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Points of View

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The Growth of Phylogenetic Information and the Need for a Phylogenetic Data Base

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In the wake of widespread acceptance of phylogenetic methods, it is appropriate to assess how fast phylogenetic knowledge is accumulating. To obtain a rough indication of this rate, we surveyed phylogenetic analyses in the recent literature. The results raise an important information management issue. The volume of phylogenetic information now becoming available may soon compel the systematics community to confront its own rapidly expanding knowledge base in a deliberate and concerted manner. In this note, we present quantitative evidence regarding the growth rate of phylogenetic information and then argue for the establishment of an electronic data base of phylogenetic data and results.

Preliminary surveys (Sanderson and Donoghue, unpubl. data) indicated that the number of phylogenetic studies has grown steadily in recent years. This finding prompted us to gather data on the three most recent years for which complete in-

formation could be obtained, 1989, 1990, and 1991. We surveyed the literature using a three-step procedure. First, a computeraided search of the BIOSIS (1990) data base was used to generate a list of prospective journals. Searches using keywords such as 'phylogenetic analysis,'' "cladogram," and "cladistic analysis" uncovered citations from 139 journals. This list of journals was then supplemented by ourselves and suggestions from colleagues. Next, these journals were searched page by page for articles in which a tree was presented. A few journals with many pages per volume (Nature, Science, Journal of Biological Chemistry, Proceedings of the National Academy of Sciences USA) were searched by examining their tables of contents for relevant titles. Third, each article was examined relative to a set of selection criteria designed to avoid including intuitive or redundant analyses. A data matrix must have been included in the paper (or cited elsewhere), and an explicit phylogenetic algorithm must have been used (parsimony, maximum likelihood, distance methods, neighbor joining, or Lake's method). Phylogenetic studies published in books, nonserial monographs, or symposium volumes were not included, mainly because of the difficulty of developing thorough search strategies. For each analysis, we recorded the

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citation, type of data, taxon, and tree-building algorithm used.

The survey was neither a complete census nor a random sample. Many journals were undoubtedly omitted, including those that publish phylogenetic studies rarely, are less widely known (particularly non-English ones), or are in fields less familiar to us. Most of us are botanists, and the botanical literature may have been surveyed more completely than the literature on other taxa (see Appendix). Some issues in several journals were not examined because the volumes were missing from the library at the time of the survey. The effect of these errors is to underestimate the rate of accumulation of phylogenetic data.

RESULTS

Information was recorded on 882 phylogenetic analyses published in 76 journals (Appendix). The large number of journals publishing phylogenetic work reflects the magnitude and diversity of interest in phylogenies. About a dozen journals that publish phylogenies frequently published fully half of all analyses; the other half were published in journals that publish phylogenetic work less frequently or publish smaller volumes. Among the five journals publishing phylogenies most often, only one, Systematic Botany, is a "systematics" journal. Occupying the leading two places are Journal of Molecular Evolution and Molecular Biology and Evolution, which underscores the central role that phylogenetic inference is playing in molecular evolutionary studies. Journal of Molecular Evolution published more phylogenies than the three top "systematics" journals combined (Systematic Botany, Copeia, and Plant Systematics and Evolution)—just under 10% of all phylogenies published during the study years. Evolution came in fourth, again ahead of the systematics journals. Systematic Zoology (as it was called during the study years) ranked 17th, which is not surprising given its emphasis on conceptual issues of broad interest regardless of taxon (see editorial policy expressed in Syst. Zool. 39: 187–191 and Syst. Biol. 41:1–3).

Despite the great interest in molecular

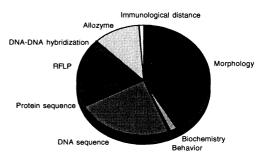


FIGURE 1. Proportion of phylogenetic articles (i.e., those using phylogenetic algorithms) relying on various kinds of data to reconstruct phylogenies (see text). RFLP = restriction fragment length polymorphism data.

data (e.g., Hillis and Moritz, 1990; Soltis et al., 1992), morphological phylogenetic studies account for almost half of the studies (Figs. 1, 4). Next most frequently used were DNA sequence data, followed by restriction site and allozyme data, DNA-DNA hybridization data, and behavioral and biochemical (excluding information macromolecular) data. One potential artifact is that studies (articles) were counted rather than some more precise measure of the amount of data (such as the size of the character-taxon matrix). This possible bias was especially worrisome for sequence information because a significant number of articles that use sequence data actually added only one or a few new sequences to the existing literature, relying on previously published data for most of the data matrix. Better estimates of the rate of accumulation of sequence data might be obtained from the rate of growth of data bases such as GenBank (Burks et al., 1990), although most sequences accessioned in those data bases are unaligned and therefore not immediately amenable to phylogenetic study.

