RÉSUMÉ. Cet article présente une mise au point sur la morphologie comparée des Rhigonematida (Nematoda) et indique les directions évolutives utilisées pour construire une reclassification du groupe. L'ordre se divise en deux superfamilles, les Rhigonematoidea et les Ransomnematoidea, et un schéma cladistique des genres est présenté pour chacune d'entre elles. Les Rhigonematoidea renferment les Rhigonematidae avec les genres *Rhigonema*, *Xustrostoma*, *Obainia* and *Glomerinema*, et les Ichthycephalidae avec les genres *Ichthyocephalus*, *Paraichthyocephalus* et *Ichthyocephaloides*. Les Ransomnematoidea renferment les Ransomnematidae avec le genre *Ransomnema*, les Hethidae avec le genre *Heth* et les Carnoyidae avec les genres *Carnoya*, *Rondonema*, *Urucua*, *Clementeia*, *Raonema*, *Brumplaemilius* et *Waerebekeia*. Le spectre d'hôtes et la répartition géographique des genres sont discutés, et il est suggéré que *Rhigonema* est un groupe paraphylétique comprenant des formes primitives de plusieurs lignées de Rhigonematidae.

Introduction

Two major groups of nematodes parasite the posterior intestine of the Diplopoda, namely rhigonematids and thelastomatids. Thelastomatids are clearly members of

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the Oxyurida but the systematic affiliations of rhigonematids are uncertain. Recent studies (Adamson, 1981 ; Inglis, 1983 ; Adamson and van Waerebeke, 1984a) support Chitwood's (1932) contention that rhigonematids are fundamentally distinct from thelastomatids and other Oxyurida and Inglis (1983) treats them as a suborder of the Ascaridida.

Existing classifications of rhigonematids (Kloss, 1960 ; Skrjabin, Schikhobalova and Lagadovskaya, 1966 ; Poinar, 1977) are inadequate on several grounds : they use taxa which include thelastomatids ; they employ many families and/or subfamilies but say little of the interrelationships of these taxa ; they were constructed when our knowledge of the group was limited and often make use of characters of dubious value.

Recent studies have greatly increased our understanding of the group and the present communication reviews comparative morphology in rhigonematids with the aim of identifying evolutionary trends to construct and justify a new classification. A cladistic representation of proposed phylogenies within the group is given ; host and geographic distributions of the genera are reviewed and the place of rhigonematids in the origins of nematode parasitism is discussed.

Proposed classification

For reasons that we will elaborate below we do not follow Inglis (1983) in including rhigonematids in the Ascaridida. Instead, we follow an earlier proposal (Adamson, 1981) and treat these nematodes as an order, the Rhigonematida. It is divided into two superfamilies, the Rhigonematoidea and the Ransomnematoida (*Table I*).

TABLE I. — Proposed reclassification of the order Rhigonematida.

<i>Rhigonematoidea</i>	Rhigonematidae	<i>Rhigonema</i> Cobb, 1898 <i>Obainia</i> Adamson, 1983 <i>Xustrostoma</i> Adamson and van Waerebeke, 1984 <i>Glomerinema</i> van Waerebeke, 1985
	Ichthyocephalidae	<i>Ichthyocephalus</i> Artigas, 1926 <i>Paraichthyocephalus</i> Travassos and Kloss, 1958 <i>Ichthyocephaloides</i> Hunt and Sutherland, 1984
<i>Ransomnematoida</i>	Ransomnematidae	<i>Ransomnema</i> Artigas, 1926
	Hethidae	<i>Heth</i> Cobb, 1898
	Carnoyidae	<i>Carnoya</i> Gilson, 1898
		<i>Rondonema</i> Artigas, 1926
		<i>Clementeia</i> Artigas, 1930 <i>Brumptaemilius</i> Dollfus, 1952 <i>Urucua</i> Kloss, 1961 <i>Raonema</i> Kloss, 1965 <i>Waerebekeia</i> Adamson and Anderson, 1985

Our classification differs little from that of Kloss (1960). We retain the families Rhigonematidae, Ichthyocephalidae, Ransomnematidae, Hethidae and Carnoyidae. The major differences lies in the fact that we oppose the first two families which make up the Rhigonematoidea, to the last three which constitute the Ransomnematoida.

We recognize the following synonymies : *Ruizia* Travassos and Kloss, 1958 ; *Dudekemia* Artigas, 1930 and *Haplacis* Baylis and Daubney, 1926 are synonyms of *Rhigonema* Cobb, 1898 (see Dollfus, 1952 ; Adamson, 1983d) ; *Dudekemnema* Skrjabin, Schikhobalova and Lagodovskaya, 1966 is a synonym of *Ransomnema* Artigas, 1929 (see Adamson, 1983a) ; *Pararondonema* Travassos and Kloss, 1960 and *Angranema* Travassos, 1949 are synonyms of *Rondonema* Artigas, 1926 (see Adamson, 1983b).

Morphology and evolutionary trends

This section is a synthesis of information presented in Osche (1960), Travassos and Kloss (1960, 1965), Kloss (1965), Rao and Kumari (1967), van Waerebeke (1984, 1985a, 1985b), van Waerebeke, Adamson and Kermarrec (1984), Hunt and Sutherland (1984), Adamson (1981, 1982, 1983a, 1983b, 1983c, 1983d, 1983e, 1983f, 1984a, 1984b), Adamson and van Waerebeke (1984a, 1984b, 1985), Adamson and Zaman (1984) and Adamson and Anderson (1985).

Primitive states of characters in each superfamily are determined using free-living rhabditids as an out-group.

