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# PHYLOGENETIC RELATIONSHIPS OF THE SOIL NEMATODE ORDERS DORYLAIMIDA, MONONCHIDA, TRIPLONCHIDA AND ALAIMIDA, WITH A REVISED CLASSIFICATION OF THE SUBCLASS ENOPLIA

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## Abstract

A study of the morphology and systematics of all the nominal genera of the orders Dorylaimida, Mononchida, Triplonchida (= Diphtherophorina) and Alaimida and of other enoplian genera outside these orders suggested that several evolutionary lines could be established in the subclass Enoplia, class Adenophorea. The most important line is that of the animal parasitic Adenophorea, *viz.* Trichinellida (= Trichocephalida) and Mermithida, which are unique within the entire Phylum in having stichosomes composed of a series of unicellular glands or stichocytes associated with the oesophagus; new subclass, Stichosomia is proposed for them. Adenophorea now contains three sub-classes: Enoplia (= Penetrantia), Chromadoria (= Torquentia) and Stichosomia.

On the basis of this study nine orders are recognized under Enoplia *viz.*, Enoplida (with Enoplina, Campydorina and Ironina n. subord.), Oncholaimida n.ord., Trefusiida (with Trefusiina n.subord. and Lauratonematina n.subord) Tripylida n.ord., Triplonchida, Mononchida, Alaimida n.ord., Bathyodontida n.ord. and Dorylaimida. New orders and suborders proposed have been diagnosed and their relationships discussed. A key to the orders of the subclass Enoplia is given.

Since Clark's (1961) and De Coninck's (1965) classifications of the subclass Enoplia, class Adenophorea, three major revised systems have appeared, *viz.*, those by Andrássy (1976), Lorenzen (1981) and Maggenti (1982). These systems are based on the morphology of nematodes and are supposed to reflect (if not show) phylogeny. Each revision has Enoplida and Dorylaimida as large heterogeneous orders based on the characters of the location of the openings of the oesophageal glands. In Enoplida, one or more glands open anterior to the nerve ring, while in Dorylaimida all the glands empty behind the nerve ring. This original concept of Chitwood (1937) has been rigidly followed and not enough consideration given to the massive convergence and parallel evolution that operates on the free-living nematodes. Undoubtedly, each of the two orders encompasses more than one major evolutionary lines worthy of separate ordinal ranks.

Other characters have been and need to be further examined to determine phylogenetic relationships. Lorenzen's (1981) finding of metanemes (stretch sense organs lying longitudinally between cuticle and hypodermis in the oesophageal and caudal regions) led to the proposal of a new order, Trefusiida, for the Enoplida that lacked metanemes, but which had one or more oesophageal glands opening anterior to the nerve ring. The validity of such an action is dubious since these two characters are not fully known for several groups of both the Enoplida and Trefusiida. Moreover, the metanemes can easily escape detection especially in small-sized nematodes and even their total absence should not be the primary basis for erection of an order. Nevertheless, the finding of metanemes has greatly helped in understanding the phylogenetic relationships of several groups and some sorting out by Lorenzen has been useful.

Lorenzen's other useful 'new' characters are the location of the excretory cell in or behind the oesophageal region, caudal glands in tail or pre-caudal region and the position of the female reproductive organs in relation to the intestine. Similarly, the location of the oesophageal gland orifices and nuclei (Coomans & Loof, 1970) and the comparative structure of the female gonads (Geraert *et al.*, 1980) and of the spicular muscles (Siddiqi, 1974) have also been very helpful. A study of these and other characters both in the literature and as studied by the present author necessitated a re-appraisal and reclassification of the subclass which is presented here.

## Historical Review

Filipjev (1934), Chitwood (1937), Thorne (1939), Chitwood in Chitood & Chitwood (1950), Clark (1961), Goodey (1965), De Coninck (1965), Andrássy (1976) and Lorenzen (1981) have made substantial original contributions to the classification of the subclass Enoplia. Under the order Enoplida, Clark (1961) recognized five suborders–Enoplina, Dorylaimina, Alaimina, Trichosyringina and Dioctophymatina, based largely on the characters of the oesophageal glands and their outlets.

Coomans & Loof (1970) increased considerably the concept of the order Dorylaimida by proposing new suborders, Diphtherophorina and Bathyodontina, placing them along with Dorylaimina, Mononchina (proposed as a suborder by Kirjanova & Krall, 1969 and as an order by Jairajpuri, 1969) and Trichosyringina under it. Andrassy (1976) also considered Mononchina and Diphtherophorina under Dorylaimida, assigning Mermithina to this order and excluding Alaimina and Trichosyringina from it. Andrássy recognized alaims as constituting only a family, Alaimidae, under the Oxystominoidea of the suborder Tripylina, order Enoplida, while Hooper (1973) suggested that alaims should be placed under a separate order.

Filipjev (1934) proposed the subfamily Mononchinae under the family Trilobidae and Chitwood & Chitwood (1937) raised it to family placing it under the superfamily Tripyloidea of the suborder Enoplina. Tripyloidea, *sensu* Chitwood (1937) contained the families Tripylidae, Mononchidae and Alaimidae and thus an assemblage of unrelated groups and of independent evolutionary lines. Thorne (1939) removed Alaimidae from the Tripyloidea to the Dorylaimina raising it to superfamily. Clark (1961) remarked that the Mononchidae have very little in common with the Tripyloidea, but share several features with the Dorylaimoidea, eg.. absence of cephalic setae, similar arrangement of the oesophageal glands and their ducts and the large number of preanal supplements. He proposed the family Bathyodontidae under the Mononchoidea and raised Diphtherophoridae to super family.

Jairajpuri & Khan (1982), Poinar (1982) and Maggenti (1982) assigned Bathyodontina to the order Mononchida, whereas Coomans & van der Heiden (1979) regarded Bathyodontina as a suborder of the Dorylaimida, and Andrássy (1976) considered bathyodonts as a superfamily of the suborder Mononchina, order Dorylaimida. Siddiqi (1980) removed Diphtherophorina from the Dorylaimida to Enoplida, and later he (1983) suppressed it in favour of Triplonchida (Triplonchia of Cobb, 1920). Lorenzen (1981) recognized under Enoplia three orders – Enoplida, Dorylaimida and Trefusiida Lorenzen, 1981. To Trefusiida, Lorenzen assigned the families Trefusiidae, Onchulidae, Xenellidae and Lauratonematidae. He did not recognize Alaimina and Diphtherophorina as suborders but assigned their families to the Dorylaimida.

