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20 ♦ Comparative Morphology in Nemic Phylogeny

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In 1945 Simpson wrote: "Phylogeny cannot be observed. It is necessarily an inference from observations that bear on it, sometimes rather distantly, and that can usually be interpreted in more than one way." Certainly this applies to a study of nemic phylogeny where our reasoning is based upon degree of resemblance and subject to confusion by convergence and reversal. Many feel that, because fossil records are lacking, it is of little purpose to indulge in speculation on nemic phylogeny. Nemic taxonomy, however, requires such speculation when it is based upon comparative morphology. Our attempts in taxonomy are really an effort to express phylogenetic relationships. These relationships have developed through time and cannot be understood without extrapolation into the past.

In presenting the modification proposed here, I have largely avoided use of zoöparasitic nemas for which a phylogeny was proposed by Dougherty in 1951. Although these are phylogenetically important, understanding the evolutionary sequence of the so-called "free-living" soil, freshwater, and marine nemas should be attempted first.

Changes in the current concepts are necessary if the classification of the Nemata is to be consistent with the available knowledge of their comparative morphology. The modifications suggested in this paper are based upon studies of the cephalic sensory structures (setae, papillae, and amphids), esophagus (its nuclear arrangement, glands and valves—fig. 20-2, A), esophago-intestinal valve, excretory system (fig. 20-2, B), reproductive system, and total number of intestinal cells. Some use is also made of the stoma, somatic sensory structures, and cuticular specializations.

Rudolphi (1808) proposed a class Helmintha that encompassed five orders, one of which was the Nematodea. Cobb (1919) proposed that the latter group be recognized as a distinct phylum, Nematodes. Chitwood and Chitwood (1950) utilized the concept that these animals represented a phylum, but used the name Nematoda for the phylum designation. Later B. G. Chitwood (1958) proposed a name change for the phylum to Nemata (Rudolphi, 1808) Cobb, 1919. In this same

paper two classes were proposed and assigned names derived from ones originated by von Linstow (1905): Adenophorea (syn. Aphasmidia) and Secernentea (syn. Phasmidia). It is the phylogenetic relationships of the orders, families, and genera within this phylum that will be discussed here.

Chitwood and Chitwood (1933) proposed an animal combining features of the Rhabditidae and Plectidae as the hypothetical primitive nema. As a consequence modern representatives of the Rhabditidae and Plectidae were considered as basic to nemec taxonomy and phylogeny (fig. 20-1). It was as a result of my studies of the morphology and biology of the genus *Plectus* that the likelihood of their being basic in the phylogeny of the Monhysterida, let alone nemec phylogeny, was subjected to suspicion. On gross examination the Plectidae and Rhabditidae seem to exhibit a resemblance of morphologic structures. Close examination reveals, however, that their similarity of structure is the result not of homologous development, but of convergent development. The modified concept presented here is still ar-

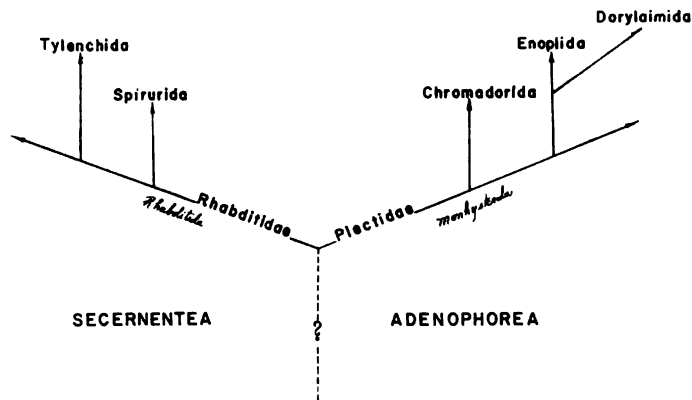


FIGURE 20-1. Current concept of the evolution of the major groups in the phylum Nemata.

ranged so that the orders Monhysterida and Rhabditida are rather closely related and represent the point of the split between the Secernentea and Adenophorea (fig. 20-2). It is not believed that either the Plectidae or Rhabditidae are basic to nemec phylogeny or to the evolution of each order. If these forms were basic, we should be led to the conclusion that the ancestral nemas not only were similar to one or both of these orders, but also resembled these two families. Yet none of the modern groups, on this basis, seem to qualify as a possible ancestor.

