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## System Analysis and Nematode Phylogeny

A. R. MAGGENTI<sup>1</sup>

The purpose here is to suggest a method which will permit understanding of the phylogenetic relationships of contemporary representatives of the phylum Nematoda without fossils. It is not my intent to again (14) offer a phylogeny for the Nematoda. To say that no real benefit or knowledge of phylogeny or evolution is possible without fossils is succumbing to apathy. One cannot deny or ignore that all systems, morphological, biological and chemical manifested in modern forms developed by evolutionary sequence. It is true that with a complete fossil record the rates of evolution and developmental pressures could be accurately evaluated. However, in the absence of a fossile record evolutionary relations and developmental tendencies can be assessed by the use of direct or corollary system analysis. Taxonomists must not overlook systems and their analysis.

Obviously, confidence would be much more complete in the presence of a complete fossil record. The fossil record provides (in addition to verification of existence) knowledge of time of existence, rates of development, and to some extent distribution and abundance. The latter have proven to be more accurate for marine life than terrestrial fauna and flora. Though often assumed, frequency of occurrence of fossils is rarely correlated with former population density or distribution but rather indicates areas and time periods favoring preservation together with optimum predisposal to fossilization.

The available fossils represent only a small fraction of the former plant and animal life on earth. That enormous numbers of animals and plants, important to the evolution of contemporary forms, must have existed and declined to extinction without leaving a trace is illustrated by an observation in recent historical times. Of the millions of buffalo (American Bison), some estimates in excess of  $100 \times 10^6$ , strewn over the Great Plains scarcely three generations ago, today there is hardly a trace. The skeletons have now largely disappeared and the bones are dissolving and crumbling into dust under the attack of weather. Without conservation of the remaining limited numbers, practically the only other evidence of their occurrence would be "buffalo wallows." Without supplementary knowledge of the buffalo, however, these would not be identifiable.

The advent of sophisticated instrumentation has permitted new research avenues heretofore impossible or impractical. Computers, electron microscopes, and the myriad of instruments available to the biochemist and physiologist have facilitated significant contributions to our store of knowledge. The impact of this rapid development of methodology, technology and instrumentation has led into an era of apparently divergent taxonomic schools. Taxonomists are categorized as numerical phenetic, cladistic or phylogenetic. It is indeed unfortunate that, perhaps through faulty communication, each school seems to lack appreciation for the others' attempt to attain the same goal from another point of view. Among the various schools the phylogenetic approach has been termed

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intuitive taxonomy because it relies upon the experience and the judgment of the observer to determine significance of characters. Some significance must be attached to the fact that the fundamental ideas of the traditional phylogenetic taxonomists have often been confirmed by the opposing schools.

The literature suggests that all too much time is spent in argument about the theoretical merits of the various methods of approach rather than the compatibility and significance of the results. Comparison of the findings of the various approaches and argument over areas of noncorrelation would seem to be much more fruitful. As in all methodology, different techniques have different inherent limitations. Therefore, it would behoove the taxonomists to recognize the restricting premises of each particular school. It would then be advantageous to combine the efforts of each system, thereby increasing the level of confidence in any phylogenetic conclusions. It is axiomatic in science that the realness of any determination should be supported by multiple evaluation using different techniques.

In attempting to form a classification of higher categories into phylogenetic units we must accept certain limitations. We are always faced with insufficient knowledge of the phylogenetically important characters of many groups. In classification, phylogenies must be presented in a linear sequence of species, genera, families and so forth, while the phylogenetic tree, more than a classification, has the added dimension of time. Therefore, no classification could be an exact representation of the phylogeny, even if all the facts were known.

The phylogenies and the evolutionary relationships of nematodes that have been proposed have usually utilized gross morphology of a single character group. For example, De Coninck (5) employed the distribution of cephalic setae and papillae;

Schuurmans Stekhoven and De Coninck (20) proposed a scheme based on amphidial shapes; Steiner (21) utilized the excretory system. The difficulty with a single gross morphological character analysis is the uncertainty whether the evolved scheme is progressive or regressive. Filipjev (8), Chitwood (3), Maggenti (14), Platonova (19) and Gerlach (9) proposed phylogenies utilizing several systems for which the most information was available. The parasitologists have supplemented these criteria by a correlation of parasite characteristics with host biology and evolution.

