

## AN OVERVIEW OF CLADISTIC APPLICATIONS

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## ABSTRACT

Circa 2486 applied cladistic papers have been published up to the year 1992: 776 (31%) to the insects, 771 (31%) to the vertebrates, 332 (13%) to the plants, 294 (12%) to the remaining arthropods and 313 (13%) to all the remaining organisms. Most of these applications are at low taxonomic levels. A broad outline of vertebrate, insect and plant evolution has been obtained, but relationships of these groups to the remaining taxa at the next successively higher taxonomic levels have been only cursorily approached. Within the Animalia, the positions of many smaller phyla remain controversial and the closest relatives of such large taxa as the Mollusca, Arthropoda and Radialia remain unknown. Too many nonmonophyletic higher taxa still recur in the system. Lack of progress at the higher taxonomic levels may be due to (1) the reductionist belief that systems have to be built upwards from populations and species, and (2) the empiricist attitude that specimens have to be examined for the obtainment of reliable results. I suggest that it is urgently necessary to attempt a true summary of all available published holomorphological information under Hennigian principles. We may in this way more rapidly obtain a general reference system for historical biology and a sounder basis for the development of macroevolutionary theory.

**Keywords:** Reference system, hierarchy of life, Hennigian synthesis, patterns in published data, morphology and molecules, Eukaryota.

**Descritores:** Sistema de referência, hierarquia da vida, síntese Hennigiana, padrões em dados publicados, morfologia e moléculas, Eukaryota.

During the last few years phylogenetic studies are accumulating at a surprisingly rapid rate. This trend is specially fast for macromolecular analyses involving sequencing and restriction site surveys. Although morphological studies are also increasing markedly, these have declined in proportion to molecular studies, and now represent less than half of the total (SANDERSON et al., 1993). In this paper I am interested in surveying the total number of strictly Hennigian applications to the study of taxonomic diversity accumulated for more than three decades. In the 1980s a virtual consensus was reached that cladistics represented the only objective method for the reconstruction of phylogeny (MAYR, 1981). The approach has since been applied to all major groups of eukaryotes (Tab. 1).

But how far have we progressed in our view of the hierarchy of life? I have tried to summarize our present knowledge on the biological system (Tab. 1), with an emphasis on unresolved portions. The indicated numbers of papers are somewhat mechanical compilations based on titles in Zoological Records, summaries in Biological Abstracts, and personal reprint surveys. All papers that seemed to apply cladistics were included. Special emphasis was placed on morphological studies, but molecular articles were

TABLE 1 – Synthesis of the number of cladistic papers published until 1992 for different groups of organisms. To obtain total applications for a higher taxon all numbers indicated for subordinated levels must be added. Author's names are indicated for recently proposed higher taxa. Taxa within quotation marks are probably nonmonophyletic; those followed by 'inc. sed.' cannot be placed precisely in the system. I have simplified some resolved portions of the system by the indication 'several groups of ...'. Indentations indicate relative subordinations of taxa.

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Biotae Christoffersen (1989) - 0
"Virus, plasmids and other noncellular replicons", inc. sed. - 0
"Bacteria" - 1
Eukaryota - 4
Plantae - 18
several groups of algae - 25
Embryophyta - 6
several groups of bryophytes - 17
Tracheophyta - 0
several groups of pteridophytes - 14
Spermatophyta - 4
several groups of gymnosperms - 2
Angiospermae - 16
several groups of dycotyledones - 181
Monocotyledones - 49
Lichenes, inc. sed. - 4
"Fungi", inc. sed. - 16
Animalia - 0
"Protozoa" - 16
Mesozoa, inc. sed. - 0
Metazoa - 9
Porifera - 8
Endodermata Jefferies (1991) - 0
Placozoa - 0
Eumetazoa - 0
Radiata - 1
Ctenophora - 0
Cnidaria (Coelenterata) - 10
Bilateria - 0
Platelmintomorpha - 1
Gnathostomulida - 0
Platyhelminthes - 66
Rhynchocoela (Nemertea) - 4
Entoprocta, inc. sed. - 0
Chaetognatha, inc. sed. - 2
"Aschelminthes" - 31
Coelomata - 0

TABLE 1 - Continued.