Other theories of nemec phylogeny, though less widely accepted, have been proposed: de Coninck and Schuurmans Stekhoven (1933) offered *Areolaimus* for consideration as the modern representative of the primitive nema; Filip'ev (1934) stated that the primitive nema probably was marine and of the group Enoplida; Hyman (1951) agreed that the primitive nema was most likely marine, but suggested that it was probably of the group Chromadorida. These conflicting hypotheses on nemec phylogeny stimulated the present study, which is based on an investigation of the comparative morphology, either in totomounts or serial sections, of all the nematodes included and of many others not specifically mentioned here.

Our concept of the primitive nema must be based on our knowledge of the

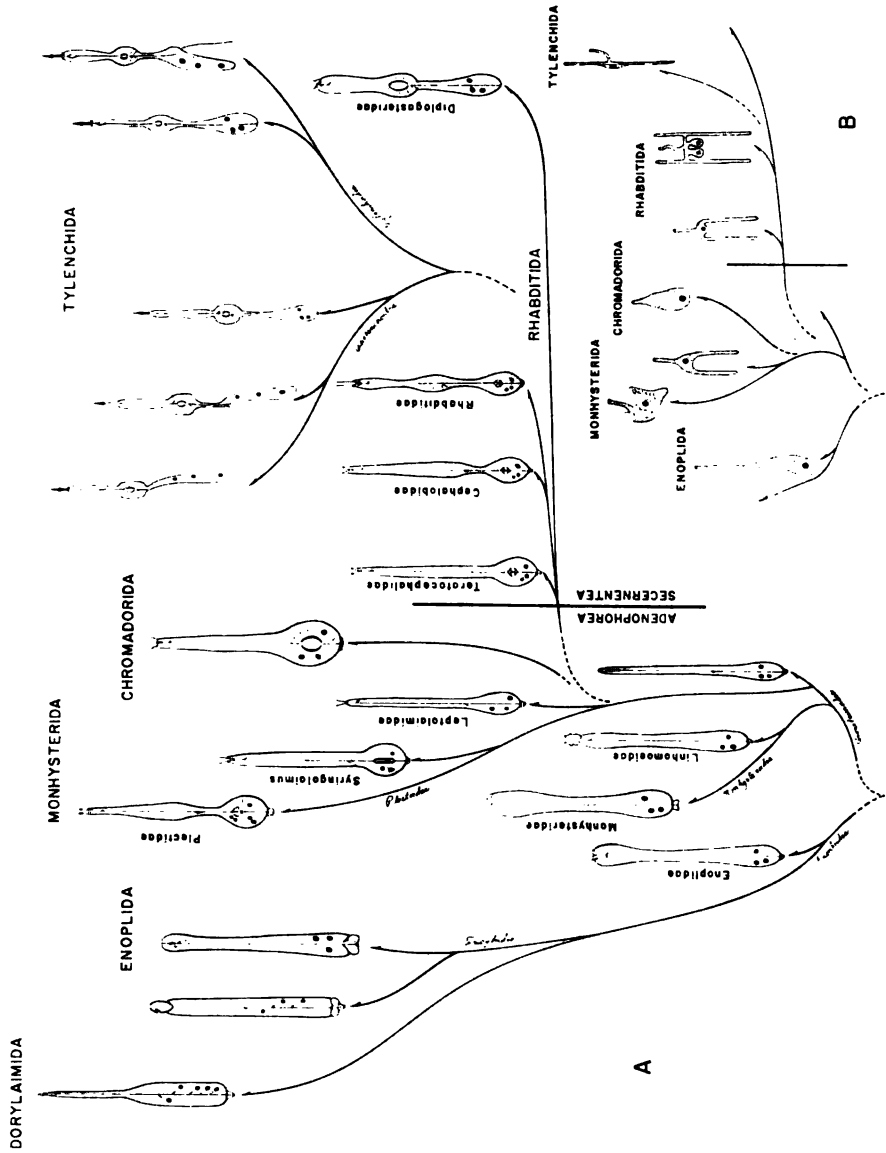


FIGURE 20-2. Modified concept of nemic phylogeny illustrating evolution of esophagi and of excretory systems.

morphology of the present forms. Such a form must include the characters common to all nematodes and to some extent those that are now limited to individual groups. Therefore, certain assumptions can be made. It had an integument, likely non-striated. The oral opening was probably surrounded by six simple lips, the cephalic sensory structures must have consisted of six circumoral setiform papillae and two post-labial whorls of six and four setiform papillae respectively and two post-labial amphids, non-spiral and not pore-like. The stoma was possibly open, cylindrical and unarmed, with the orifices of the esophageal glands opening into or near it. The esophagus was likely to have been of one part, non-valvated and muscular with esophageal glands enclosed posteriorly. The esophago-intestinal valve probably had a triradiate lumen. Little speculation can be made concerning the remainder of the alimentary canal except that it probably consisted of relatively many cells and possibly had a bacillary layer. The female gonads were didelphic and amphidelphic, and outstretched with the equatorial vulva opening separately from the alimentary canal. The male probably had two testes, opposed and uniting with the rectum to form a cloaca with two spicules and a gubernaculum. There was possibly a single ventral row of supplementary tubuli and also genital tactile papillae coincident with this system. The excretory system was almost certainly a single cell connected with a ventral excretory pore. Caudal glands and spinneret were present. The presence of two sublateral rows of hypodermal glands and possession of pigment spots and ocelli should be considered. These characters are commonly put forward for the primitive nema (Chitwood and Chitwood, 1933) with the exception of the one part, non-valved posterior bulb of the esophagus.