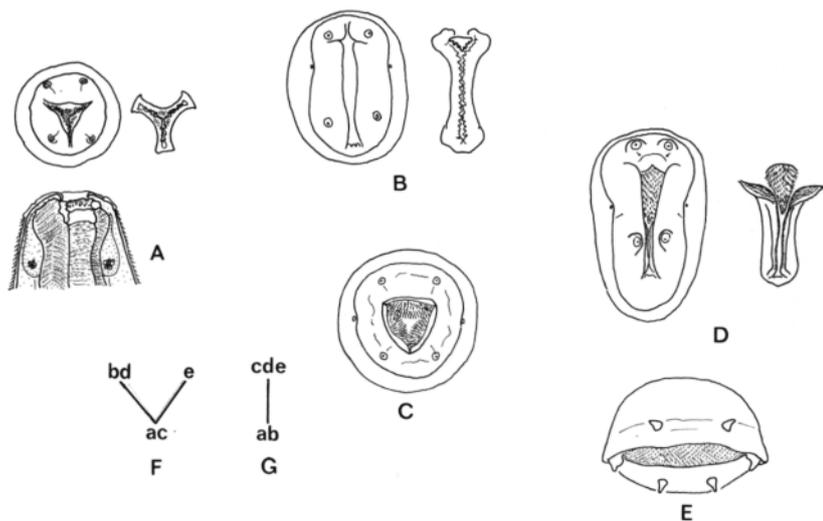
Labial Structures and Oral Opening

We consider both superfamilies to have arisen from six-lipped ancestors with hexagonal oral openings.

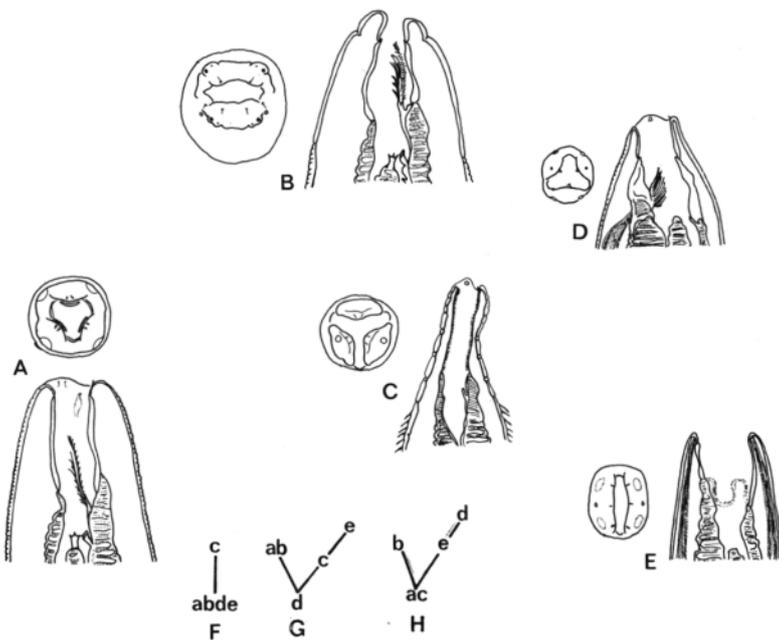
Lips are absent in the Rhigonematoidea. The oral opening is subtriangular in the Rhigonematidae but forms a lateral slit in the Ichthyocephalidae (*fig. 1*). In *Rhigonema* and *Glomerinema* the three sides of the oral opening are about equal whereas in *Obaina* and *Xuistrostoma* the dorsal side is reduced and the oral opening is dorso-ventrally elongate.

Aside from *Ransomnema* the Ransomnematoida display a pronounced sexual dimorphism in labial structures, the male exhibiting the more primitive pattern. In all genera lips are reduced (at least in number) and/or absent. In males of the Carnoyidae, *Carnoya* and *Brumptaemilius* there are one dorsal and two subventral lips and the oral opening forms a triangle whose apices are subdorsal and ventral in position. In males of *Rondonema* there are no lips and the oral opening is dorso-ventrally elongate ; in those of *Waerebekeia* dorsal and ventral lips surround a laterally elongate oral opening. Females of the Carnoyidae lack lips and the oral opening is subcircular.

Three lips are present in *Ransomnema* ; they are ventral and subdorsal and the corners of the subtriangular oral opening are dorsal and subventral in position. This pattern may have evolved directly from a six-lipped pattern but we treat it as a



RHIGONEMATOIDEA



RANSOMNEMATOIDEA

FIG. 1. — Variations in cephalic structures and stoma in the Rhigonematida.
 Rhigonematoida : A, *Rhigonema* ; B, *Obainia* ; C, *Glomerinema* ; D, *Xustrostoma* ; E, Ichthyocephalidae ; F and G, phylogenetic trees based on characters 3 and 7 respectively.
 Ransomnematoidea : A, *Brumptaemilius* ; B, *Waerebekia* ; C, *Carnoya* ; D, *Ransomnema* ; E, *Rondonema* ; F, G and H, phylogenetic trees based on characters 2, 3 and 11 respectively.

secondary inversion of a *Brumptaemilius*-like three-lipped pattern. In males of *Heth* there are no lips and the oral opening is dorsoventrally elongate as in *Rondonema*. In females, highly developed lateral pseudolabia expand anteriorly to form large plates with pectinate outer edges.

Cephalic Papillae

The primitive complement of papillae in parasitic nematodes consists of six inner and six outer labial, and four cephalic papillae. In the Rhigonematoidea the lateral outer labial papillae are absent and the submedian outer labial papillae are fused to varying degrees with the cephalic papillae. These form mammiliform structures in the Rhigonematidae and conical structures in the Ichthyoccephalidae. Inner papillae may be reduced to varying degrees depending on the species.

The complete complement of papillae occurs in one member of the Ransomnematodea, namely *Brumptaemilius justini* Adamson and Anderson, 1985. In other members of the superfamily the lateral outer labial papillae are absent. In females of the Carnoyidae the submedian outer labial papillae are fused with the cephalic papillae to form four semispherical circumoral protuberances.

Buccal Capsule and Cavity

According to Chitwood (1950b) the buccal cavity of a typical rhabditid consists of a cheilostome or lip cavity, a protostome and a telostome which is partially surrounded by oesophageal tissue.

In the Rhigonematoidea the protostome and telostome are fused and completely surrounded by oesophageal tissue. In the Rhigonematidae the buccal capsule takes the form of three sclerotized plates which articulate to form a jaw-apparatus (*fig. 1*). In *Rhigonema* and *Obaina* the plates have tooth-like excrescences and tiny bosses on their luminal surfaces whereas in *Glomerinema* and *Xustrostoma* each plate is covered with rows of tiny spines. Primitively, the three plates are identical but in *Obaina* the dorsal plate is reduced and in *Xustrostoma* it is laterally compressed. In the Ichthyoccephalidae the buccal capsule lines much of the oesophageal corpus and consists of dorsal and ventral cuticular plates bearing rows of tiny spines.

