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COELOMATE SUPERPHYLA

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Abstract

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phyla. Syst. Zool. 22:97–102.—It is proposed that regular use be made of the superphylum
as a formal taxonomic category for coelomates. Taxa at this level would serve several impor-
tant purposes: 1, they are of particular use to paleontologists as a basis for the subdivision of
the Animalia during the late Precambrian, before the advent of many modern phyla; 2, they
serve to embrace fossils of all ages that do not belong to living phyla; 3, they form a basis
for phylogenetic models concerned with the origin of major grades of organization; and 4,
they serve simply as a means of organizing phyla, which are now multiplying. [Coelomates;
superphyla.]

INTRODUCTION

The systematic hierarchy has proven to be an extremely powerful tool in organizing and containing taxonomic concepts for the entire world of life. This is not to say that it has worked perfectly, for there are certainly problems inherent in the use of such a hierarchical structure. One problem is that distantly related taxa in the same category need not have a similar significance. Most of the practical difficulties arise because we wish to have a phylogenetic systematics and cannot agree on a phylogeny, but this is certainly not the fault of the systematic architecture.

The number of categories that are regularly employed as useful organizational levels varies among different taxa, naturally enough, according to the numbers of radiations that have occurred, the numbers of branches that have appeared, and the taste of the taxonomist. There now appear to be strong theoretical and practical reasons that a category above the level of the phylum, a superphylum category, should be employed regularly for the coelomates. The purpose of this paper is to present arguments favoring such a practice.

TAXONOMIC MODELS AT THE SUPERPHYLUM LEVEL

Early authors such as Linnaeus and Lamarck employed phyla that were broad by present standards; Linnaeus used five taxa at this approximate level in 1758. Of course, the grouping of organisms in such broad units as "Vermes" proved to be unwieldy and commonly polyphyletic, and these early taxa have been split into what are regarded as distinctive and more or less monophyletic clades; many modern authors employ around 20 or more animal phyla (Hyman, 1940, has 22). Sometimes phyla are grouped into subkingdoms, which for animals usually consist of the Parazoa and Eumetazoa. Hadzi (1963) returned to an almost Linnaean plan of phylogenetic branching in using three subkingdoms (Protozoa, Parazoa, Eumetazoa), and only four phyla of Eumetazoa, but with 42 classes. The severe objections raised to his scheme have been critical of his phylogeny but not necessarily of his philosophy of categorization.