By far the most common method for reconstructing phylogenies was parsimony (Fig. 2), accounting for 60% of the analyses (the number of "analyses" is greater than the number of "studies" because some studies included multiple analyses using different algorithms). A significant fraction of the parsimony analyses (20%) used manual parsimony or "Hennigian argu-

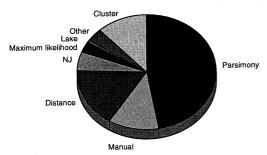


FIGURE 2. Proportion of analyses employing various algorithms to reconstruct trees. The number of analyses is greater than the number of articles because many articles included more than one analysis (usually using different algorithms). Cluster analyses were recorded only when found in articles with other explicitly phylogenetic analyses. NJ = neighbor joining; Manual = manual parsimony.

mentation." Manual reconstruction was mostly confined to insect and vertebrate studies and was never used in data sets with more than a handful of taxa. Distance methods (excluding neighbor joining; Saitou and Nei, 1987) were the next most common algorithm (16%), used especially with sequence and allozyme data. Neighbor joining accounted for 5% of all analyses. Maximum likelihood (e.g., Felsenstein, 1981; Kishino and Hasegawa, 1989) was

used less often (3%), usually in conjunction with other methods. Lake's algorithm (Lake, 1987) was only used in 0.6% of analyses, but this percentage may reflect its current restriction to data sets with very few taxa. A diverse array of other methods was found in 4% of the studies. These methods include those that are familiar but now out of fashion, such as compatibility analysis, and specialized phylogenetic methods developed by the authors of the study but not used widely elsewhere.

The diversity of organisms that have been the subjects of phylogenetic study is remarkable (Fig. 3): from nematodes to colonial green algae to influenza viruses to a fossil Magnolia. Yet despite the breadth of organisms studied, several taxonomic biases were evident. Most of the studies fell into one of three clades: insects, vertebrates, and angiosperms, but a significant number occurred in the paraphyletic "rest of life." Various "fungi," "algae," "bryophytes," nonangiosperm vascular plants, and nonarthropod invertebrates were seriously underrepresented in comparison to their species diversity (Fig. 3). Thus, mammals, a group with some 5,000 species, were studied five times as often as fungi, which

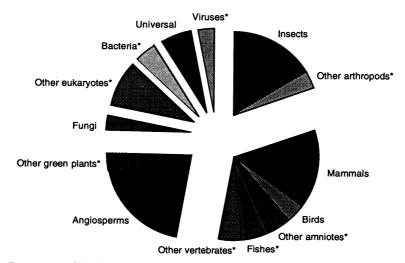


FIGURE 3. Proportion of phylogenetic studies focused on various taxonomic groups. Groups marked by asterisks are probably paraphyletic. "Universal" refers to studies with a taxonomic scope so broad that it corresponds to most of life (e.g., certain molecular phylogenetic studies of highly conserved genes, such as 16S ribosomal RNA).

may include 100,000 species (Margulis and Schwartz, 1982). However, bacteria, a comparatively less diverse group, were studied surprisingly often, possibly in large part because of the utility and accessibility of homologous ribosomal RNA sequences.

Taxonomic biases also emerged within the three major clades. Mammals made up just under half of all vertebrate studies, with primates comprising 24% (=32 studies) of mammals and hominoids comprising 66% of all primates. Within angiosperms, there were 30 studies of Asteraceae (ca. 20,000 spp. [Cronquist, 1981]), and 15 of Fabaceae (17,000 spp.), two of the largest families, but only 4 studies of Orchidaceae (20,000-30,000 spp.). Primates and Asteraceae were each studied more often than were all fungal groups combined. Within insects, the most studied taxon was the order Diptera (46 studies), but half of these studies were of the single large genus Drosophila; other large orders received less attention: Coleoptera (33), Hymenoptera (20), and Lepidoptera (9).

The rate of publication of phylogenetic studies averaged 294/year, increasing by 20% in 1990 and 16% in 1991 (Fig. 4). The rate increase held among all major taxonomic groups and types of data. Macromolecular analyses involving sequencing and restriction site surveys increased especially fast, but the rate of accumulation of morphological studies also increased markedly (Fig. 4). However, as a proportion of all studies per year, morphological studies have declined. The sampling bias introduced by sequence studies that actually involved very little new data may account for part of this trend, but this is impossible to discern without a more accurate assessment of the rate of accumulation of information as opposed to studies of phylogenetic trees.