Some representatives of the Enoploidea (Leptosomatidae) come closest to resembling such an animal. The Enoplida are also for the most part marine, therefore consistent with the concept of the origin of life in the sea. The general opinion has been that nemas did arise in the shallow intertidal zones of an oceanic habitat. The concept that the primitive nema was of the Rhabditidae-Plectidae type does not conform well with this idea. This is because in both of these families marine forms are rare.

The first major division in the Nemata probably was the segregation of the order Enoplida. At present the Enoplida are divided into the Enoploidea and Tripyloidea and as a group maintain many characters considered to be primitive. Reviewing the primitive characters we note that they generally exhibit a non-striated integument that, as far as we know, lacks lateral longitudinal alae. The males commonly have a series of preanal supplements in a single ventral row. The esophagus is one part non-valvated and shows a random placement of both marginal and radial nuclei; that is, they are not congregated anteriorly and posteriorly. The esophageal glands open anteriorly in the region of the stoma—at least, in the Enoploidea. The Enoplida have, with few exceptions, a polycytic intestine (256 or more cells). The somatic musculature usually exhibits a polymyarian condition. Normally they possess caudal glands and a spinneret. The excretory system is a single cell opening through a ventral pore.

Some characters that are considered non-primitive are also represented. The amphids are post-labial but relatively anteriorly placed; usually they are found in the region where the lips join the body. The females usually have short didelphic amphidelphic gonads with few developing oöcytes, and they are reflexed.

The Dorylaimida may have had their origin from forms near the Ironidae of

Triploidea because the internal morphology of the esophagus shows the same type of cuticular thickenings for muscle attachments. This relationship of Dorylaimida is substantiated, at least in part, by what we know occurs in the production of stomatal teeth of the triploid *Ironus*. An adult *Ironus* has a well-armed stoma, and the ontogenetic development of these teeth is in the nearby tissue of the esophagus. As the larva progresses in age the developing teeth migrate forward until at the time of molting they are positioned in the stomatal wall. This same migration of the stomatal armature, though more pronounced, can be observed in the development of the spear of the Dorylaimidae. The Dorylaimoidea are rare in oceanic habitats; the great majority are found in a terrestrial habitat.