Whether formally or informally, most authors do group the phyla, for ease of treatment at least, into associations that have similar features of ground-plan or of early ontogeny. Take for example the coelomate metazoa, which are frequently subdivided into the Protostomia and Deuterostomia (Grobben, 1908). In the plan of the phylogenetic tree (Fig. 1A), this leads at once to a major bifurcation, usually beginning just above the flatworms, which creates two relatively equal branches, each replete with a number of side branches, but each leading eventually to the most "advanced" phyla and presumably to their ultimate products, butterflies and man.
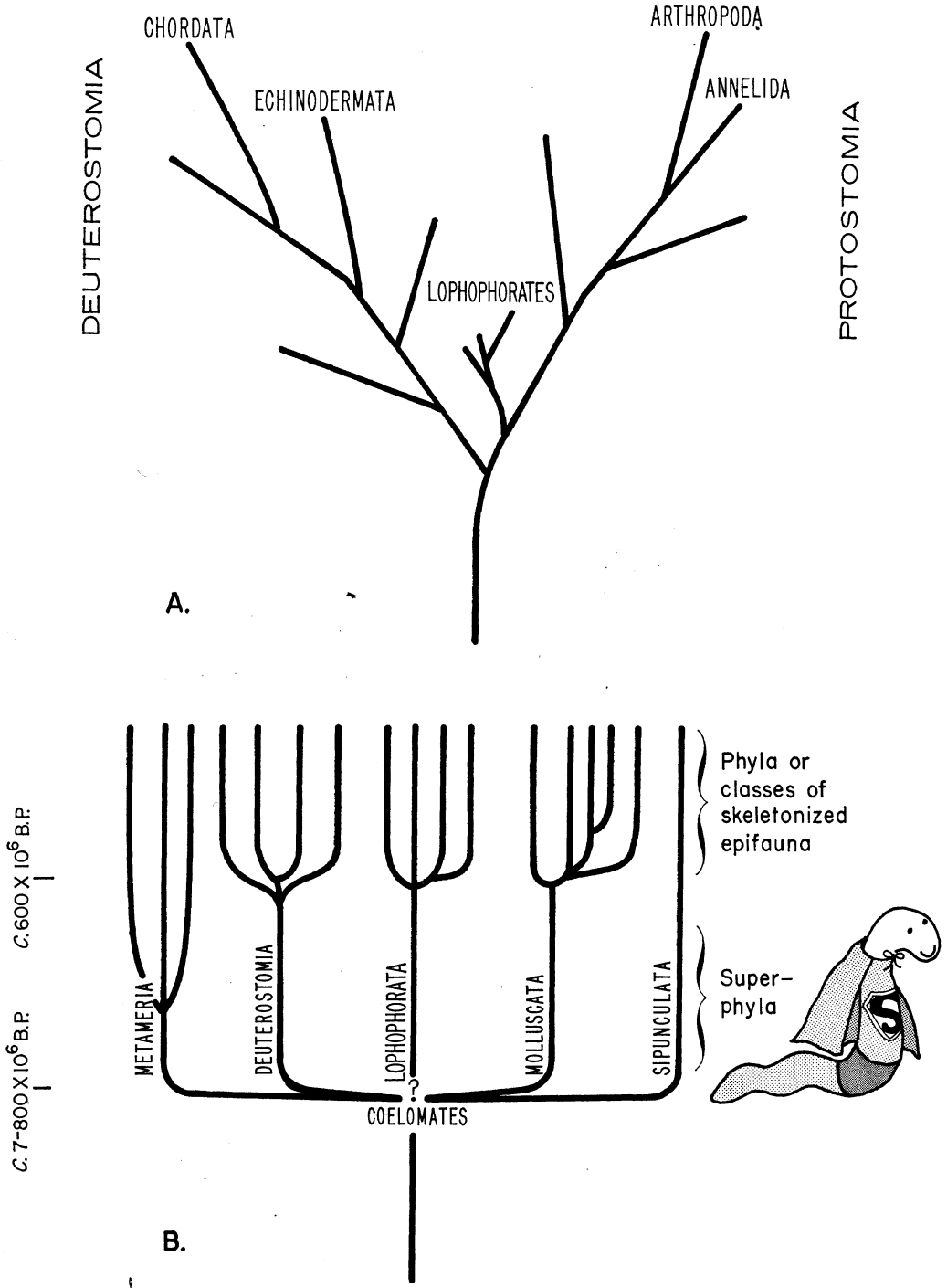
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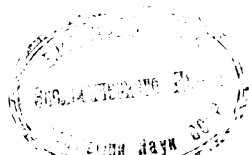
FIG. 1.—Coelomate phylogenetic models. A. Conventional phylogenetic tree, differing in detail from those in the literature but reflecting their usual pattern. B. Phylogenetic pattern based on models of adaptive pathways and using a time scale. Coelomate superphyla appear as natural taxa. Their value for classifying Precambrian organisms is apparent.

this sort of arrangement. A point that has been made repeatedly is that some coelomates, especially the lophophorate protostomes, display mixtures of features that supposedly characterize the deuterostomes and protostomes. The lophophorate branch is therefore commonly located near the major divergence into the two main branches of the coelomates. As the tree has a dendritic branching pattern, it is necessary to commit the origin of the group to a definite position with respect to other major lineages; uncertainty is difficult to diagram. Furthermore, this placement does not really help to solve the problems posed by the mixed characters of the lophophorates.

Actually, the coelomates can be placed into four or five groups that differ in their basic coelomic architectures. The primitive functions of the various architectures have been analyzed (see especially Clark, 1964); they seem to have to do chiefly with the locomotory mechanism employed, which in turn depends chiefly upon feeding habit. Perhaps one group (annelids, etc.) descended from vagile burrowing infaunal detritus feeders primitively, and developed a metamerous coelomic structure; while a second (phoronids, etc.) was primitively composed of relatively sessile burrowing infaunal suspension feeders with oligomerous coeloms; a third (mollusks) became creeping epifaunal or semiinfaunal detritus feeders with seriated organ systems but an unsegmented coelom; and a fourth (sipunculids) contained infaunal burrowers, unsegmented with an introvert, probably surface detritus feeders. Probably a distinctive fifth group was oligomerous much like the phoronids, with which it may share a common root, and was composed of burrowers that fed on surface detritus by means of coelomic tentacles (the deuterostomes). It appears that the coelom was chiefly a hydrostatic skeleton that was employed for burrowing and also was exploited in tentacular extensions and introvert mechanisms. Only for the mollusks is a primitive infaunal burrowing ancestor not required by this

model, and even there it is perfectly possible–there is simply no strong evidence one way or the other (see Stasek, 1972).