A new suborder, Nygolaimina, was proposed by Ahmad & Jairajpuri (1979) for the superfamily Nygolaimoidea, but Coomans & van der Heiden (1978) showed that phylogenetically nygolaims were acceptable only as a superfamily of the suborder Dorylaimina. Maggenti (1982) recognizes seven orders and eleven suborders under Enoplia, *viz.,* Enoplida (Enoplina, Oncholaimina. Tripylina), Dorylaimida (Dorylaimina, Alaimina, Diphtherophorina, Nygolaimina), Isolaimida, Mermithida (Mermithina), Mononchida (Mononchina, Bathyodontina), Muspiceida and Trichocephalida.

## Discussion

The two orders, Dorylaimida and Enoplida, are restudied here in order to establish and elucidate major evolutionary trends shown by their members. As a test case, the discussion here is centred on the phylogenetic relationships of the suborders Dorylaimina, Mononchina, Diphtherophorina and Alaimina which have been considered by several workers to belong to one order, the Dorylaimida. As will be seen from below, it appears that each of these suborders represents a different evolutionary line and merits the rank of an order. This conclusion is based entirely on the study of the morphological characters although some ecological and ethological characters have also been considered. The use of one character, *viz.*, the location of the orifices of all the oesophageal glands behind the nerve ring, to characterize the order Dorylaimida (Coomans & Loof, 1970; Lorenzen, 1981, etc.), has resulted in making it a 'dumping ground' for such distantly related taxa as Mononchida, Triplonchida (= Diphtherophorina) and Alaimida. The study presented here necessitates a reclassification of the subclass Enoplia (see Table 1).

The most obvious reasons in favour of considering these groups as separate orders are as follows: (i) The stomatal armature in the Mononchida is primarily a dorsal immovable tooth formed as a part of the metarhabdions (subventral teeth on metarhabdions, if present, are in pairs, similar, and never larger than the dorsal tooth), in the Triplonchida, it is a protrusible onchiostyle whose tip is solid and derived from a dorsal tooth formed *in situ;* in the Dorylaimida it is a protrusible odontostyle (axial or mural on left subventral sector) that develops in special cell(s) in the oesophageal tissue; while in the Alaimida the stomatal armature is absent. (ii) Only in the Mononchida is the stomatal cavity large and has heavily sclerotized rhabdions and five geusids (gustatory chemoreceptors, H see Fig.2,~~F~~) and is not surrounded by the oesophageal tissue except at the base. (iii) The fovea of the amphids are gaping, pocket-like and immediately followed by the sensillar pouch in the Mononchida and Triplonchida (Fig.5,A) while in the Dorylaimida and Alaimida there is a distinct ductus connecting the fovea and sensillar pouch. (iv) The cephalic sensilla of Mononchida comprises 14 (6+4+4) papillae or pits in one circlet (Fig.2J & 5D) as compared to 10 in the Triplonchida and Dorylaimida; only in Alaimida being separated into two circlets. (v) There is a distinct cuticularized excretory duct only in the Triplonchida and a medio-ventral excretory duct bifurcating posteriorly to have an inverted Y-shaped excretory system in Mononchida (Fig. 2,I) and Dorylaimida. (vi) The usual presence of three caudal glands and a spinneret only in the Mononchida. (vii) A spermatheca is formed in females of Triplonchida and Alaimida and not in those of the Dorylaimida and Mononchida. (viii) A pair of adanal (or just preanal) ventro-sublateral supplementary papillae in male and a prerectum are present only in the Dorylaimida. (ix) A single anteriorly outstretched testis in the Triplonchida and Alaimida as compared to two testes, one anteriorly outstretched, the other reflexed, in the Dorylaimida and Mononchida. (x) Different types of spicular protractor muscles being attached to the subventral body-wall in the Mononchida, while in the Dorylaimida they are attached mostly to the subdorsal body-wall and in the Triplochida form a capsule around spicules and are not attached to the body-wall (being called suspensor muscles, see Siddiqi, 1974) (Fig.6). These groups, therefore, are not so related to each other as to be grouped under the single order Dorylaimida (see other differentiating characters in the diagnoses of ordinal ranks).

Maggenti (1982) accepts Nygolaimina as a suborder "so that their characters do not cause ambiguities to arise in other taxa in the Dorylaimida", since previously the nygolaims "have been treated as genera in the Dorylaimoidea, as a family in the Leptonchoidea, and as superfamily in the Dorylaimina". This expediency in classification was achieved by regarding the stomatal armature as the primary distinguishing character of the suborder—a mural tooth in the Nygolaimina vs. an axial odontostyle in the Dorylaimina. The mural tooth of *Campydora* was claimed to be homologous with that of the Nygolaimina. This is not true as *Campydora* is not a dorylaim. The tooth of *Campydora* is placed in the dorsal sector of the stoma and is not a longitudinally movable structure. The oesophagus of *Campydora* is also not dorylaimoid and the amphidial fovea is not separated from the sensillar pouch by a ductus as in the Dorylaimida (including nygolaims). The genus is best accommodated under the suborder Campydorina which is here assigned to the order Enoplida.

It should be noted here that there are other dorylaims besides nygolaims which have a mural tooth homologous with the mural tooth of the nygolaims. Examples are found in the Sectonematinae (Siddiqi, 1969) (Dorylaimina) which have a mural tooth located in the left subventral sector of the oesophastoma, as in members of the Nygolaimoidea. The Sectonematinae have close relatives in the Aporcelaiminae which have an axial odontostyle. In nygolaims, sectonematids and aporcelaims the odontophore (=oesophastoma) is an axial tubular feeding organ and is provided with protractor muscles of oesophageal origion.. The tooth (whether mural or axial) develops in the left subventral sector of the oesophagus. The positions of the anterior subventral oesophageal gland nuclei and orifices at about the same level, and the occurrence of three cardiac glands in Nygolaimoidea are also sometimes seen in the members of the Dorylaimoidea and these characters cannot be regarded as diagnostic at the subordinal rank. As suggested by Coomans & van der Heiden (1978), nygolaims merit only superfamily rank under the Dorylaimina.