Within the Monhysterida there are forms reminiscent of the Enoplida. An example of such a form is the genus *Sphaerolaimus* (Monhysterida: Linhomoeidae). In this genus the lip region, stoma, esophagus, and cephalic sensory setae are very similar to those of some Enoplida. Cross sections of the esophagus show the same type of cuticular thickenings for muscle attachments as is found in some of the Triploidea of the Enoplida. The lumen of the esophago-intestinal valve is, however, dorso-ventrally flattened. The nuclear arrangement of the esophagus is unknown.

The Monhysterida are not a homogeneous group. This is mainly because the order contains forms representing the various stages in the development of the three-part esophagus from a one-part. The order Monhysterida has been separated into three superfamilies: Plectoidea, Axonolaimoidea, and Monhysteroidea. A change in the accepted concept of the superfamily arrangements is necessitated within the Monhysterida in order to bring those forms most closely resembling the concept of the primitive Monhysterida into a basic position. Thus, the superfamily Axonolaimoidea (subfamily *Cylindrolaiminae*) becomes closer to a likely basic form, and the superfamily Plectoidea, previously considered basic, assumes the position of the most advanced group in the Monhysterida.

It seems that segregation occurred early, and that the Monhysteroidea and Axonolaimoidea developed almost coincidentally. Both have characters considered basic or primitive, and at this time they should be considered of equal primitiveness. The Monhysteroidea are here treated as a separate line of development and the Axonolaimoidea as that part of the Monhysterida more likely to be basic to the remaining Nemata.

The significant primitive characters of the Monhysteroidea are the oligocytic nature of the intestine (26–128 cells) and the convergent ends of the esophageal radii. The form of the esophagus and the long outstretched ovary make it difficult to conceive of these forms as basic to Nemata. The Axonolaimoidea have numerous characters illustrating a relationship to the Plectoidea as well as to the order Chromadorida and the class Secernentea. The tuboid ending of the esophageal radii is a feature common to the Axonolaimoidea and Plectoidea and to the Rhabditida of the Secernentea. Some representatives of the Axonolaimidae also exhibit an almost one-part esophagus with the first set of nuclei in the esophagus being the marginals. In addition the radial nuclei tend to aggregate anteriorly and posteriorly. These are significant points and are important to the development of the two- and three-part esophagus. Such a feature prepares the way for the division of labor of parts of the esophagus. This pre-adaptation, through natural selection, could finally give rise to the three-part esophagus.

The female gonads of the Axonolaimidae differ somewhat from those of the remaining Nemata, but form a foundation consistent with the development noted in the remainder of the phylum. The gonads of the Axonolaimoidea are outstretched and have a very shortened area for oöcyte development, generally only 20–25 oöcytes in each ovary. The Plectoidea have a reflexed ovary, very short and club-shaped, very similar to the type found in the Chromadorida and Enoplida. In these there are generally less than 20 developing oöcytes. The Monhysteroidea have the long, outstretched ovary with a greatly lengthened area of oöcyte development containing many more than 25 oöcytes. Most of the Secernentea also have the elongated gonads, but these may or may not be reflexed. In this type of gonad there may be more than a hundred developing oöcytes.