Goodey (10) states, "classification of any group of organisms is a matter of convenience" and that the "collection and cataloguing of nematodes have not yet progressed far enough for their interrelationships to be seriously studied." It is essential for the growth and progress of this science that we do not allow ourselves to be deceived by this type of reasoning. The best classification according to Mayr (16) is not that which guarantees rapid unambiguous identification but that which has the highest predictive value. Thus nematode taxonomists must decide to accept the limitations enforced by the lack of a fossil record and attempt to formalize a phylogeny on the basis of tested evolutionary principles and methods for evolutionary resolution or forego the phylogenetic concept of classification and replace it with a "practical" classification permitting rapid identification.

I do not accept Goodey's philosophy; therefore, the proposal here is to describe a means whereby alternate phylogenetic schemes based upon thorough detailed system and character group analysis can be compared; the regions of superimposition would then suggest the most probable line of descent. The approach is not original; it has been tested and utilized successfully in other disciplines. The basic idea is to utilize

diverse systems of all types, morphological, hormonal, chromosomal, immunological, biological, physiological or biochemical. The effectiveness of the system is predicated upon each system being analyzed independently and objectively. The confidence in determinations by approaches used heretofore is limited by the subjective decision-making requisite in character selection and estimation of profundity at each successive level. That taxonomy can and should require the use of supplemental systems and properties other than the gross morphology of simple characters has been well established. Nadler (17) employed chromosomal characters in his study of the taxonomy of ground squirrels; Kelly (12) used comparative endocrinology in his investigation of the evolution of invertebrates and vertebrates; and Barrington (1) utilized comparative hormone studies in his book on evolution. Within nematology, immunology has been used in the systematic studies of both plant parasitic and free living nematodes by Bird (2), Lee (13), and El-Sherif and Mai (7).

Without an analysis such as employed by the numerical taxonomists there is danger of subjective bias. The model scheme being presented here could be quantitatively analyzed. However, for the purpose of discussion and in order to illustrate the approach, this technique has not been applied. Each system was analyzed independently with deliberate effort not to weight the characteristics within each system, to estimate evolutionary significance, or to relate one system to another. The features selected were the esophagus, the male reproductive system and the systems of excretion. Characteristics for each major group were listed and organized according to order of frequency of occurrence so that the initial features are common to large groups of nematodes, then each progresses to features present in select groups. No attempt was made to define the feature com-

mon to all except in the systems of excretion. The reason for this will become obvious when the system is discussed. In other than a model system many more features of each system would have to be discussed. However, for simplicity in illustrating the feasibility of the approach, these were kept to a minimum. These particular systems were chosen because of their variability throughout the Nematoda.

Within Nematoda other systems have value at different levels of investigation. The stoma, for instance, is of little value in system analysis because it is likely to be greatly influenced by environment. Analysis of this feature rapidly reduces to circumlocution; however, this does not negate its usefulness at lower category levels of investigation. The same may be said of the amphid, even though it appears to be more conservative and less susceptible to environmental influence. Until we know more about amphidial structure and function this organ does not lend itself to analysis. An important aspect of system study is to recognize those features which analyze in a linear fashion. The position and form of cephalic setae and papillae is such a case. The pattern of progression is toward cephalization and reduction in setal size with the eventual replacement by papillae (15). This development is useless for main dichotomic separation but extremely useful in confirming the progression in any dichotomic line. The female reproductive system was not utilized in this study because of the clarity of the features of the male system as well as the obvious complementary development of these systems. However, it should be emphasized that for a thorough analysis as many systems as possible need to be included.

The diagrammatic illustration of the analysis of the esophageal system is shown in Figure 1. The category names are not indicated; the concern at this time is analysis of the system. This discussion is not being