Maggenti (1981) speculates that the Nygolaimina split off from the Dorylaimida-stock earlier, in the Devonian period, than the Diphtherophorina which arose from the same stock in the late Triassic, (this means that the Diphtherophorina is closer to the Dorylaimina than the Nygolaimina). Obviously this speculation is false, firstly because Nygolaimina/ Dorylaimina separation cannot be so ancient if the former represents only a superfamily of the latter, as just discussed, and secondly, because the Diphtherophorina represents a different evolutionary line than the Dorylaimida (Siddiqi, 1980, 1983 a) and cannot be derived from it.

Bathyodontina and Dorylaimida appear to have a common ancestor because both the groups have a stomatal armature that develops in the left subventral sector of the oesophagus, the stoma is elongated and mostly surrounded by the oesophagus thus representing an oesophastoma and the stomatal muscles attach posteriorly to the eosophagus (and not to the body-wall) suggesting an oesophageal origin. Both have similar oesophageal glands (one dorsal, two pairs of subventrals) opening behind the nerve ring and similar cephalic sensilla. But there are fundamental differences between the two groups. The presence in Dorylaimida of a protrusible odontostyle, a ductus between the amphidial fovea and sensillar pouch, a prerectum, a pair of adanal or just preanal male supplementary papillae clearly differentiates it from the Bathyodontina. I agree with Lorenzen's (1983) statement that "The buccal armature of the Mononchina and Bathyodontina cannot be derived from an onchiostyle like that of the Dorylamimida".

Coomans & Loof (1970) considered Bathyodontina to occupy an intermediate position between Mononchida and Dorylaimida but Jairajpuri & Khan (1982) and Maggenti (1982) treated Bathyodontina as a suborder of the Mononchida and Andrássy (1976) regarded Bathyodontoidea as a superfamily of the suborder Mononchina. On the basis of the above discussion, it is most desirable to consider the Bathyodontina as an order separate from the Mononchida and Dorylaimida. (Mononchida stands apart from them in having a basically dorsal stomatal armature, the stomatal muscles of somatic origin and attached to the body-wall, a different arrangement of oesophageal glands and cephalic sensilla). The new order Bathyodontida is closer to the Dorylaimida than the Mononchida, originating from an ancestor whose stoma was surrounded by the oesophagus and the stomatal armature was dominantly subventral in origin and location. The modern Oncholaimina have representatives in which a left subventral hollow tooth is a dominant stomatal armature (see Fig. 2, A–C) and thus on the basis of the homology of the stomatal armature, the soil inhabiting dorylaims and bathyodonts may appear to share a common ancestor with the oncholaims.

Coomans & Loof (1970) assigned the genus *Cryptonchus* Cobb, 1913 to the family Bathyodontidae Clark, 1961. However, as pointed out by Lorenzen (1981), Cryptonchinae Chitwood, 1937 has priority over Bathyodontidae Clark, 1961 and hence Bathyodontidae and Bathyodontoidea Clark, 1961 (Jairajpuri, 1969) are here synonymized with Cryptonchidae Chitwood, 1937 (Gerlach, 1966) and Cryptonchoidea Chitwood, 1937 (n. rank), respectively. Bathyodontida n.ord. (type-genus *Bathyodontus* Fielding, 1950) contains two superfamilies, *viz.*, Cryptonchoidea Chitwood, 1937 (n.rank) and Mononchuloidea De Coninck, 1965 (Coomans & Loof, 1970).

The order Isolaimida is monotypic for the genus *Isolaimium* Cobb, 1920. Its systematic position is uncertain; Andrássy (1976) and Lorenzen (1981) assigned the family Isolaimidae to Mermithina and Bathyodontina (Dorylaimida), respectively.

## Reclassification of the subclass Enoplia

The subclass Enoplia (= Penetrantia) contains mostly free-living nematodes, but animal parasitic nematodes of the orders Trichinellida Ward, 1907 (=Trichocephalida) and Mermithida have also been assigned to it (Chitwood, 1950; Clark, 1961; Théodoridès, 1965; Maggenti, 1982). Clark (1961) assigned Trichosyringina Ward, 1917 (with Mermithoidea, Trichuroidea and Dioctophymatina) to Enoplida and Coomans & Loof (1970) classified it under Dorylaimida. Maggenti (1982) considered Trichocephalida (with Trichuroidea, Trichinelloidea and Cystoopsoidea) and Mermithida (with Mermithoidea and Tetradonematoidea) under Enoplida. Poinar (1982) recognized two suborders, Mermithina and Echinomermellina under Mermithida which he also considered under Enoplia. M.B. Chitwood (1969) assigned the order Trichinellida to Adenophorea and stated "these nematodes usually have direct life cycles, but differ radically in structure and development from all other known nematodes". Recently, Lorenzen (1983) suggested the removal of Trichosyringida (Trichuroidea and Mermithoidea) and Dioctophymatoidea from the Adenophorea to the Secernentea because "phasmid-like organs" found by Kaiser (1977) in three species of Mermithidae are, accordingto Lorenzen, homologous to the phasmids of the Secernentea and the stylet found in the juveniles of these nematodes is not homologous to the odontostyle of the dorylaims because Richter (1971) showed that the stylet of *Hydromermis contorta* (Mermithina) is a formation of the ventral wall of the buccal cavity.

Maggenti (1982) predicted the creation of a new subclass for the "animal-parasitic Enoplia" on the basis of the presence of stichosomes comprising serially arranged unicellular oesophageal glandular cells or stichocytes. However, in 1983, he proposed a new order name, Stichosomida, for these nematodes. As this name is based on a characteristic feature and not on a type-genus, and previously proposed order names are available for its members, Stichosomida is not acceptable. These nematodes are unique in having stichosomes and due to their peculiar organisation, biology and development stand apart from the two subclasses of the class Adenophorea, and from the class Secernentea. Therefore a new subclass, Stichosomia is porposed here for the two orders Trichinellida (=Trichocephalida Skrjabrin & Schulz, 1928) (animal-parasitic) and Mermithida (insect-parasitic). The Class Adenophorea henceforth should comprise three subclasses – Enoplia (=Penetrantia), Chromadoria (=Torquentia) and Stichosomia.