Thus there may well have been five Precambrian groups of worm-like organisms from which the coelomate phyla that we know have descended. Probably, some of the living worm phyla have descended without major changes in ground plan from late Precambrian precursors. However, the coelomate phyla that are not worm-like seem to owe their present ground-plans to modifications and elaborations of vermiform ground-plans to adaptations for epifaunal existence (Clark, 1964; Valentine, *in press*). Most of the infaunal vermiform stocks have radiated into a few distinctive epifaunal lineages, each originally exploiting a separate mode of life (Fig. 1B). Many of these newly organized ground-plans were coadapted with skeletons. Indeed, it is suggested that the Precambrian-Cambrian boundary represents the first emergence of a diverse coelomate epifauna. The development of this epifauna may have been permitted by a trend towards the stabilization of trophic resources (see Valentine and Moores, 1972), or perhaps by a rise in the level of atmospheric oxygen (see Rhoads and Morse, 1972). At any rate, the phylogenetic "tree" that best depicts this pattern (Fig. 1B) has a hierarchical aspect itself and focuses interest, not on which lineage arose from which, but on the events responsible for a series of adaptive radiations of ground-plans. Furthermore, the feeling that the history of life represents a long struggle upwards to a few advanced forms, as conveyed by the pattern in Fig. 1A, is replaced by the feeling conveyed by the pattern of Fig. 1B that the radiations responsible for diversity at higher taxonomic levels produced numbers of lineages that were more or less equally well-adapted, but to a number of distinctive life modes. Thus in establishing superphyla, the emphasis is to be upon adaptive divergences and adaptive pathways rather than upon morphology alone.

From several lines of evidence, then, including comparative anatomical, embryological and paleontological, and from theoretical considerations, it is possible to group the coelomate phyla into a few associations that appear to represent true clades. At least, the evidence favoring such an arrangement is no worse than the evidence favoring most taxonomic models that are in common use for lower levels. What are the advantages, if any, of employing these groupings formally?

THE SUPERPHYLUM AS A PRACTICAL TAXON

The phylum has certainly been about the most useful of all the systematic categories, with the possible exception of the species. The kingdom, on the other hand, has hardly mattered to most biological scientists until rather recently, when a marked renewal of interest occurred (Whittaker, 1969; Margulis, 1970a). This rising interest correlates very closely with new work on the very early history of life, including descriptions of early fossil procaryotes (see Schopf, 1970), work on the early state of the environment (for example, Cloud, 1968), and on the evolutionary pathways that have led to the major life forms (Margulis, 1970b). Curiously, some of the proposed kingdoms are explicitly polyphyletic. At any rate, the point is that consideration of the systematics of this level follows naturally from the active consideration of the origin of these fundamental subdivisions of life.

In a similar way, the potential usefulness of the superphylum can be correlated with a new round of active work on the origin of phyla involving interest in the adaptive pathways along which they have evolved. As this work goes forward, two main sets of conclusions appear to be emerging. The first is that several of the accepted phyla are polyphyletic. For one example take the Brachiopoda. It has long been suspected that the Articulata and Inarticulata might not be conphyletic, for they have very distinctive larval lives and several basic and consistent anatomical differences. A new

adaptive model of their origin (Cowen and Valentine, in press) suggests strongly that each arose from a phoronid-like infaunal worm but along separate adaptive pathways, each of which led to skeletonization primarily to internalize feeding currents as an adaptation to epifaunal life. Indeed, early inarticulates themselves seem to be divided into several distinct lineages, all epifaunal. The linguloids reentered the infauna during the Ordovician (Rudwick, 1970). Therefore the nearest common ancestor of these various branchiopod stocks was not a brachiopod, and brachiopods form a grade, not a clade. It appears necessary to raise the articulates to the rank of phylum, and perhaps to erect several phyla among the inarticulates, in order to achieve monophyletic taxa. Another example is found among the Arthropoda, which probably take their origins from more than one vermiform ancestor (Manton, 1964, 1972) in which case the phylum will have to be split to achieve a monophyletic classification. Some other phyla may also require such splitting. Therefore the number of phyla will probably increase, and so will the advantages of organizing them taxonomically into allied groups.