DISCUSSION

The most striking result of this survey is the increase in the rate of accumulation of phylogenetic data in 1989–1991. It is difficult to imagine how the sampling strategy could have been biased in such a way that a false increasing trend would emerge

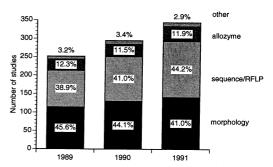


FIGURE 4. Phylogenetic studies surveyed for the period 1989–1991. Within each year, the type of data used is expressed as a proportion of the total for that year.

(one reviewer did suggest that the trend toward publishing shorter papers and reanalyzing previous work might explain this pattern, but such sociological processes would have had to increase exceptionally rapidly in a short period of time). Moreover, the estimates of rate of accumulation can only be underestimates of the true rates, given the many studies that have been published outside of journals. Thus, phylogenetic studies are accumulating at a surprisingly rapid rate, and the rate itself has increased markedly even over the brief time span considered here.

Paradoxically, despite this burgeoning information base, we systematists remain poorly equipped to answer certain basic questions about the state of knowledge about the phylogeny of life. It will soon become a hindrance and may even become something of an embarrassment that the systematics community cannot provide a cogent assessment of the current state of phylogenetic knowledge. One problem is that the tools to make inferences across phylogenetic studies are not presently available. For example, despite great interest in methods for combining different kinds of data for the same taxa (e.g., Kluge, 1989; Doyle, 1992), little attention has been paid to the problem of combining data sets on different taxa—either studies of the same group using different exemplars or studies on entirely different groups (although, see Finden and Gordon [1985] for consensus methods aimed at representing taxa common to several studies). The phylogenetic literature includes studies at all levels in the hierarchy of life, and informative synthetic statements about the phylogeny of life can only be made if methods are developed for integrating studies across taxa.

However, even if such tools were to appear tomorrow, a more basic practical problem would hinder progress: inaccessibility of the relevant studies in an easily retrievable form. Imagine the difficulty of acquiring all the relevant data sets from the literature on vertebrates or angiosperms, for example. Even if an investigator were willing to spend the time and resources to find the relevant studies, he or she would then be faced with the prospect of entering the data into a computer so that synthetic analyses could be undertaken. A computerized data base of phylogenetic data and trees would relieve interested investigators of routine tasks such as data reentry.

Similar issues confronted the molecular biology community with regard to the rapid accumulation of DNA and protein sequence information. They responded by establishing computer data bases and by aggressively enforcing the electronic deposition of data as a corequisite of publication (Burks et al., 1990; Cinkosky et al., 1991). The rapid accumulation of phylogenetic data makes a compelling case for similar measures. An effort to establish a data base of phylogenetic studies would catalyze standardization of formats for data matrices, trees, and character and taxon information and would stimulate efficient means for the transmission, storage, and retrieval of phylogenetic information, making it readily accessible both to the systematics community and to the largest number of interested scientists outside of systematics. A phylogenetic information system would permit sophisticated queries and searches not possible (or at least extremely impractical) by traditional means. It could also serve as a useful link to the molecular sequence data bases. The reciprocal flow of information between these systems would benefit both.

The practical problems in establishing

such a data base are many. Entry, annotation, and maintenance of data would require a sustained commitment of personnel. The endorsement of journal editors would be an essential element in providing a tangible motivation for electronic deposition of data sets. A significant initial investment would be required to develop standard data formats, allocate computer resources, and establish protocols for standardization and submission. Because much phylogenetic research will continue to be undertaken on a variety of computers, the issue of cross-platform standardization will be critical. The flexibility of the "Nexus" file format used in PAUP 3.0 and MacClade 3.0 provides one possible starting point, but it is limited to discrete character data and requires access to a Macintosh or to a UNIX system running PAUP. Nomenclatural issues regarding the terminal taxa will be important, because these names provide both for retrieval of phylogenies and connection to other phylogenies at lower or higher taxonomic levels. In short, the task of establishing this data base is something that would require a significant investment and hence a commitment from the systematics community as a whole. We have established a small computer data base of information on the studies reported here, including bibliographic information and broad information on the characteristics of the studies (but lacking data sets or trees). Even this primitive, preliminary data base has proven useful for retrieving studies on particular taxa or kinds of data (such as particular genes) for research and teaching purposes.