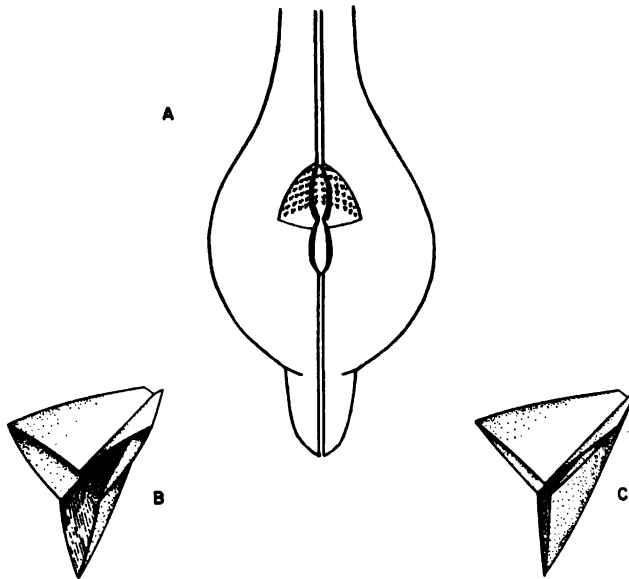
The Plectidae probably represent the most advanced Monhysterida and exemplify the highest development of the three-part esophagus in this order. The groups mentioned above consist for the most part of marine forms, whereas the Plectidae with a well-developed three-part esophagus are mainly terrestrial. Therefore it seems possible that this development is correlated with the invasion of the terrestrial habitat.

The family Leptolaimidae can be placed somewhere between the Axonolaimidae (Cylindrolaiminae) and the Plectidae. The ontogeny of *Plectus parietinus* lends evidence to the development of the three-part esophagus from a two-part esophagus. The first larval stage of *P. parietinus* has a very weakly developed two-part esophagus (Maggenti, 1961). The posterior portion of the esophagus shows only a slight swelling, which contains a simple valve. The gross appearance of this larval esophagus is very similar to that found in the adults of *Leptolaimus*. The valve of the posterior bulb is entirely different from that which is found in the adult. In the first larval stage of *Plectus parietinus* the valve consists merely of three longitudinal plates. These plates amount to little more than a thickening of the cuticular lining of the posterior bulb and are constructed much the same as the valve of *Syringolaimus* and *Rhabdolaimus*.

In the later larval stages and adult, the valve differs from that found in the first stage larvae in having a complex triradiate valve. In later larvae and adults each radial arm of the valve is, in cross section, triangular; longitudinally, each arm is arched so that it is narrowest anteriorly and widest posteriorly (fig. 20-3,A). The whole structure can be considered a reservoir, and it functions as a bellows. The expansion of this reservoir, with the corresponding closure of the lumen in the posterior portion of the bulb, acts to draw in food (fig. 20-3,B). Contraction of the reservoir, with the coincident dilatation of the esophageal lumen in the posterior portion of the bulb, forces food out posteriorly and into the intestine (fig. 20-3,C). Dilatation of the valve (reservoir) is owing to muscular contraction; the collapsing of the reservoir is coincident with muscle relaxation.

The construction and operation of the valve in the Plectidae is different from that found in the Rhabditida (Secernentea). This is one of the evidences supporting the hypothesis that the similarity of these animals is due to convergent development. In the Rhabditida the lumen of the posterior bulb expands to a trilobed reservoir; into this reservoir project three muscular lobes (fig. 20-3,D,E). The face of each lobe is lined with cuticle. The action of this valve involves more than the dilatation and contraction of a reservoir. Muscular contraction rotates the three lobes posteriorly, thus drawing food into the reservoir formed in the lumen pos-

PLECTIDAE



RHABDITIDAE

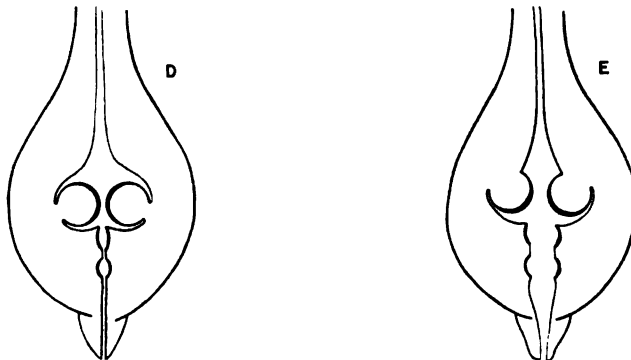


FIGURE 20-3. Diagrammatic illustrations, action of valve in the posterior bulbs of Plectidae (A-C) and Rhabditidae (D-E): A, posterior bulb and valve, adult Plectidae; B, contracted, valve reservoir open; C, at rest, valve reservoir collapsed; D, at rest; E, contracted. (D-E after Chitwood and Chitwood, 1950.)

terior to the lobes. Muscle relaxation permits the movement of the lobes to be reversed, and this collapses the reservoir and forces food posteriorly into the intestine.