Maggenti (1983) speculated that Enoplia developed primarily along two lines, one marine, the other terrestrial, and proposed superorders Marenoplica and Terraenoplica (also spelt Terrenoplica), respectively, for them. The latter line included Mononchida, Dorylaimida and Stichosomida. The present analysis of Enoplia rejects this concept and points out that nematodes representing different evolutionary lines independently invaded the niche "land" and successfully occupied it. The marine orders Enoplida and Oncholaimida have Ironidae and Oncholaimidae on the land, Tripylida occupy both land and sea as indicated by Onchuloidea, and Alaimida have one suborder (Alaimina) on the land and another (Oxystominina) in the sea. Maggenti's (l.c.) contention that Marenoplica generally have 10 cephalic sensilla posterior to the lip region, oesophageal glands opening anterior to the nerve ring, commonly a single excretory cell is persent, and prominant male preanal supplements occur in a single row, is likewise rejected as the land Enoplia (Ironidae, Oncholaimidae, Tripylidae, Onchulidae and Alaimina) more or less show thess features.

Lorenzen (1981) restricted the order Enoplida to those members which have metanemes. Metanemes are stretch sense receptors in the form of a neuron having a long anterior axon or "frontal filament" and a posterior "caudal filament". They are found between the cuticle and hypodermis in the oesophageal and caudal regions and are placed longitudinally or obliquely on the body. Straight and curved metanemes are called orthometaneme and loxometaneme, respectively.

The discovery of metanemes should help solve systematic problems in Enoplia. For example, (i) members of Ironidae have and Cryptonchidae lack metanemes and these families should not be placed together (as was done by several workers – Goodey, 1963; Andrássy, 1976; Maggenti, 1982; but Coomans & Loof (1970) have shown that *Cryptonchus*, and not *Ironus*, is close to *Bathyodontus* in having similar oesophageal glands which open posterior to the nerve ring); (ii) Tripylidae have and Prismatolaimidae lack metanemes and so they should not be placed together under one superfamily, the Tripyloidea (as was done by Andrássy, 1976; Maggenti, 1982); (iii) Oxystominidae have and Alaimidae lack metanemes and members of these two families should not be grouped together (as was done by Gerlach, 1966, Andrássy, 1976, etc.). However, the absence of metanemes should not be the sole character in recognizing the order Trefusiida, because the absence of these sense organs may have been the ancestral character (or the derived character) of different evolutionary lines. For example, the absence of metanemes in the Onchulidae led Lorenzen (1981) to classify it under the Trefusiida although it is a relative of the Tripylidae which have metanemes (see under diagnosis of Tripylida n.ord.). Lorenzen (1981) recognized that Trefusiida is paraphyletic (or polyphyletic) and not halophyletic (or monophyletic).

Other sense organs should also be given due phylogenetic importance. The subclasses Torquentia and Penetrantia were proposed by Andrássy (1974) primarily on the basis of the structure of the amphid (fovea). In Torquentia, the amphids are spiral or twisted and lie close to the cuticle, whereas in Penetrantia the amphids are pouch-like and 'penetrate' into the body-wall. Lorenzen (1981) did not attach as much phylogenetic importance to amphids as he did to the metanemes since he shifted Prismatolaiminae, Odontolaiminae and *Tobrilia*, which have pouch-like amphids, from Enoplia to Chromadoria (= Torquentia) and brought back some with twisted amphids into the Enoplida. Ocelli and pseudocelli (photo receptors) may also be of phylogenetic significance because they occur in some (Enoplina and Oncholaimina) and not in others.

Lorenzen (1978) concluded that the gonadal characters (structure and arrangement with respect to intestine) indicate that the Adenophorea contains polyphyletic taxa from generic to ordinal rank. All genera in this class have antidromously reflexed ovaries (proximal end pointing away from the vulva), and the presence of two ovaries and two testes is considered to be a plesiomorphic (ancestral) character. Examination of a large number of species allowed Lorenzen (1978) to show that Prismatolaiminae in most cases have both ovaries either on the left or on the right side of the intestine (or gonoduct); Lauratonematidae have the ovary on the left of the intestine, Enoplidae, Phanodermatidae, Anticomidae and Anoplostomatidae (all within the order Enoplida as redefined here) have both ovaries on the left, while *Parironus* and *Trissonchulus* (suborder Ironina as proposed here), and Oncholaimidae and Enchelidiidae (order Oncholaimida as proposed here) have ovaries on the right of the intestine. However, this gonadal character is variable in some other groups.

The protractor muscles of the spicules forming a capsule and appearing not to be attached to the body-wall is the most important characteristic of the Triplonchida and Tripylida. Siddiqi (1974) called these protrators 'suspensor muscles' in which the spicules remain suspended. The two suspensor muscles surround the spicular capsule which is filled with a hydrostatic tissue surrounding the spicules (Fig 6 ) and a contraction of the suspensor muscle would force the spicules out by a squeezing effect. Siddiqi (1974, 1983a) and Riemann (1972) have discussed the phylogenetic importance of these muscles.