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Sipuncula, inc. sed. - 3	
Echiura, inc. sed. - 0	55 - Siphonophora
Mollusca, inc. sed. - 42	several groups of fishes - 228
"Articulata" - 0	Tetrapoda - 20
"Annelida" - 42	Amphibia - 28
"†Trilobita" - 20	Amniota - 9
Arthropoda - 10	several groups of reptiles - 141
"Protoarthropoda" - 0	Aves - 78
Tardigrada - 6	Mammalia - 223
Onychophora - 1	
Pentastomida (Linguatulida), inc. sed. - 1	
Euarthropoda - 5	
Cheliceromorpha - 0	
Pycnogonida (Pantopoda) - 0	
Chelicerata - 105	
Mandibulata - 3	
"Crustacea" - 123	
Tracheata - 1	
"Myriapoda" - 19	
Insecta - 23	
Hemiptera - 83	
Coleoptera - 218	
Hymenoptera - 109	
Lepidoptera - 116	
Diptera - 131	
remaining groups of insects - 96	
Vestimentifera, inc. sed. - 0	
Rodionophora, inc. sed. - 0	
Radialia Jefferies (1991) - 0	
"Tentaculata" (Lophophorata) - 0	
Phoronida - 2	
Brachyopoda - 1	
Ectoprocta (Bryozoa) - 5	
Deuterostomia - 1	
†Graptolithina, inc. sed. - 2	
"Hemichordata" - 0	
Dexiothetica Jefferies (1988) - 3	
Echinodermata - 26	
Chordata - 12	
†Conodonts, inc. sed. - 1	
Cephalochordata - 0	
Tunicata - 0	



TABLE 1 – Continued.

Vertebrata - 22
several groups of fishes - 228
Tetrapoda - 20
Amphibia - 49
Amniota - 9
several groups of reptiles - 141
Aves - 79
Mammalia - 223

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included when based on parsimony methods of data analysis. Phylogenetic analysis of molecular data by distance, cluster, neighbour joining, maximum likelihood, and other tree-building algorithms were excluded from these counts. Evidently, such a compilation must contain both underestimations — cladistic papers unknown to me — and overestimations — papers that under closer scrutiny would not be judged to be truly Hennigian in outlook.

Under the considerable restrictions noted above, the present compilation (Tab. 1) may still reflect or suggest some important aspects and trends of the present state-of-the-art in cladistics.

Most remarkable from the table is the small amount of papers establishing relationships across taxa traditionally ranked as phyla, divisions and kingdoms. I find this scarcity of broad perspective in the applications quite disappointing, particularly because HENNIG (1950) showed so convincingly that his method was useful at all levels of inquiry in historical biology. Within systematics he himself was interested not only in the broad features of dipteran phylogeny (HENNIG, 1973), but also in insect (HENNIG, 1981) and metazoan phylogeny (HENNIG, 1980, 1983). When one remembers that the Hennigian method is available for a full generation span, progress in our knowledge of the hierarchy of life in space and time, on a broad scale, seems to be quite limited.

So limited, in fact, that there is a growing belief among systematists that morphology is incapable of resolving phylogenetic relationships at the highest taxonomic levels. Many are convinced that the only way to know the broad evolutionary history of living beings is through the application of the latest sophisticated techniques of biochemical systematics (e.g. HILLIS and MORITZ, 1990). I find such a reductionist view almost preposterous: no single molecule, in principle, is adequate as a criterion to reconstruct the history of the evolution of a group of living beings (MARGULIS, 1990: 809). Furthermore, in sexual organisms only nonrecombinant maternally inherited alleles or fixed attributes will form hierarchic patterns above the species level (DAVIS and NIXON, 1992: 422). Thus the greatest responsibility for phylogenetic reconstruction still remains with systematists.