The Ransomnematodea are characterized by the presence of three cuticular projections at the base of the protostome which we refer to as metastomal projections (see Osche, 1960 for a discussion of the occurrence of these structures throughout the Nematoda). These may be reduced or absent in females but some vestige of them always remains in males. We consider the most primitive conformation in the superfamily to consist of a stalk upon which lamellae are arranged like petals on a flower (*fig. 2*). Such metastomal projections occur in *Ransomnema*, males of *Heth*, and probably those of *Clementeia*. In general the evolutionary trend has been towards reduction but in males of *Brumptaemilius* and *Waerebekeia* they are hypertrophied.

A second evolutionary trend in the buccal capsule of the Ransomnematodea is towards lengthening. The *Brumptaemilius* males serves as an example of the primitive type: the buccal capsule consists of a short cheilostome, an urceolate protostome and a telostome partially surrounded by oesophageal tissue. A similar conformation occurs

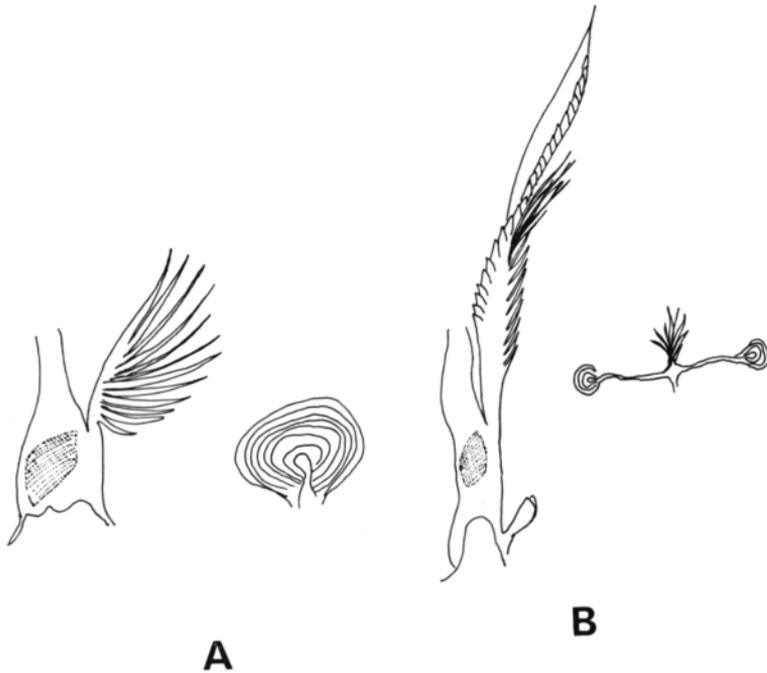


FIG. 2. — Schematic representation of metastomal modifications in the Ransomnematodea. A, lateral and apical views of *Ransomnema*-type. B, lateral and apical views of *Brumptaemilius*-type.

in *Ransomnema* and in males of *Heth*, *Waerebekeia* and *Rondonema*, and probably also those of *Raonema* and *Clementeia*. In male *Carnoya* the protostome takes the form of a long tube of striated cuticle and this tendency is carried further in female Carnoyidae where the base of the buccal capsule lies some distance down the oesophagus at the junction between the narrow and broad portions of the corpus. The buccal capsule is also secondarily lengthened in female *Heth* but this is accomplished by the encorporation of a long tubular cuticular segment posterior to the telostome and is therefore an instance of convergence.

Oesophagus (fig. 3)

The oesophagus of a typical Rhabditidae consists of a corpus with a posterior swelling, a long cylindrical isthmus and a valved bulb.

In the Rhigonematoidea the corpus is robust; it is clavate and relatively long in *Rhigonema* but longitudinally compressed in *Obainia*, *Xustrostoma* and *Glomerinema*, and forms an ovoid mass around the buccal capsule in the Ichthyocephalidae. The isthmus is reduced in the Rhigonematidae and this is most pronounced in *Rhigonema*; it is slightly reduced in *Ichthyocephalus* and *Ichthyocephaloides*. The bulb is hypertrophied in *Obainia*, *Glomerinema* and *Xustrostoma*.

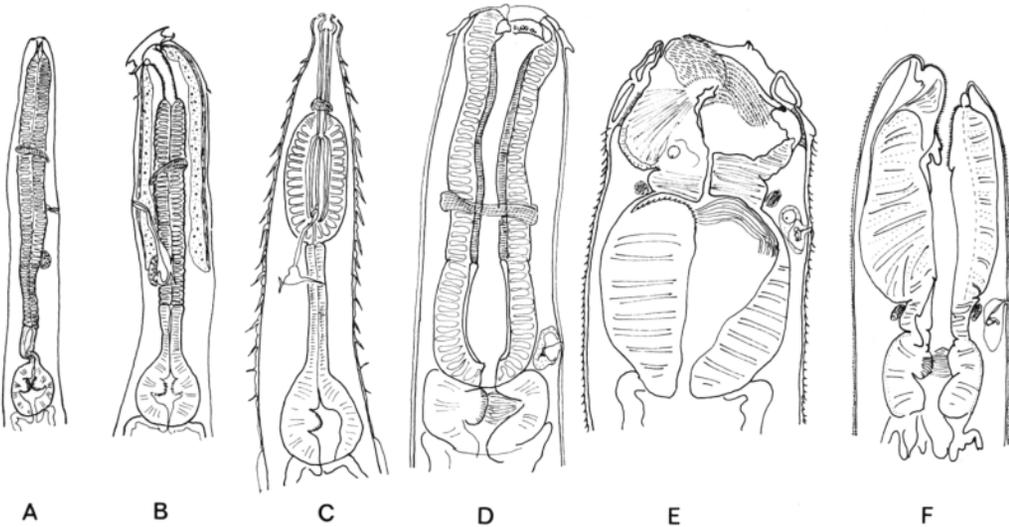


FIG. 3. — Variation in oesophageal morphology in the Rhigonematida.
 A, male *Heth*; B, female *Heth*; C, female *Carnoya*; D, *Rhigonema*;
 E, *Xustrostoma*; F, *Ichthyocephalus*.