## DIAGNOSES OF ORDINAL RANKS

### Enoplida Filipjev, 1929 ( = Enoplata Filipjev, 1929; Enoplida Chitwood, 1933)

(Fig. 1)

*Diagnosis* (amended): Enoplia. Cuticle smooth. Metanemes present. Ocelli and pseudocelli usually present. Cephalic cuticle reduplicate, may form two capsules – an anterior cephalic capsule formed by the thickening of the inner layers of the body cuticle and stomodaeal capsule formed by the outer sheath covering of the oesophagus (see Inglis, 1962, 1964). Amphids pocket-like at base of cephalic region, a distinct ductus between fovea and sensillar pouch lacking. Stoma mostly surrounded by oesophageal tissue and thus mostly comprises oesophastoma and is usually armed with movable solid mandibles (or jaws) (Fig.1, A&B) and onchia (Fig.1, D & E); orifices of dorsal and two subventral glands open in stoma behind the stomatal armature (and not through it); orifices of subventral glands usually anterior to that of dorsal gland. Oesophagus usually cylindrical, with straight walls. Renette cell single, located in oesophageal

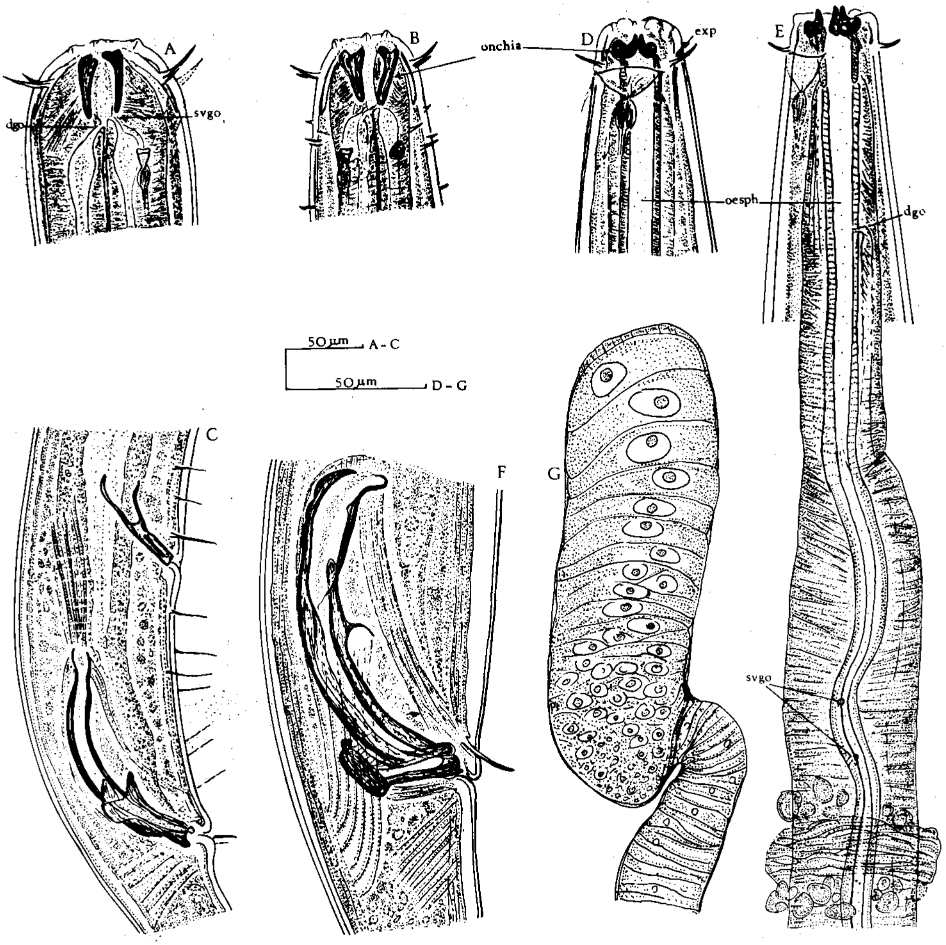

Fig. 1. Order Enoplida. A–C. Enoplina. D–G. Ironina. A. Head end of *Enoplus behringicus* female from a fiord in Greenland. B & C. *Enoplus quadridentatus* male from Isles of Scilly. B. Head end. C. Spicule region. D–G. *Ironus* sp. from a lake in Tasmania. D & E. Head ends. F. Spicule region. G. Anterior ovary and oviduct. (dgo = dorsal gland orifice; exp = excretory pore; oesph = oesophastoma; svgo = subventral gland orifice.)

(Enoplina) or post-oesophageal (Ironina) region, opening usually near head. Three caudal glands and a spinneret usually present, former generally not extending into precaudal region. Ovaries usually paired, antidromously reflexed, lying usually on left (Enoplina) or right (Ironina) of intestine; oviduct attached near germinal region. Testes also paired. Ejaculatory duct strongly muscular. Spicules well developed, protractor muscles not capsuliform, attaching to body-wall mostly subventrally (Enoplina) or subdorsally (Ironina). Male preanal ventromedian supplement few, usually one, or absent, tuboid (Enoplina) or setose (Ironina). Gubernaculum large, with large lateral pieces on the corpus.

Type-genus: *Enoplus* Dujardin, 1845.
Suborders: Enoplina Chitwood & Chitwood, 1937
Campydorina Jairajpuri, 1983.
Ironina n. subord.

## Suborder Ironina n.subord.
(Fig.1,D–G)

*Diagnosis:* Enoplida. Metanemes present. Ocelli or pseudocelli usually absent. Cephalic region usually offset and with three lips; cephalic capsule reduced or absent. Labial sensilla papilliform. Cephalic sensilla in two circlets of 6 inner and 4 outer papillae or setae. Amphids pocket-like, dorsoventrally flattened, aperture slit-like, at base of cephalic region; fovea and sensillar pouch close together, not separated by a ductus. Stoma anteriorly capsuliform, posteriorly elongated into a prominent oesophastoma surrounded by oesophageal tissue and having cuticularized lumen walls forming an odontophore. Stomatal armature evertible, comprises claw-like, solid onchia, which in juveniles develop much behind the active ones in the oesophastoma, one or two in dorsal sectors of anterior capsuliform stoma; subventral onchia usually larger than dorsal onchia. Oesophastomatal odontophore provided with intra-oesophageal protractor muscles and retractor muscles outside oesophagus. Oesophagus cylindrical, very muscular; dorsal and a pair of subventral glands located in posterior region of oesophagus, but open in oesophastomatal region at some distance behind the onchia, orifices of subventral glands anterior or posterior to that of the dorsal gland. Excretory duct opens between two circlets of cephalic sensilla (Fig.1,E) or behind cephalic region; renette single, post-oesophageal, or may rarely be in oesophageal region. Cardiac glands absent. Ovaries paired, rarely single (prodelphic), usually lying on right of intestine; oviduct joining ovary in latter's distal region (Fig.1,G). Testes paired. Caudal glands generally present. Male preanal, ventromedian supplement setiform, usually single (Fig.1,F). Spicules well developed, with median stiffening piece and ventral flanges, or tubiform; protractors of spicules attached to body-wall mostly subdorsally; gubernaculum present, with thickened margins of the corpus (Fig.1,F). Marine, freshwater or soil-inhabiting, mostly predators and carnivores.