Awareness of and access to a computer data base of phylogenetic data will become critical as interest grows in the use of phylogenies outside of systematics. For example, students of coevolution will want access to phylogenies of particular kinds of organisms. Ready access to a wide array of phylogenies would facilitate the study of general patterns of character evolution, such as homoplasy (e.g., Archie, 1989; Sanderson and Donoghue, 1989; Sanderson, 1991, 1993; Janson, 1992; Brooks and McLennan, 1993) and correlation (e.g.,

Donoghue, 1989; Maddison, 1990; Martins and Garland, 1991), and the study of evolutionary success and general patterns of evolutionary diversification (Mitter et al., 1988; Guyer and Slowinski, 1993) and evolutionary rates (Cracraft, 1984). Knowledge of the availability of phylogenies could substantially alter the design of all such research. A phylogenetic data base would also facilitate the comparison of results based on different sources of data (e.g., Bledsoe and Raikow, 1990; de Queiroz and Wimberger, 1993) and would encourage the combination of data sets on particular taxa (Kluge, 1989; Barrett et al., 1991; Doyle, 1992).

The utility of such a phylogenetic data base for systematists interested in higher level phylogenetic synthesis is also clear. However, for systematists less interested in making statements across taxa outside of their particular group, the availability of such a data base might initially seem of limited value. Experts on particular taxa are presumably well aware of relevant studies. However, the broadening of scope entailed by outgroup analysis inevitably leads to progressively less familiar groups and less familiar literature, and the search for outgroups would be aided by access to a phylogenetic data base. Systematists interested in developing and testing new methods of data analysis, algorithms, or computer programs could also take advantage of an extensive supply of test data from actual studies (e.g., Platnick, 1989; Maddison, 1991). Use of area cladograms to reconstruct biogeographic history would be facilitated by instant access to all the phylogenies of taxa found in particular geographic areas (Nelson and Platnick, 1981; Page, 1988). Finally, a phylogenetic data base would be an invaluable tool for identifying critical taxa in need of research and for developing a comprehensive, longterm strategy for reconstructing the phylogeny of life.

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APPENDIX

The following is a list of 76 journals publishing phylogenetic analyses. These journals were found in a literature survey for 1989–1991, and the number of studies published in that period is indicated in parentheses. Journal abbreviations are according to Serial Sources for the BIOSIS Previews Database (BIOSIS, 1990)

J. Mol. Evol. (84), Mol. Biol. Evol. (58), Evolution (46), Proc. Natl. Acad. Sci. USA (46), Syst. Bot. (36), Copeia (24), Zool. J. Linn. Soc. (24), Am. J. Bot. (23), Plant Syst. Evol. (22), Am. Mus. Novit. (20), Nature (20), Ann. Mo. Bot. Gard. (19), Can. J. Zool. (19), Genetics (18), J. Nat. Hist. (18), Syst. Entomol. (18), Syst. Zool. (18), Bull. Am. Mus. Nat. Hist. (17), J. Mammal. (16), Z. Zool. Syst. Evolutionsforsch. (16), J. Bacteriol. (15), Cladistics (14), J. Virol. (14), Ann. Entomol. Soc. Am. (13), Int. J. Syst. Bacteriol. (13), Can. J. Bot. (11), J. Phycol. (11), Auk (10), Herpetologica (10), J. Parasitol. (10), J. Biol. Chem. (10), Proc. Entomol. Soc. Wash. (10), Quaest. Entomol. (9), Science (9), Bot. J. Linn. Soc. (8), Condor (8), Trans. Am. Entomol. Soc. (Phila.) (8), Can. Entomol. (7), J. Herpetol. (7), J. Zool. (7), Opera Bot. (7), Taxon (6), Aust. Syst. Bot. (5), Entomol. Scand. (5), J. Evol. Biol. (5), J. N.Y. Entomol. Soc. (5), Mycologia (5), Phycologia (5), Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr. (4), Heredity (4), J. Crustacean Biol. (4), Ann. Soc. Entomol. Fr. (3), Bull. Br. Mus. (Nat. Hist.) Entomol. (3), Blumea (3), Brittonia (3), Bryologist (3), Malacologia (3), Mem. N.Y. Bot. Gard. (3), Mycol. Res. (3), Nord. J. Bot. (3), S. Afr. J. Bot. (3), Syst. Parasitol. (3), Veliger (3), Wilson Bull. (3), Am. Fern J. (2), Aust. J. Zool. (2), Beaufortia (2), Invertebr. Taxon. (2), Mycotaxon (2), N.Z. J. Zool. (2), Paleobiology (2), S. Afr. J. Zool. (2), Bull. Br. Mus. (Nat. Hist.) Bot. (1), J. Arnold Arbor. Harv. Univ. (1), Malacol. Rev. (1), Smithson. Contrib. Zool. (1).