In both sexes of *Ransomnema* and in males and larvae of the other Ransomnematoidae the corpus is spindle shaped and distinctly set off from the isthmus and bulb. In females of *Heth* the corpus is slightly modified being roughly cylindrical and in females of the Carnoyidae it is divided into narrow anterior and broad posterior portions.

Excretory System

The excretory system is H-shaped in both superfamilies. However the terminal duct is vesicular in the Rhigonematoidae whereas the Ransomnematoidae have retained the tubular terminal duct.

Female Reproductive System (fig. 4)

The reproductive system of female Rhabditidae characteristically consists of a median vulva and a short, poorly muscularized vagina leading to amphidelphic uteri and reflexed ovaries.

The vagina is generally long and muscular in the Rhigonematoidae; it may include a more glandular vaginal chamber, or a blind vaginal diverticulum. A well differentiated oval seminal receptacle is present. *Ichthyocephaloides* is monodelphic as a result of complete atrophy of the posterior reproductive horn.

The Ransomnematoidae are monodelphic and digonant, and the vagina is well muscled and long. In *Ransomnema* the vulva is markedly posterior to midbody and the vagina leads anteriorly to the uterus. The short pyriform ovaries are opposed and reflexed; one opens into the posterior end of the uterus, adjacent to the vaginal

opening, and the other opens into the anterior end of the uterus. The vulva is also posterior to midbody in *Heth*; the vagina leads anteriorly through the uterus to a single oval seminal receptacle from which leave two oviducts and parallel ovaries. In the Carnoyidae the vulva lies about midway between the cephalic extremity and the anus. The most primitive pattern is exhibited by *Carnoya*; the vagina runs posteriorly from the vulva to a posteriorly directed uterus from which two reflexed oviducts lead anteriorly to parallel anteriorly directed ovaries. The pattern is similar in other Carnoyidae except that the vagina leads anteriorly before flexing posteriorly to join the uterus.

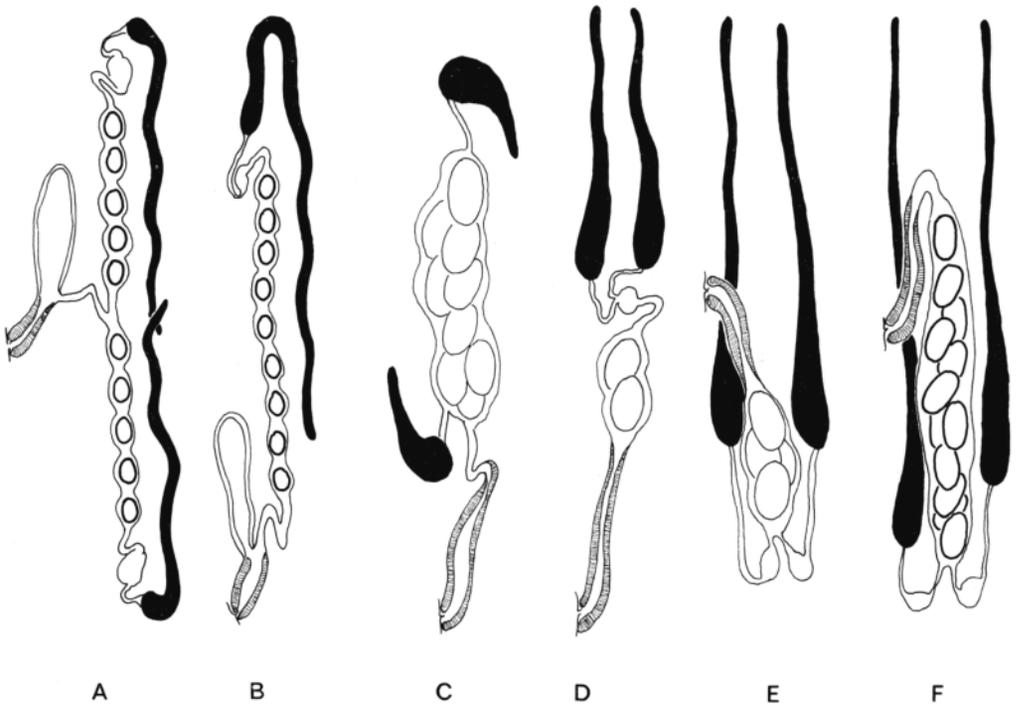


FIG. 4. — Variations in female reproductive morphology in the Rhigonematida. A, rhigonematoid-type; a vaginal sac has been included but may be absent depending on the species; B, *Ichthyocephaloides*; C, *Ransomnema*; D, *Heth*; E, *Carnoya*; F, *Brumptaemilius*/*Waerebekeia*/*Rondonema*/*Raonema*/*Urucuia*.

Egg Morphology

The rhabditid egg is surrounded by a thin flexible membranous shell. Eggs in the Rhigonematoidea have a thick smooth shell; the thickness of the shell is probably due to a highly developed chitinous layer. In some members of the Ransomnematoida (*Ransomnema*, *Heth* and *Carnoya*) the egg shell is thin and flexible like that in rhabditids. In *Rondonema* and *Urucuia* the shell is thin but relatively inflexible; in *Brumptaemilius*, *Waerebekeia* and probably also in *Raonema* the egg shell is thickened by the presence of a sculptured outer protein layer.

Male Reproductive Structures— Caudal Papillae (*fig. 5*)

Osche (1958) established homologies between the caudal papillae of *Rhabditis* and the bursal rays of the Strongylida, and Chabaud and Petter (1961) extended these homologies to include the Ascaridida and Spirurida. According to the latter authors, primitively there are ten pairs and one unpaired caudal papillae of which three pairs (the first, fourth and eighth) are sublateral to subdorsal in position.

The most primitive papilla pattern in the Rhigonematoidea is exhibited by *Xuistrostoma*, *Obainia* and African and Indian *Rhigonema*; the full complement is often present (there may be supernumerary pairs) and three sublateral pairs exist. In *Glomerinema*, *Rhigonema* from the New World and Pacific region, and the Ichthyocephalidae, the first, fourth and eighth papilla pairs are subventral and the number of papillae may be reduced. *Ichthyocephaloides* apparently has supernumerary papillae.