Type-genus: *Ironus* Bastian, 1865 (syn. *Cephalonema* Cobb, 1893; *Nanonema* Cobb in Stiles & Hassal, 1905).

Superfamily: Ironoidea de Man, 1876, (with families Ironidae de Man, 1876, and Thalassironidae Andrássy, 1976 (n. rank)).

*Relationship:* Ironina n.subord. differs from Enoplina in having cephalic sensilla in 2 circlets, an elongated oesophastomatal odontophore, evertible solid onchia which in juveniles develop at some distance behind the functional ones, oesophageal glands opening at some distance behind stomatal onchia, excretory gland usually lying behind the oesophagus and ventromedian supplement of male setiform and not tuboid.

Lorenzen (1981) recognized the superfamily Ironoidea with three families; Ironidae, Leptosomatidae Filipjev, 1916 and Oxystominidae. Ironidae is here placed under the Ironina n.subord. and Oxystominidae is moved to the Alaimida n.ord.

Maggenti (1971) considers Ironidae and Bathyodontidae as showing the characters of early Dorylaimida since in Ironidae, the teeth migrate from within the oesophageal tissue to final placement in the stoma in much the same way as they do in the Dorylaimida. This migration is necessitated due to elongation of the oesophastoma which forms the odontophore. Coomans & van der Heiden (1979) argue that the elongation of the anterior feeding apparatus in Dorylaimida was not present in their ancestral forms and has originated within the group, and the condition in which the replacement tooth is stored at some distance behind the functional one has been achieved independently in Ironidae and Dorylaimida, since the most primitive Dorylaimida have the replacement tooth inside or immediately behind the functional one. There is also a difference in the origin of the protractor muscles of the feeding apparatus of the two groups. In Ironidae the protractors are intra-oesophageal (van der Heiden, 1975) but in Dorylaimida they may be somatic in origin or derived from the oesophageal sheath tissues. Other characteristics of Ironidae given under the diagnosis of the suborder Ironina do not support the view that

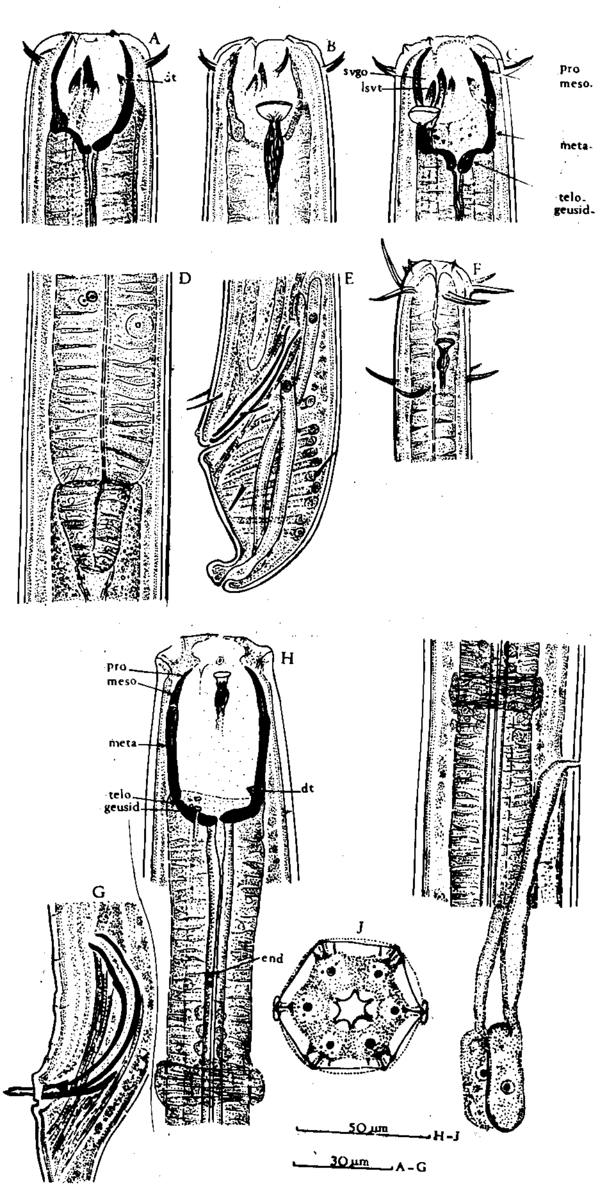

Fig. 2. A–E. Order Oncholaimida. A–C. Head ends of *Oncholaimus brevicercus* from Northern Ireland. D & E. Basal portion of oesophagus and tail end, respectively, of *O. brevicercus* male. F & G. Order Trefusiida, *Trefusia zostericola* from Scotland. F. Head end of male. G. Spicule region. H – J. Order Mononchida. H. Anterior region of *Iotonchus* sp. female from Fiji. I. Excretory system of *Prionchulus* sp. female from Scotland. J. *En face* view of *Clarkus* sp. female from England. (dt = dorsal tooth; meso = mesorhabdion; meta = metarhabdion; pro= prorhabdion; svgo = subventral gland orifice; telo = telorhabdion.)

Ironidae share ancestral characters with the Dorylaimida.