Another outstanding feature in Tab. 1 is that cladistic methods are applied almost exclusively to groups of interest to specialists, rather than to groups of particular importance to the uncovering of the history of life. Of the 2486 published papers, 776 (31%) apply to the Insecta and 771 (31%) to the Vertebrata, accounting together for almost two-thirds of the total. Plants received another 332 papers (13%), followed by 294 (12%) for the remaining arthropods. That leaves 313 papers (13%) for all of the remaining organisms. Interestingly, broad phylogenies are largely resolved within vertebrates, insects and plants, but the relationships of these groups to the remaining taxa at the next successively higher taxonomic levels are still controversial and only cursorily approached.

Actually, the majority of cladistic works are even more specialized than the present tabulation is able to show. Although some outstanding papers evidently provide saltatory progress in our knowledge independently of level it is obvious that many published cladograms are only appendages or afterthoughts to traditional monographic studies. Others are based on a restricted set or only one particular kind of data. The great majority of papers apply to single genera or species-groups. While such a taxon as Coleoptera may appear to be relatively well studied for containing the largest number of applications within the insects (218), most of these are low-level analyses. We still lack solid hypotheses for a complete phylogeny of such major taxa as the Coleoptera, Hemiptera and Hymenoptera.

I suggest that our lack of progress at the higher taxonomic levels is largely due to two prejudices inherited from traditional taxonomy: (a) the persistent reductionist belief that biological systems have to be built upwards starting with populations and species; (b) the widespread inductivist and empiricist attitude that biological specimens always have to be examined in cladistic analyses for the obtaining of objective data and reliable results.

I believe that just the opposite trends are the most necessary for quicker progress: (a) high-level phylogenies are most urgently required for adequate polarizations of characters in lower-level studies; (b) the primary literature may be most profitably used as the empirical knowledge on which to base phylogenetic inferences at the highest taxonomic levels.

When broader level phylogenies are attempted, it is a common practice to select representative specimens for whole genera or families — even phyla or kingdoms in molecular cladistics — and then to conduct an objective analysis based on characters from those specimens alone. In principle such cladistic analyses should provide a satisfactory preliminary outline of the group. Given appropriately chosen and analyzed characters, three-taxon statements are possible for any combination of taxa. In practice, however, reliance on too small a sample or an ill-chosen portion of the available information often leads to underestimations of the true generalities of characters and consequently to incorrect polarity decisions and spurious taxa.

Construction of lower level phylogenies for diverse species groups and genera requires taxonomic expertise and examination of as much biological material as possible. This is because we need detailed information on every single species, and the published data sources, usually gathered for non-cladistic purposes, are often too

incomplete and non-uniformly recorded. But at the higher hierarchical levels, missing data on particular species become progressively less critical for recognizing a congruent phylogenetic pattern. Furthermore, our level of ignorance can always be objectively coded in data matrices. In any case, the establishment of approximately correct levels of the generality of characters and the recognition of extended transformation series, particularly at high levels of diversity, requires broad perspective and perceptive interpretation, rather than taxonomic specialization and empirical observation. It may be wise in some cases to value imperfect cladistic hypotheses in contrast to perfect ignorance.

Unfortunately, the value of good taxonomic literature for the construction of broad phylogenies has been underestimated. Detailed illustrations are particularly useful because enormous quantities of empirical data may be assessed at a glance, especially when adequately organized onto pictorial plates.

By literature work I do not mean that such simplistic textbook approaches as those of BRUSCA and BRUSCA (1990), SCHRAM (1991; also in MEGLITCH and SCHRAM, 1991) and EERNISSE, ALBERT and ANDERSON (1992), based largely on secondary literature, are entirely satisfactory. No matter how objective and orderly such data matrices and final cladograms may appear, these attempts do not really advance our phylogenetic knowledge on any solid grounds. It does not make much sense to produce cladograms of fictitious groups like the "Invertebrata", "Spiralia", "Protostomia", "Eutrochozoa", "Articulata", "Annelida", "Polychaeta" and "Crustacea". Also, just too many taxa and traditional characters are simply left out of the data matrices. But the main problem with such attempts lies in the shallowness of the presence-absence character matrices, with hardly no regard for the extended transformation series which must become evidenced both within and across very diverse basic plans.