Other evidences of convergent rather than homologous development are: the marginal nuclei are the most anterior in the esophagus of the Plectidae, and the

esophago-intestinal valve is dorso-ventrally flattened. In the Rhabditidae the radial nuclei are the most anterior set, and the esophago-intestinal valve is triradiate.

It appears that the Chromadorida as well as the Secernentea have their origin in closely related forms of the Monhysterida. In both of these groups the radial nuclei of the esophagus are the most anterior set and both groups have the triradiate esophago-intestinal valve. The Secernentea seem to have undergone their main development terrestrially, whereas the majority of the Monhysterida and Chromadorida occupy a marine habitat. The tremendous array of niches that are available in terrestrial habitats can account for the Secernentea's diverse morphologic development.

Within the Chromadorida the line of development seems to be two-directional: the Chromadoroidea represent one line; the Desmodoroidea and Desmoscolecoida, the other. It is within the Chromadoroidea that one finds forms most reminiscent of the Monhysterida. This is especially true of the family Microlaimidae.

The characters exhibited by the Monhysterida are important to our understanding the subsequent class and ordinal divisions. The Secernentea probably developed out of the Monhysterida; characters common to the two groups support a phylogenetic relationship. A significant character that is unknown except in the esophagus of the Axonolaimoidea, Plectoidea, and Secernentea is the radial tubuli on the arms of the lumen of the corpus. Other common features are the transverse annulation on the integument commonly interrupted by lateral longitudinal alae. Certain features of the divergence of these two groups are strikingly apparent: the loss of caudal glands and the coincident acquisition of phasmids. It is unfortunate that more is not known concerning the histology and function of these structures. The cephalization of the sensory structures onto the lips is significant. It is a rare exception in the Secernentea that does not have the full complement of 16 papillae (or their remnants) and the two amphids on the lips.

The triradiate esophago-intestinal valve is a common feature of the Secernentea. The dorso-ventrally flattened valve, however, does occur in the Spirurida and Camallanida. The triradiate valve is also common to the Chromadorida (Adenophorea) and is general in the Enoplida. The Spirurida have a two-part esophagus and both forms of the esophago-intestinal valve. In this order as well as the Camallanida, however, all known forms are parasitic, and therefore these features may be not primitive, but rather the result of a secondary development.

Within the Secernentea the pattern of esophageal development is more nearly complete than in the Adenophorea. A logical serial development can be reconstructed from the modern forms of the Rhabditida and Tylenchida. The same is also true of the excretory system (fig. 20-2,B). Such a scheme, however, does involve certain changes in the accepted concept of family positions. In the organization of the order Rhabditida the family Rhabditidae has been considered basic, and we should, if this were true, be able to link it with the Adenophorea. The Teratocephalidae should really assume this position, for they exhibit more characters in common with the Monhysterida than any other secernenteans. Members of the genus *Euteratocephalus* have post-labial, circular amphids, and cephalic setae, and the males have a ventromedian tubular supplement as in the Monhysterida. The esophagus is two-part with little or no evidence of an isthmus. At present nothing is known of the excretory system of this genus or family. In the family Cephalobidae, however, to which the Teratocephalidae are closely related, the

excretory system is described (Chitwood, 1950) and seems to be the simplest of the secernentean types. The construction of this system is: from the ventral excretory pore there is an excretory tube leading to the ventral sinus cell, and from this cell extend two posteriorly directed lateral longitudinal collecting tubules (fig. 20-2,B). The gonads of the Teratocephalidae have the structure common to the Adenophorea. The gonads are short, contain less than 20 developing oöcytes, and are reflexed at the junction of the oviduct and ovary. This is in contrast to the majority of the Secernentea, wherein usually the ovaries are long, commonly with 100 or more developing oöcytes, outstretched, and "reflexures" occur anywhere along the area of oöcyte development.