The number of caudal papillae is reduced to seventeen or fewer in the Ransomematoidea. In *Brumptaemilius*, *Raonema*, *Waerebekeia* and *Urucuia* there are fifteen or more papillae of which two pairs (one adanal and one postanal) are subdorsal or lateral in position. In *Heth* there are thirteen to fifteen papillae depending on whether or not the adanal lateral pair (presumably papilla 4) is present. In *Rondonema*, *Carnoya* and *Ransomnema* there are thirteen caudal papillae, the adanal sublateral pair being absent.

— Spicules and Gubernaculum

The primitive state is two similar and equal, convergent spicules and a gubernaculum.

In the Rhigonematoidea there are two convergent spicules but the gubernaculum is reduced or absent. Spicules are similar and equal in the Rhigonematidae and in *Paraichthycephalus*, but they are dissimilar in *Ichthycephalus* and *Ichthyocephaloides*.

Spicules are similar and parallel (not convergent) in the Carnoyidae. A gubernaculum is present in all genera but reduced in *Raonema*. In *Ransomnema* spicules are convergent and dissimilar; the gubernaculum is absent and its role is assumed by the left spicule. Spicules are convergent and fused in *Heth*.

— Miscellaneous Structures.

A ventral sucker occurs in males of *Ransomnema* and *Heth*. This structure was also reported in the original description of *Clementeia* but Kloss (1956) suggested that Artigas (1930) had mistaken a male of *Heth* for one of *Clementeia*. Little is known about the anatomy of *Clementeia* and this suggestion awaits confirmation.

In *Urucuia* the ventral cuticle on the caudal extremity of the male bears reinforced striations which presumably aid in holding the female during copulation. In males of *Brumptaemilius* there is a prominent *area rugosa*.

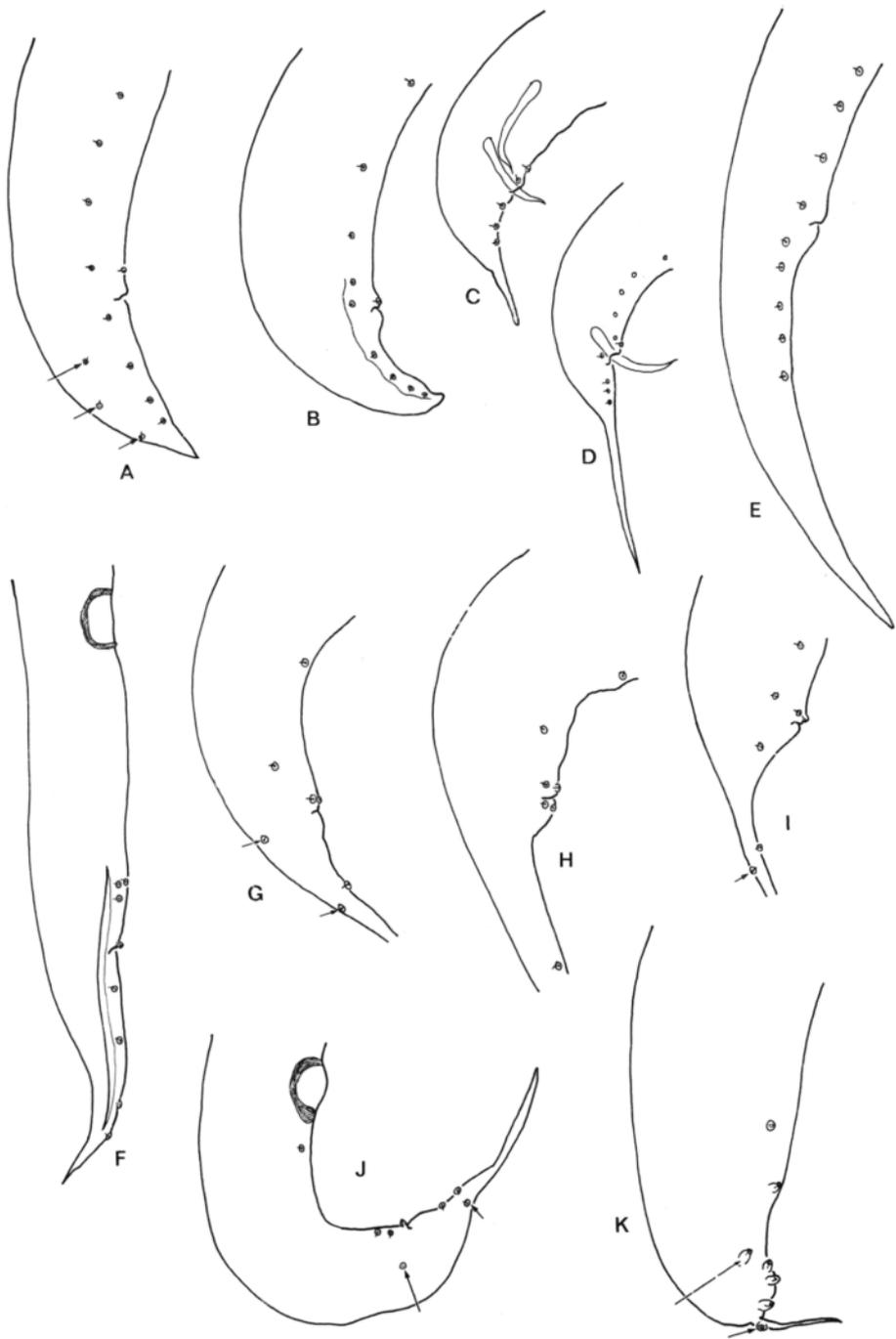


FIG. 5. — Variation in male caudal morphology in the Rhigonematida.

A to E : Rhigonematoidea : A, African *Rhigonema* and *Obainia* ; B, New World *Rhigonema* ; C, *Rhigonema* from New Zealand Sphaerotoeroidea (Glomerida) ; D, *Glomerinema* from Madagascar Sphaerotoeroidea ; E, *Ichthyocephaloides*. Note presence of subdorsal papillae in A (arrows) and similarity between C and D.

F to K : Ransomnematoidea : F, *Ransomnema* ; G, *Waerebekeia* ; H, *Carnoya* ; I, *Rondonema* ; J, *Heth* ; K, *Brumplaemilius*. Note presence of sublateral to subdorsal papillae (arrows) : two in G, J and K, one in I and nine in F and H.