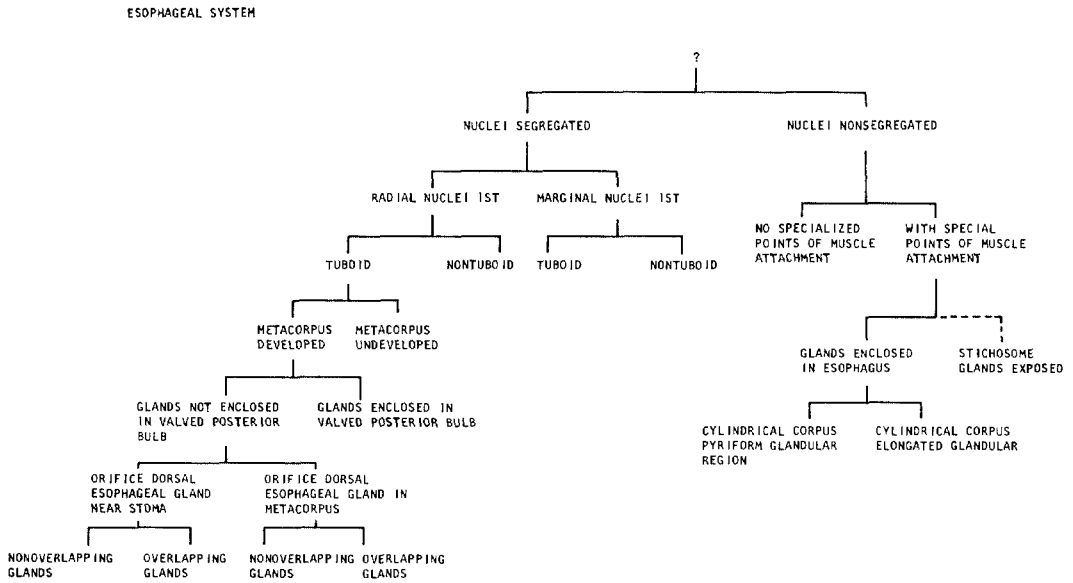


FIG. 1. Analysis of morphologic and histologic characteristics of esophagi in Nematoda.

presented as an exhaustive analysis of the selected systems; it has been kept intentionally brief in order to facilitate an understanding of the approach.

Form and function of any cell, tissue, or organ is determined by its nuclear components, and nuclear distribution within the esophagi of nematodes falls into two groups. In one group the nuclei are dispersed throughout the esophagus, whereas in the other the nuclei segregate anteriorly and posteriorly. The latter is extremely interesting because such a condition supplies the foundation for the specialization of the diverse characteristics exhibited in nematode esophagi. It is also in the segregated esophagus that the so-called isthmus is manifested. Continuing down the left hand dichotomy, nuclear arrangement can be further divided as to type of nuclei, their order of appearance, and coincident structure. Thus basically two groups segregate on the position of radial or marginal nuclei being the first to

appear in the esophagus. Each of these groups can be further subdivided on the presence or absence of tuboid endings on the esophageal radii of the corpus. Those esophagi having segregated nuclei, radial nuclei first and tuboid endings on the radii define two other subdivisions: those with and those without muscular development of the metacarpus. Coincident with metacarpal development is the increased development of esophageal glands. Where these glands open into the esophagus identifies another dichotomy, that is, whether the dorsal gland opens into the corpus or into the metacarpus. As glandular volume increases there is a progressive reduction in posterior musculature which eventually results in the glands overlapping the intestine. The latter character is useful only in individual taxa.

Returning to the right hand of the scheme presented in Figure 1 it will be seen that in the case of non-segregated nuclei within the esophagus that musculature and glands seem