The Rhabditidae should be considered more advanced than the Teratocephalidae and Cephalobidae because they not only have the well-developed three-part esophagus but they also show an advancement of the excretory system and in some forms evidence of the formation of the median bulb in the posterior region of the corpus. The rhabditid excretory system has two anteriorly directed lateral longitudinal collecting tubules in addition to the posterior pair (fig. 20-2,B). It seems that the diplogasterid group separated from the Rhabditida and possibly should be considered as a distinct line of development. Genera now being considered as likely transitional forms are: *Pseudodiplogasteroides*, *Diplogasteroides*, and *Pseudodiplogaster*.

In the diplogasterids the anterior portion of the esophagus (corpus) is very muscular with a rather well-developed median bulb that is valved, behind which is a glandular terminal bulb. An example of this esophagus is found in the genus *Diplogaster*. Also within this family are the genera *Tylopharynx* and *Neodiplogaster*, which seem to be a logical step toward the Tylenchida. *Tylopharynx* shows possible evidence of a primitive stomatal stylet as well as the tylenchid-like esophagus. The next step is the typical tylenchid esophagus with the corpus, valved median bulb, isthmus, and a glandular posterior bulb (fig. 20-2,A). Modifications of this occur in some tylenchoids, where the glands increase in size and overlap the anterior portion of the intestine. The excretory system of the Tylenchida is restricted to one side of the body, but still with the anterior and posterior collecting tubules; that is, a unilateral reduction of the rhabditid type (fig. 20-2,B). The excretory system of *Tylopharynx* and *Neodiplogaster* has not been described.

From the similarity of esophagi it seems that the Aphelenchoidea developed from very near the family Tylenchidae; but they also show affinities to the diplogasterids. They differ from the Tylenchoidea in that the orifices of all the esophageal glands open posteriorly. The dorsal gland opens just anterior to the valve in the median bulb and the subventral glands open posterior to it. A possible phylogenetic sequence of the aphelenchoid esophagus is illustrated (fig. 20-2,A) by three modern genera: *Paraphelenchus*, *Aphelenchus*, and *Aphelenchoides* respectively. *Paraphelenchus* is basic because the esophagus is without overlapping glands; one species retains the remnant of caudal alae, genital tactile papillae, and a gubernaculum associated with the spicules and is thus reminiscent of the Diplogasteridae. These are considered basic even though most of the species lack caudal alae and retain only genital tactile papillae and a gubernaculum. The loss of caudal alae probably represents a secondary modification. The species of the genus *Aphelenchus* have well-developed caudal alae containing genital papillae and a gubernaculum associated with the spicules. In my opinion, however, the overlapping esopha-

geal glands and the retention of the isthmus place it in an intermediate position in this group. *Aphelenchoides* is considered the most advanced of these because it has genital papillae and no gubernaculum, and the esophagus has overlapping glands and has lost the isthmus.

The modifications that have been proposed here for nemic phylogeny certainly do not represent the final answers. Yet they open the door to many complex questions. At present we are attempting to clarify as many cases of convergence as possible through a study of the histologic morphology of the various groups within the Nemata.

The implications of the valvular apparatus in the posterior bulb of the Plectidae and Rhabditidae offer a striking example of how a common feature, when more fully understood, can change our concepts of classification. It is also obvious that we need more knowledge of the comparative morphology of the Monhysterida and Enoplida. If and when such information becomes available, we may be able to sort secondary developments from primitiveness. It is only when we can make these decisions with some authority that we shall be able to approach an even closer understanding of nemic phylogeny.

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