## Order Oncholaimida n.ord.

(Fig. 2, A–E)

*Diagnosis:* Enoplia. Cuticle thin, smooth or finely annulated. Metanemes and somatic setae present; ocelli and pseudocelli present. Cephalic cuticle thick but not reduplicate to form a helmet or cap; cephalic and stomodaeal capsules not formed. Labial sensilla papilliform, cephalic sensilla usually setiform, in one circlet of 6 + 4 setae. Amphids pocket-like or cyathiform, aperture transversely oval, just post-cephalic, ductus between fovea and sensillar pouch short or absent. Stoma mostly cheilostomatal, capsuliform, with sclerotized walls, at base and up to dorsal and subventral teeth surrounded by oesophageal tissues (teeth are therefore oesophastomatal in origin); anteriorly oesophagus not attached to the body-wall. One dorsal and two subventral teeth not individually movable; left subventral tooth is often the largest (Oncholaimoidea), hollow and with orifice of left subventral oesophageal gland subterminally (Fig.2,A & C) or dorsal tooth may be the largest. Orifice of dorsal oesophageal gland posterior to those of subventral glands; teeth may be absent as in Pelagonematoidea, and stoma may be reduced in males of some groups; a series of denticles may be present (eg. Eurystominidae). Oesophagus muscular, cylindrical, posteriorly enlarged or multibulbar. Cardia without glands (Fig.2,D). Excretory pore near or behind stoma; renette cell single, usually posterior to oesophagus on right of intestine. Caudal glands usually extending well into precaudal region. Didelphic or monodelphic, with antidromously reflexed ovaries lying mostly on right of intestine. A demanian system representing modified receptaculum seminis and having external pores near the tail may be present; during copulation sperm are known to be transferred to the uterus through one of these pores and not through the vulva. Testes paired. Ejaculatory duct poorly muscular. Spicules simple, straight to arcuate, with protractors mostly attached to the subventral body-wall. Gubernaculum poorly developed or often absent. Bursa present in some genera. Marine, very rarely occurring in fresh water.

Type-genus: *Oncholaimus* Dujardin, 1845
Suborder: Oncholaimina De Coninck, 1965.
Superfamilies: Oncholaimoidea Filipjev, 1916
Enchelidioidea Filipjev, 1918
Pelagonematoidea De Coninck, 1965.

*Relationship and discussion:* Oncholaimida n.ord. differs from the Enoplida in having the cephalic cuticle not reduplicated to form a helmet or cap, oesophagus not attached to the body-wall at or near the cephalic region, stoma mostly cheilostomatal, with teeth which are not individually movable, but may be hollow and bear orifices of the oesophageal glands, renette cell usually post-oesophageal, ovaries lying mostly on right side of intestine, a demanian system in females may be present and male preanal, ventromedian supplement never tuboid or setiform and gubernaculum never well developed.

Oncholaimida is related to Mononchida through Pelagonematoidea, but differs in having metanemes, setae, dorsal and subventral glands opening anterior to the nerve ring, a single post-oesophageal renette cell (Mononchida have two renette cells forming an inverted Y-shaped system behind the nerve ring, Fig.2,I), and gubernaculum being poorly developed or absent.

The large, hollow, left subventral tooth of the Oncholaimida points towards the evolution of the Dorylaimida whose stomatal armature is basically a hollow left subventral tooth. However, in the Dorylaimida the oesophageal glands open behind the nerve ring, never anterior to it or through the teeth.

Some members of the Oncholaimida have recently been transferred to the Mononchina. The genus *Thalassogenus* Andrássy, 1973 of the Pelagonematidae De Coninck, 1965 (Andrássy, 1976) was tranferred to the Mononchidae by Lorenzen (1981) who also proposed the synonymy of Dioncholaiminae De Coninck, 1965 (Oncholaimida) with the Mononchidae. This shows that Oncholaimida and Mononchida are related to each other. However, unlike Mononchida, *Thalassogenus* has telorhabdial dorsal and a pair of subventral teeth and merits a new subfamily, Thalassogeninae, under Pelagonematidae. Thalassogeninae differ from Pelagonematinae in having stomatal teeth.

The dorsal and subventral teeth of *Oncholaimus* and *Metaparoncholaimus* De Coninck & Sch. Stekh., 1933 and the dorsal tooth of *Dioncholaimus* Kreis, 1933 (? syn. of *Mononchus*) and *Mononcholaimus* Kreis, 1924 are metarhabdial (see figures in De Coninck, 1965). The mesorhabdial denticles are found in Eurystomininae (Oncholaimida) and Mylonchulinae (Mononchida). The toothless condition of the stoma is similar between *Pelagonema* and *Pelagonemella* (Oncholaimida) and a new genus of the toothless mononchs I found in samples from rain forest of Colombia. The most important distinguishing character between the two orders appears to be the location of the orifices of all the oesophageal glands behind the nerve ring in the Mononchida and not so in the Oncholaimida.

## Order Tripylida n.ord.
(Fig.3)

*Diagnosis:* Enoplia. Cuticle annulated or smooth, usually loosely fitting on body and swelling upon fixation. Metanemes present (Tripyloidea) or absent (Onchuloidea). Cephalic region with cuticle not reduplicate to form a helmet or cap. Labial sensilla papilliform or setiform; cephalic sensilla setiform usually in two well separated circlets of 6 large anterior and 4 smaller posterior setae. Amphids pocket-like immediately followed by sensillar pouch, aperture transversely oval, well behind oral aperture. In Tripyloidae stoma collapsed or funnel-shaped, tri-radiate with long radii, mostly comprising oesophastoma surrounded by oesophageal tissue, not sclerotized, teeth inconspicuous elevations on oesophastomatal wall at different levels, dorsal tooth in median region anterior to subventrals. In Onchuloidea the stoma is capsuliform and has a large dorsal tooth and may have subventral teeth and bristles. Orifice of dorsal gland at the tip of the dorsal tooth (Onchuloidea) or just behind it (Tripyloidea); orifices of subventral glands near that of dorsal gland. Oesophagus cylindrical or sometimes enlarged posteriorly, lumen with long radial arms; muscular tissue areolated. Cardia with large glands. One (prodelphic) or two (amphidelphic) antidromously reflexed ovaries lying on lateral (Onchuloidea) or ventral (Tripyloidea) of intestine. Spermatheca present. Prerectum absent. Caudal glands not extending into pre-caudal region, and spinneret generally present. Male usually with a series of ventromedian cervical papillae which may be continuous with the preanal ventromedian supplements. Latter papilliform, vesiculate, or setiform, spaced; adanal or postanal pair of papillae absent. Testes paired or rarely single. Ejaculatory duct nonmuscular or poorly muscular. Spicules simple; protractors of spicules in th form of suspensor muscles (see Siddiqi, 1974) forming a capsule around the spicule, apparently not attached to the body-wall. A simple gubernaculum usually present. Mostly predators and carnivores, found in fresh water and wet soils; some genera are marine.