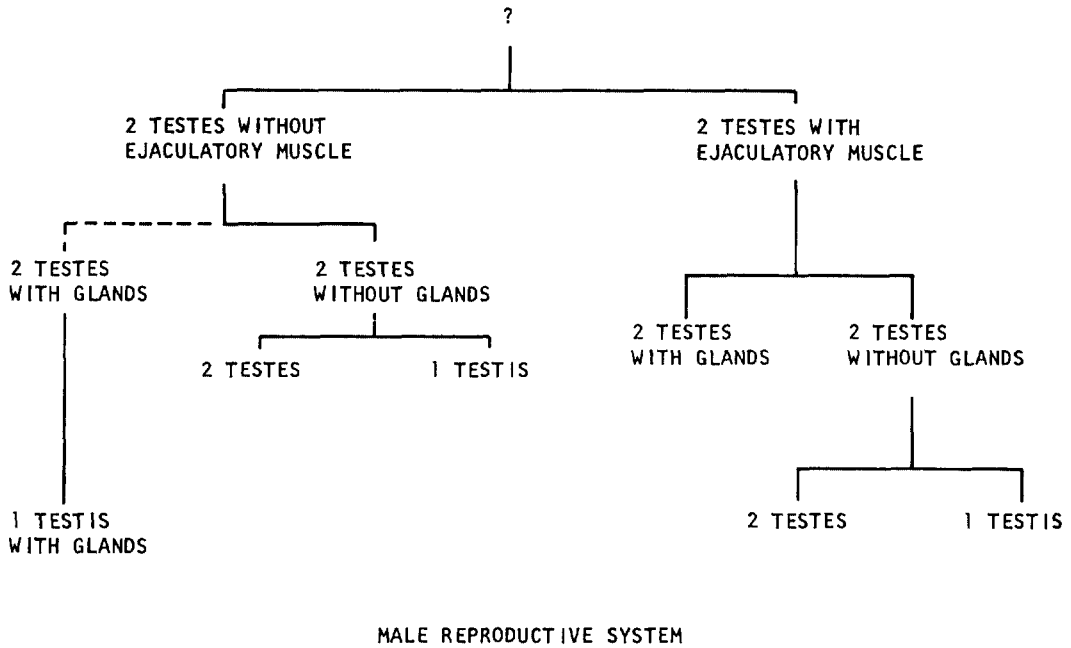


FIG. 2. Analysis of the male reproductive system in Nematoda.

to lend themselves to further analysis. On the basis of musculature esophagi segregate into those forms without specialized areas of the lumen for muscle attachment and those forms with specialized areas of attachment. It is among the latter group that esophagi with more than three glands can be found. In some the development goes so far as to be described as a stichosome, that is, a multiple exposed glandular structure on one or both sides of the esophagus. Because a well defined dichotomy does not present itself, this section is connected by a broken line. The last dichotomy is really a manifestation of the external form of the posterior bulb of the esophagus.

Figure 2 illustrates the analysis for the male reproductive system. Nematodes fall into two groups, each with consistent characteristics and each with two testes. It is not assumed here, however, that the primitive nematode had two opposed testes. We have

little information concerning the testis itself; however, we do recognize many features associated with the male reproductive system. The divergence expressed by the presence or absence of ejaculatory muscles manifests in both branches an interesting dichotomy of the presence or absence of ejaculatory glands. It is interesting to note that ejaculatory glands are associated with terrestrial nemas of widely divergent types. In the left-hand group of Figure 2 no nematode is known with two testes plus ejaculatory glands; this is indicated in the diagram by a broken line. Discrepancies and gaps in available information are readily recognized. If the analysis is correct then predictions can be made as to what areas need further investigation for additional knowledge or unsuspected species. It must be realized that in many instances the extinction of an animal may forever exclude the completion of our knowledge.

The right hand dichotomous branch of

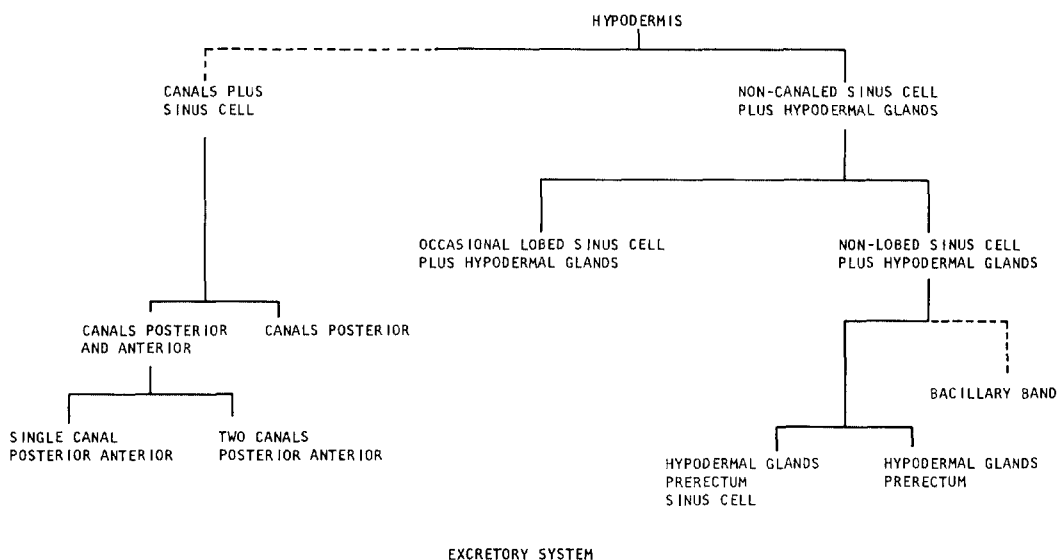


FIG. 3. Analysis of the excretory systems in Nematoda.

Figure 2 is also based on the presence or absence of glands associated with the testes. The final dichotomy separates those forms with either one or two testes.