A set of considerations that is of particular interest to paleontologists concerns those fossil organisms that do not fall into any of the living phyla. Such remains are commonly unskeletonized body fossils that have had exceptional histories of preservation. They appear to be particularly common in the late Precambrian Ediacara beds (Glaessner and Wade, 1966). Classing such fossils as Animalia or Metazoa is not very helpful, and calling them "annelid-like" or using some other informal descriptive phrase may be quite misleading. To assign them to a superphylum, when possible, would be much more appropriate and satisfactory. Today most of the superphyla contain a vast diversity, but in the late Precambrian they probably embraced only modest numbers of lower taxa and formed the natural major subdivisions of animals, since they preceded

the evolution of the ground-plans that characterize most of the skeletonized phyla (Fig. 1B). Even after the appearance of modern phyla in the early Paleozoic, some problems arise in assigning some extinct groups to modern phyla, both among skeletonized forms (such as the tentaculitids) and among the unusual soft-bodied fossils such as are represented in the Middle Cambrian Burgess shale (Whittington, 1969 and personal communication), and even as late as the Pennsylvanian (Richardson, 1966).

One additional important use for the superphylum category is to provide a taxonomic receptacle for very early lineages for which we do not now have (and probably never shall) any actual fossil remains excepting trace fossils. The superphyla should certainly not be based upon imaginary organisms, but once defined they may serve to embrace the concepts of appropriate primitive lineages of soft-bodied forms that preceded the recorded phyla.

COELOMATE SUPERPHYLA

Five coelomate superphyla are suggested (Fig. 1B). The Metameria include the Annelida, Arthropoda, Onychophora, and other primitively eumetamerous lineages that share common ancestors with these groups. Epifaunal radiation within the Metameria evidently produced new phyla such as the Arthropoda well before the advent of Cambrian time (see Glaessner and Wade, 1966). The Lophophorata (Tentaculata of Hatschek, 1888 and others) include the Phoronida, Brachiopoda, Ectoprocta, and other oligomerous lineages that share common ancestors with these groups. The Deuterostomia include the Echinodermata, Chordata, and the usual groups of oligomerous lineages that are believed to share common ancestors with these phyla. Presumably the developmental peculiarities of the deuterostomes, including the cleavage pattern, arose in a primitive common ancestor. The Molluscata are monotypic, including only the Mollusca but potentially

including any coelomates that share a common pseudometameric ancestry with them. Actually, the distinctiveness of the molluscan classes rivals or surpasses the distinctiveness of the lophophorate phyla. And finally the Sipunculata, also monotypic so far as is known, includes the phylum Sipunculida and any lineages that share a common ancestral ground-plan and a common origin with them. This is the least diverse of the suggested superphyla by far. Nearly all these superphyla have some special importance; Metameria are most diverse on land at present; Lophophorata dominated Paleozoic benthic shelf communities; Molluscata are most diverse in the sea at present; and the Deuterostomia have produced us. Only the Sipunculata have no special claim to fame. The groupings share much in common with those of Hatschek (1888) and many later authors.

Coelomates may well be monophyletic, in which case the primitive stock of one of these superphyla is *most* primitive among them (unless the primitive coelomate stock is unknown and had an entirely distinctive coelomic architecture). It is possible to imagine any of the superphyla as ancestral, and most have been previously suggested. On the other hand, coelomates may be polyphyletic, and their interrelationships may be lost among a maze of lower metazoan ancestors. Although many investigators have despaired of ever reaching answers to the questions of phylogenetic origins at this level, such pessimism may prove unwarranted. A functional-ecological approach to the origin of higher taxa produces models of adaptive pathways that have much explanatory power and when joined with emerging information of past environmental regimes may yet serve to constrain the possibilities so that a well-supported model of coelomate phylogeny will emerge.

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