Type-genus: *Tripyla* Bastian, 1865.
Suborder: Tripylina Andrássy, 1974.
Superfamilies: Tripyloidea de Man, 1876 (Chitwood, 1937)
Onchuloidea Andrássy, 1973 (n.rank).

*Relationship and discussion:* Tripylida n.ord. has a cuticle swelling upon

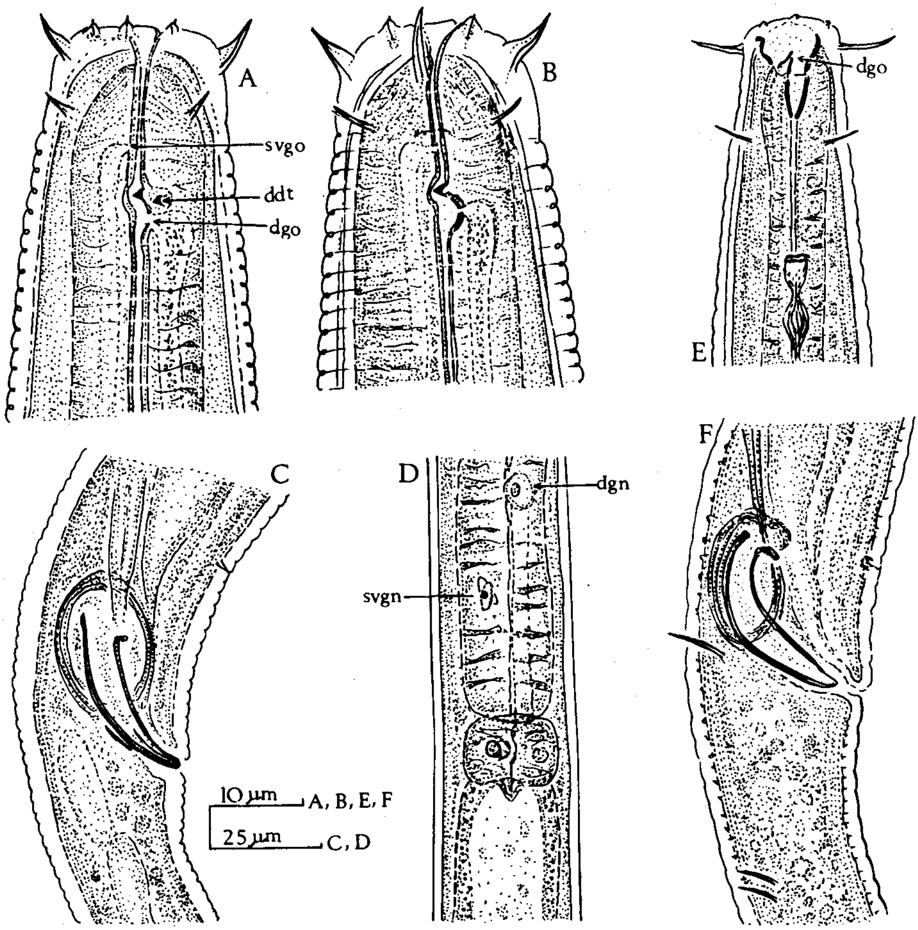

Fig. 3. Order Tripylida. A–D. *Tripyla* sp. from England. A. Fourth stage juvenile stoma showing developing tooth and orifices of oesophageal glands. B. Female stoma region. C. Male spicule region. D. Female basal region of oesophagus and cardia. E & F. *Onchulus* sp. from Colombian rain forest, male anterior and spicule regions respectively. (dgn = dorsal gland nucleus; dgo = dorsal gland orifice; ddt = developing dorsal tooth; svgn = subventral gland nucleus; svgo = subventral gland orifice.)

fixation, an evertible stoma which is mostly an oesophastoma, spermatheca usually present and the protractors of the spicules are in the form of suspensors forming a capsule around each spicule and apparently are not attached to the body-wall. In these characters it is related to the order Triplonchida Cobb, 1920 (syn. Diphtherophorina Coomans & Loof, 1970, *apud* Siddiqi, 1983) but differs from it in having the cephalic sensilla in two circlets, amphids located well behind the cephalic region, dorsal oesophageal gland opening in the stomatal region and in lacking a protrusible stylet and its associated protractor muscles and cardiac glands.

On the basis of the remote positions of the posterior circlet of the cephalic setae and amphids, Onchuloidea are considered the more primitive than Tripyloidea and Triplonchida (see Riemann, 1972; De Coninck, 1965). Triplonchida, with their adaptations of a protursible stylet to feed on plant roots appear to be relatively modern, but the resulting changes that took place in triplonchs are sufficient to assign them to a separate order from Tripylida.

De Coninck (1965) regarded *Tripyla* as a primitive Enoplia, which through forms such as *Bastiania* (Bastianiidae) points towards the evolution of the Chromadoria. He considered two subfamilies, Tripylinae Örley 1880 and Tobrilinae Andrássy, 1959 (syn. Trilobinae Micoletzky, 1922) under Tripylidae de Man, 1876 which together with Ironidae de Man, 1876 constituted the superfamily Tripyloidea de Man, 1976 (Chitwood, 1937). Andrassy (1976) classified Tripylidae, Lauratonematidae Gerlach, 1953 and Prismatolaimidae Micoletzky, 1922 under Tripyloidea and Onchulinae under Prismatolaimidae. Lorenzen (1981) transferred Prismatolaimidae to Chromadoria and assigned Onchulidae and Lauratonematidae to Trefusiida. Tripylidae and Onchulidae are here accommodated under Tripylida n.ord.

Tripylida and Triplonchida are easily recognized amongst the Enoplia by their suspensor muscles which act as protractors for the spicules and which form a capsule around each spicule and apparently are not attached to the body wall (see Siddiqi, 1974). Riemann (1972) noted the characteristic ellipsoidal suspensor muscles of the Tripyloidea *(Kinonchulus* and *Tripyla)* and pointed out their similarity to those found in the Diphthero-