The third system to be analyzed here is that of excretion, Figure 3. Vital processes are less susceptible to subjective interpretation than their morphological manifestation. The analysis begins with the hypodermis. All alleged excretory systems in Nematoda are derived from hypodermal tissue. However, all processes of excretion are not necessarily hypodermal in origin. For lack of critical information the initial division is determined by whether or not the specialized hypodermal cell (rennete, sinus cell, ventral gland) is associated with a canal system or not. If it is, then the position and number of canals is to be considered, that is, whether they are found both posterior and anterior to the sinus cell or only posterior. Among those forms possessing canals both anteriorly and posteriorly we note that the canals may be present on both sides of the body or confined to only one side.

The system without true canals is by far the most interesting. In most forms with the simple sinus cell there is generally a corresponding development of other hypodermal glands. Jägerskiöld (11) associated the existence of sublateral hypodermal glands with degeneracy of the excretory system in Adenophorea. The term sinus cell is used throughout in order to maintain consistency between Adenophorea and Secernentea. The diagram also illustrates that in some instances the simple sinus cell may be modified by posterior lobes; and in others these are well developed and extend posteriorly for a considerable distance. When no sinus cell is present, the hypodermal glands are often well developed and in some forms are manifested in bizarre structures such as the bacillary band in trichurids. Furthermore, an additional important feature of some nematodes with the simple sinus cell is the presence of a pre-rectum. It is found in forms with hypodermal glands and presumed sinus cells, as well as in the absence of the sinus cell. It is also worth noting that when the

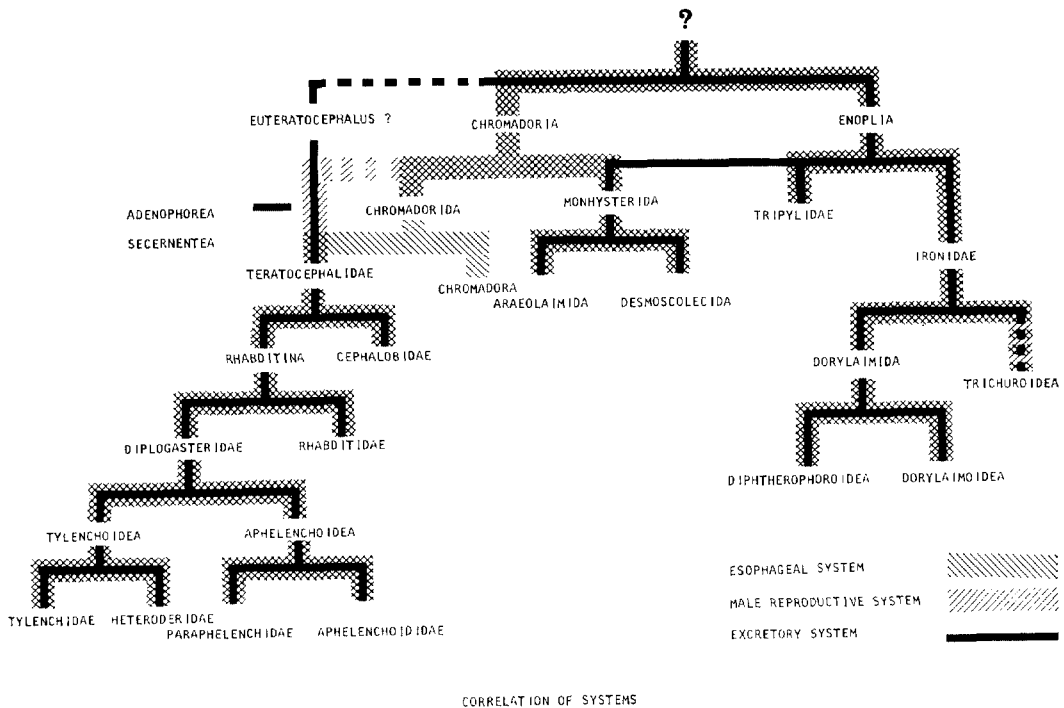


FIG. 4. Correlation of systems: superimposition of analyses of nematode esophagi, male reproductive system, and systems of excretion.

pre-rectum is extensive the hypodermal glands are not and conversely a shorter pre-rectum is found with well developed hypodermal glands. The origin or function of the pre-rectum in nematodes has not yet been established. The circumstantial implication that it may be important in the function of excretion in the nematodes in which it is found should not be ignored.

The final step is the superimposition of the individual models to detect correlation, discrepancies or lack of information, Figure 4. Category names have been included for better orientation. As one might have expected the highest degree of correlation is found in the Secernentea, enoplids and among the dorylaims. The apparent discrepancy among the Monhysterida, Araeolaimida and Chromadorida would indicate that these groups are not as well understood as they

ought to be. Furthermore this uncertainty would suggest that a closer inspection of their internal relationships is in order. Any phylogeny or classification with these as foundation groups should be subjected to severe scrutiny. Unfortunately this criticism applies to all the classifications widely used today.