Modifications of the External Cuticle— Cephalic Modifications (*fig. 6*)

Tiny transverse striations occur on the cuticle of most Nematoda and can be considered a primitive feature of both superfamilies considered here. Primitively striations begin immediately posterior to the lip region but in the Rhigonematoidea the cuticle of the cephalic extremity is devoid of striations and forms a smooth cap. In the Rhigonematidae the cephalic cap is accompanied by a posterior collar separated from the cap by a deep groove; the posterior edge of the collar forms a prominent overhang and striations begin posterior to it. The cuticle of the cephalic extremity forms a smooth cap in three genera of the Carnoyidae, namely, *Urucuia*, *Waerebekeia* and *Raonema*.

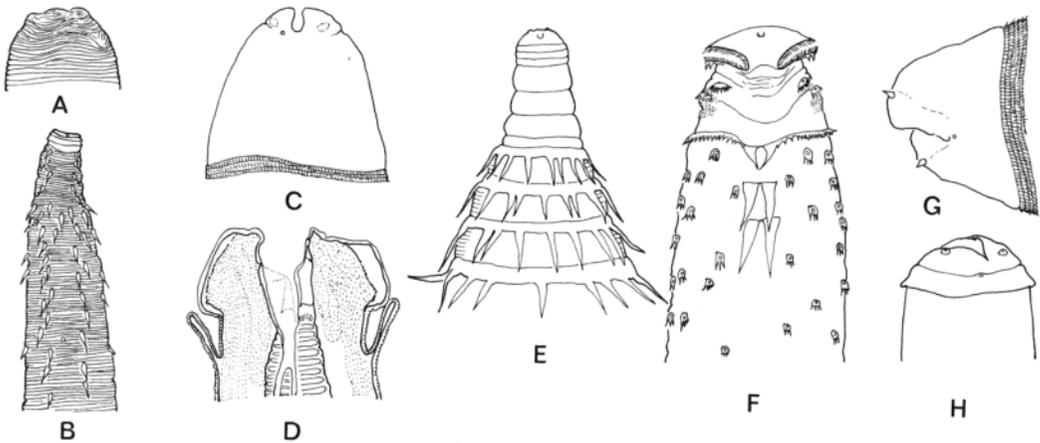


FIG. 6. — Modifications of the external cuticle in the Rhigonematida.

A, male and B, female *Brumptaemilius*; C, male *Waerebekeia*; D, male *Urucuia*; E, female *Carnoya*; F, female *Heth*; G, *Ichthyocephalus* showing cephalic cap.; H, *Rhigonema* with cephalic cap and collar.

— Annulations

Annulations are deep transverse grooves which may be separated by one or more striations. They have arisen in many parasitic nematodes and occur in three genera of the Carnoyidae: *Brumptaemilius*, *Raonema* and *Carnoya*. In the first two genera they occur only in females.

— Spines

In the Rhigonematoidea spines are arranged in transverse rows, each row corresponding to a stria. Spines are generally more pronounced anteriorly and may become scale-like or disappear posteriorly. Such spination may assist in anchoring the worm between folds of the intestine. Spines are secondarily absent in a number of South American species of *Rhigonema* considered by Travassos and Kloss (1959) to comprise the genus *Ruizia*.

A number of different spination patterns occur in the Ransomnematodea. The type of spination is characteristic of a given genus but little can be concluded from the absence of spines and the character is therefore of limited value beyond the species level.

Rows of tiny spines occur on the striae of females of certain *Brumptaemilius* and *Waerebekeia*. In other *Brumptaemilius* large spines are arranged in several longitudinal rows in the oesophageal region ; similar spination occurs in *Raonema* and *Urucuia*. In *Rondonema* spines are restricted to the lateral region and are apparently anterior modifications of the lateral alae. In *Carnoya* spines are arranged in a series of spiny collars in the oesophageal region ; the more anterior collars represent annules but posteriorly annules are absent and spines are smaller and less regularly disposed. Females of *Heth* exhibit a variety of spine-like formations including isolated simple spines, comb-like or button-like compound spines, and spiny collars.

Biological considerations

Very little is known of the biology of rhigonematids. We know that they must be monoxenous since they are restricted to the Diplopoda which feed entirely on decaying vegetation. We report here on some observations previous authors or ourselves have made on the biology of the group. Life history tactics in the two rhigonematid superfamilies are apparently different.

The Rhigonematoidea are generally large worms which produced large numbers of thick-shelled eggs. Some authors (Leidy, 1853 ; Clark, 1978) have observed them attached to the intestinal wall of the host by their jaw apparatus. *Rhigonema infecta* in southern Canada are wedged in large numbers in the sphincter region between mid- and hindgut, with their anterior extremities projecting into the midgut. We have observed *Ichthyocephalus* wedged between folds in the intestinal wall. Parasitic females in this superfamily deposit eggs at about the four-cell stage ; these pass to the external environment, larvate and are then presumably infective.

The Ransomnematodea are commonly less than 3 mm long and live unattached in the lumen of the hindgut. Primitively, females produce small numbers of large thin-shelled eggs which do not develop beyond the four-cell stage in the parasitic female. We have not observed egg deposition in such females ; females of *Heth mauriesi* isolated from the host and placed in aged tap water remain active for up to two weeks, during which time their eggs larvate. We do not know whether such eggs are infective or if larva must hatch and undergo further development in the external environment. Female *Brumptaemilius* are among the largest ransomnematoids ; they produce large numbers of thick-shelled eggs which they deposit readily in tap water. The eggs larvate and hatch spontaneously presumably releasing infective larvae.

Cladistic representation

For each character used we have defined a primitive state (0) and one or more evolved states (1, 2, 3, ... ; -1, -2, -3, ...). Negative numbers are used to indicate a second evolutionary direction represented by an encircled number in the cladogram. In legends to the characters used to construct cladograms we give the character number, followed by a description of its various states with their evolutionary score in parentheses.