Although EERNISSE et al. (1992) have provided a useful historical summary of metazoan phylogenies in the form of cladograms, I cannot accept that such characters as spiral and radial cleavage, metameric and trimeric body plans, schizocoelous and enterocoelous coeloms, should represent six independent characters, rather than three transformation series, with the implication that the spiralian groups do not form a monophyletic taxon. In my opinion, *FX* (1989) and JEFFERIES (1991) provide more solid, even if less quantitative, hypotheses for the systematization of the Metazoa. In systematics, it will always remain a truism that "garbage that has been thrown at a computer" (GHISELIN, 1993) or any kind of ill-chosen or poorly analyzed data — even expensive molecular data — will result in crap and cannot be expected to produce a convincing phylogenetic hypothesis.

Of course, the study of "all" published holomorphological information for a given group can only be approached in a piecemeal and somewhat exploratory fashion, while only part of the results will be satisfactorily interpreted in any one analysis. But phylogenetic logic provides objective ways of choosing key portions of the hierarchy on which to focus detailed examination. For example, Mollusca is a major group of Metazoa, with a higher diversity (50,000 species) than all of the Vertebrata (40,000 species) (BARNES, 1987). Remarkably few cladistic analyses (42) have been applied to this group and the majority of these deal with terminal groups of Gastropoda, particularly



pulmonates. Furthermore, there is notable controversy on the positioning of the Mollusca in the biological system, with opinions ranging from acoelomate flatworm origins to coelomate metamerism-worm origins. But if we can accept a few guiding principles, for example that Conchifera is subordinated to a larger monophyletic Mollusca (LAUTERBACH, 1983; SALVINI-PLAWEN, 1984), then a detailed study of all that has been published on the circa 250 species of aplousobranch molluscs (BOSS, 1982) — a manageable diversity — should be rewarding. Knowledge on this neglected group will be paramount not only for the resolution of a framework for molluscan phylogeny, in which Conchifera will represent but one specialized branch, but also for a more meaningful search for the closest relatives of the Mollusca.

After more than 40 years of cladistics we know a little more about the phylogeny of the groups that most interest biologists (vertebrates, insects, and plants), but are still not able to answer important questions such as: (a) where do the various groups of viruses and their allies come from? (b) how and where do we include the symbiotic lichens in the system?; (c) how many groups of fungi and protists do we have and where do they fit into the system? (d) which are the closest relatives of such major lineages as the Arthropoda, Mollusca and Radialia? (e) why do such obvious candidates of nonmonophyly, like "Virus", "Bacteria", "Monera", "Prokaryota", "Protista", "Protoctista", "Protozoa", "Invertebrata", "Pseudocoelomata", "Aschelminthes", "Protostomia", "Spiralia", "Trochozoa", "Schizocoela", "Articulata", "Annelida", "Polychaeta", "Oligochaeta", "†Trilobita", "Protoarthropoda", "Crustacea", "Myriapoda", "Lophophorata", and "Hemichordata" keep popping up even in the works of cladists?; (f) where do such minor phyla as the Mesozoa, Entoprocta, Chaetognatha, Sipuncula, Echiura, Pentastomida (Linguatulida), Vestimentifera, Pogonophora, and †Graptolithina definitely belong?

I think it is time some of us leave our pet groups aside and concentrate work where it is most needed. Metazoan phylogeny basically involves establishing a plausible sequence for the free-living, marine, vermiform groups, into which the skeletonized, colonial, terrestrial, parasitic and other diversely specialized groups will be conveniently fitted. Nonparasitic worms are precisely the most neglected zoological groups by taxonomists and cladists alike.

If more of us would join the effort of attempting an honest synthesis of available biological information under Hennigian principles, we would be contributing more effectively to the completion of the indispensable general reference system for biology and to the faster development of macroevolutionary theory. Towards this aim we do not have to wait until all the tropical beetles and mites become described, nor neglect everything that has been published as unreliable, neither start collecting specimens and examining museum material from scrap, or even abandon comparative morphology in favour of an exclusively molecular approach to phylogeny reconstruction.

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