Of additional interest is the position of trichurids. Only the male reproductive system in Figure 4 shows a distinct dichotomy with the Dorylaimida. The other two systems analyzed, though not so clearly, also indicate a closeness to Dorylaimida, as was suggested by Chitwood (3).

The superimposition further indicates the all too apparent lack of information concerning the relationship of the secernentean excretory system and male reproductive system to those of the adenophoreans. Perhaps,



when fully described, a nematode like *Euteratocephalus* may clarify many questions in this region.

In Figure 4 the division of the nominal classes Adenophorea and Secernentea is indicated. The scheme, however, would indicate that three groups are evident: the first in very broad terminology embraces enoplids, the second chromadorids and the third rhabditids. If classes are accepted in Nematoda then it is apparent from the analysis illustrated in Figure 4 that the conventional class division as it is currently accepted is not sufficient. This scheme corroborates the subclass division of Chromadoria and Enoplia Pearse (18).

The analytical separation of Chromadorida does not lend any confidence to the assumption that they are basic members of Chromadoria. The systematics of this whole group should be carefully investigated. Any such investigation will necessarily involve much more than just the single character of amphid shape. For instance in the Monhysterida we find forms with smooth cuticle without lateral fields, undivided esophagi with wide stomatal attachment, a lack of specialized areas for muscle attachment and with the cephalic setae in two sublabbial circles of six and four. These are nearly the same characters that could be listed for Enoplia. Yet they are discussed as advanced Chromadoria that have undergone regression. There is no evidence for such a premise; furthermore, none is necessary. It would seem rather important but overlooked that the marginal nuclei are the most anterior nuclei in the esophagus of Monhysterida. The transition from marginal nuclei to radial nuclei anteriormost (Chromadorida and Secernentea) and then back again requires too many unwarranted assumptions. Accepting and working with the systems and morphology as expressed in contemporary species is more objective and the resulting scheme more feasible.

The four major classifications available at present are Filipjev (8), Chitwood (3), Goodey (10) and De Coninck (6). Goodey's classification, as he clearly states, makes no effort to reflect relationship; therefore, it is irrelevant to this discussion. His classification is predicated on convenience, economic importance, and consequently lacks the fundamental phylogenetic property, predictability. Each of the remaining three classifications has strong features well worth considering.

Filipjev proposed a classification that present knowledge would lead us to conclude was extremely perceptive. He reviewed the then known nematodes as representative specimens and was unbiased by relative abundance, economic importance or bulk of information on specific nematodes. His conclusions were formulated from observation of total morphology. He recognized the overall basic features of Enoplida and accepting the Leptosomatidae as primitive he built his classification. Filipjev, however, rejected the idea of nematodes being subdivided into classes. In addition to Filipjev, Maggenti (14) and Platonova (19) also proposed phylogenies based on Leptosomatidae as primitive.

Chitwood's published phylogeny and classification has *Rhabditis* and *Plectus* as contemporary representatives of the foundation group. From Rhabditida there is progression toward the other Secernentea; however, from *Plectus* there is regression away from the remaining Adenophorea. Most important to this discussion of Chitwood's (4) classification is his establishment of the two classes Adenophorea and Secernentea. In addition to the class divisions Chitwood had an unusual grasp of the organization of the Secernentea; aside from category modifications his basic organization of Secernentea has stood sound and workable for thirty years.

Pearse (18) made the important contribu-

tion of further dividing the Adenophorea into two subclasses: Chromadoria and Enoplia. De Coninck (6) recognized this division but termed the categories infra-classes. It would be difficult to argue with his knowledge and interpretation of the individuality of the Chromadoria. A disturbing fact, however, is that the internal arrangement of the group Chromadoria is based almost solely on the amphidial form.

The model system analysis presented here indicates that further in-depth analysis of all systems would reveal a phylogeny consistent with the manifested development of contemporary representatives. From this phylogeny it should be possible to devise a sound classification that will in all probability reflect the best qualities of the classifications of Filipjev, Chitwood, and Pearse, *i.e.* the organization of Filipjev, the classes of Chitwood, and the subclasses of Pearse. I have no doubt that given this foundation we can construct a sound classification based upon phylogeny and therefore manifesting inherent predictability.

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