The Rhigonematida are placed in the class Rhabditea (*sensu* Inglis, 1983) characterized by the following synapomorphies : buccal capsule consisting of a cheilostome, protostome and telostome, and males with ten paired and one unpaired caudal papillae of which three pairs are lateral in position. The order is characterized by the following : the posterior portion of the buccal capsule consists of a telostome fused with part or all of the protostome, and is surrounded by oesophageal tissue ; the vagina is long and heavily muscled. The Rhigonematida is divided into two superfamilies which have apparently evolved in quite different directions and which may be descendants of distinct parasitic events.

RHIGONEMATOIDEA (*fig. 7*)

The superfamily is characterized by the following : presence, at least primitively, of spines ; cephalic extremity in form of cephalic cap with or without posterior collar ; oesophageal corpus robust ; protostome and telostome fused, completely surrounded by oesophageal tissue ; terminal duct of excretory system vesiculate ; egg with thick, smooth shell.

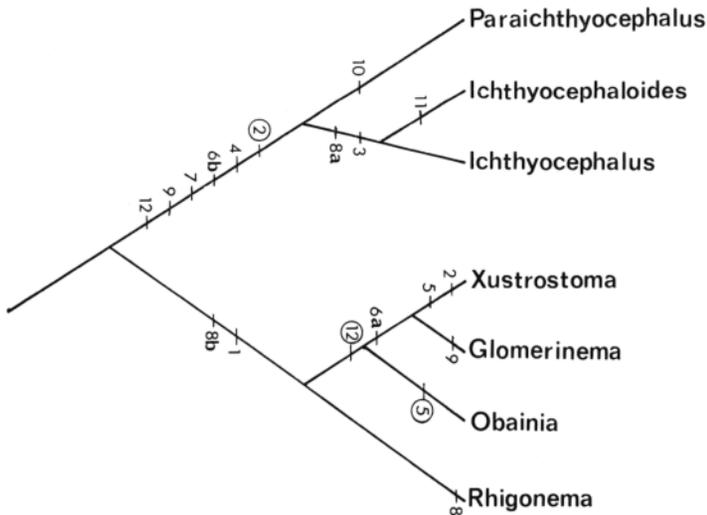


FIG. 7. — Cladogram to genera of the Rhigonematoidea. Synapomorphies are indicated by slash marks and identified by a number (see text for legend). Encircled numbers indicate a second evolutionary series. 6b and 8b are more evolved than 6a and 8a.

1. Cephalic collar absent (0), present (1).
2. Oral opening in form of equal sided triangle (0), dorsoventrally elongate (1), laterally elongate (-1).
3. Spicules similar (0), dissimilar (1).
4. Buccal capsule in form of three articulating pieces (0), in form of one dorsal and one ventral plate (1).
5. Dorsal jaw-piece similar to subventral piece (0), dissimilar and well-developed (1), dissimilar and reduced (-1).
6. Jaw-pieces with tooth-like excrescences (0), with spine rows (1).
7. Submedian outer cephalic papillae mammiliform (0), conical (1).
8. Oesophageal isthmus longer than width of bulb (0), about half as long as bulb width (1), less than half as long as bulb width but forming distinct cylindrical portion (2), represented only by constriction between corpus and bulb (3).
9. Three sublateral to subdorsal papilla pairs present (0), subdorsal and sublateral papillae pairs absent (1).
10. Spicules without (0), with (1) surface sculpturing.
11. Female reproductive system didelphic (0), monodelphic (1).
12. Oesophageal corpus clavate and long (0), ovoid (1), much shorter than bulb (-1).

RANSOMNEMATOIDEA (*fig. 8*)

The superfamily is characterised by the following : reduced number of caudal

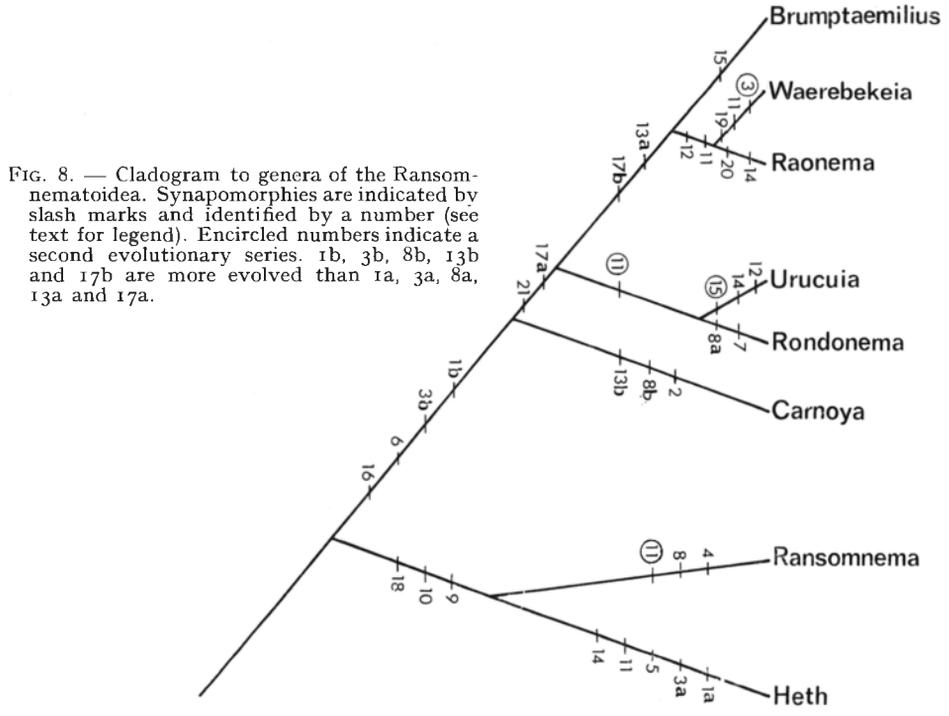


FIG. 8. — Cladogram to genera of the Ransomnematoidae. Synapomorphies are indicated by slash marks and identified by a number (see text for legend). Encircled numbers indicate a second evolutionary series. 1b, 3b, 8b, 13b and 17b are more evolved than 1a, 3a, 8a, 13a and 17a.

papillae ; monodelphy ; presence, primitively of three pennate cuticular metastomal projections ; corpus primitively spindle-shaped and sharply demarcated from isthmus and bulb.

1. Oesophageal corpus spindle-shaped in both sexes (0), spindle shaped in male, cylindrical in female (1), spindle shaped in male, divided in female (2).
2. Protostome urceolate in male (0), long and tubular in male (1).
3. Metastomal projections present in both sexes, of *Ransomnema*-type (0), developed only in male, of *Ransomnema*-type (1), reduced in both sexes (2), developed only in male, *Brumptacmilius*-type (-1).
4. Spicules similar (0), dissimilar (1).
5. Spicules separate (0), fused (1).
6. Spicules convergent (0), parallel (1).
7. Number of caudal papillae : fifteen or more (0), thirteen (1).
8. Subdorsal or sublateral caudal pipalla pairs : two (0), one (1), none (2).
9. Vulva about half way between cephalic extremity and anus (0), vulva markedly posterior (1).
10. Spermatids subspherical (0), elongate (1).
11. Lips of male : one dorsal and two subventral (0), one dorsal and one ventral (1), Lips absent (-1), one ventral and two subdorsal (-2).
12. Cephalic cap absent (0), present (1).
13. Annulations absent (0), present in female (1), present in both sexes (2).
14. Tail of male tapering gently form anus (0), subulate (1), abruptly truncate with caudal appendage (2).
15. *Area rugosa* absent (0), ventral striae reinforced in caudal region of male (-1), present (1).
16. Outer submedian cephalic papillae of female non-salient (0), forming sub-spherical saliences (1).
17. Egg shell thin and flexible (0), thin and inflexible (1), thick and with surface sculpturing (2).
18. Ventral sucker absent (0), present (1).
19. Spicules smooth (0), with surface sculpturing (1).
20. Gubernaculum well-developed, subtriangular in lateral view (0), reduced, dorso-ventrally flattened (1).
21. Vagina directed posteriorly from vulva (0), anteriorly from vulva (1).

Host and geographical distribution

RHIGONEMATOIDEA

Ichthyocephalids occur essentially in South American Rhinocrididae (Spirobolida). However, the monotypic *Ichthyocephaloides* comes from an unidentified New Guinea diplopod (Hunt and Sutherland, 1984) and the family may be more widely distributed in the Pacific region.

The Rhigonematidae are known from all southern continents and North America. *Xustrostoma* and *Glomerinema* occur in the Sphaerotoeroidea (Glomerida) in Madagascar and the only described species of *Obainia* comes from *Pachybolus* sp. in Gabon. Over 35 species of *Rhigonema* have been described from Africa, North and South America, Australia, New Zealand, India, Malaysia and Polynesia. This genus includes the most primitive of the rhigonematoids and they occur in all of the host groups parasitized by the superfamily. African and Indian forms resemble *Obainia* and *Xustrostoma* in disposition of postanal caudal papillae, i.e. they possess three pairs lateral to subdorsal (Adamson, 1983d ; Adamson and van Waerebeke, 1984b). Forms from New Zealand and Sumatran Sphaerotoeroidea (Parona, 1896 ; Clarke, 1978) resemble Madagascan *Glomerinema*, also from the Sphaerotoeroidea (van Waerebeke, 1985a, 1985b) in disposition of caudal papillae as well as in general form of the male tail and spicules. Thus, *Rhigonema* may represent a paraphyletic group of primitive forms of several lineages of the Rhigonematidae.

RANSOMNEMATOIDEA

Ransomnematoids are known from the Polydesmida, Spirobolida and Spirostreptida but none has been reported from the Glomerida. The Hethidae and Ransomnematidae are most common in South American Rhinocricidae although species of *Heth* occur in the Polydesmida and other are known from the Pacific region. The Carnoyidae can be divided into two branches : one African/Indian and the other from South America and the Pacific. Most *Brumptaemilius* spp. have been described from African Spirostreptida although the genus is probably also common in African Spirobolida. The monotypic *Waerebekeia* comes from a spirostreptid from Malawi and *Raonema* occurs in Indian Spirostreptida.

Carnoya is the most widely distributed carnoyid and occurs in South America and the Pacific region ; most species come from the Rhinocricidae. The monotypic *Urucuia* is from a Brazilian spirostreptid. *Rondonema* spp. have been described from several unidentified diplopods and from *Pseudonannolenou tricolor* (Spirobolida), all in South America.

Systematic affiliations of the Rhigonematida with other parasitic Nematoda

As mentioned above, we consider the Rhigonematida to belong to the Rhabditea. Two other parasitic orders of this class have been affiliated with rhigonematids at one time or another, namely the Ascaridida and the Oxyurida. The fundamental distinctness of the Oxyurida and the Rhigonematida has been treated in earlier articles (Adamson, 1981 ; Adamson and van Waerebeke, 1984) and we will not repeat the arguments here. However, Chitwood (1950a) placed some rhigonematids (the Ransomnematodea in our classification) in the Atractidae (Ascaridida) and Inglis (1983) has considered rhigonematids as a suborder of the Ascaridida. Inglis gave no

morphological justifications for his decision and we argue here that the only similarities between rhigonematids and ascarids are plesiomorphic characters : oesophagus consisting of corpus, isthmus and valved bulb ; presence of two spicules ; relatively unreduced number of caudal papillae, etc. Such characters give us no information concerning phylogenetic relationships beyond the fact that both groups evolved from rhabditid like ancestors.

Presumed synapomorphies of the Ransomnematodea and some primitive Ascaridida (especially the Atractidae) are due to convergence. Thus monodelphy of ransomnematooids has little in common with that of attractids. In the latter group there is one ovary ; thin shelled eggs larvate and hatch *in utero* and play a role in a highly evolved endogenous (autoinfective) cycle. In ransomnematooids, ovaries and oviducts are paired. The thin shelled eggs do not develop beyond the four cell stage in the parasitic female. They embryonate in the external environment and are presumably a primitive element in an exogenous cycle. Similarly the ventral sucker of the Ransomnematodea has little in common with that of the Cosmocercoidea.

In summary, the Rhigonematida, Ascaridida and Oxyurida are considered distinct orders of the class Rhabditea. We cannot say whether rhigonematids are more closely related to oxyurids or to ascarids but Inglis (1983) separates the Oxyurida (subclass Rhabditia) from the rhigonematids and ascarids which he places in the subclass Diplogasteria.

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