

FORUM

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THE SIXTH ANNUAL MEETING OF THE WILLI HENNIG SOCIETY

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The sixth annual meeting of the Willi Hennig Society convened November 7-10, 1986, at the American Museum of Natural History in New York City, under the joint sponsorship of the AMNH and the New York Botanical Garden. Roughly 220 people registered, and 41 talks were scheduled. As in the past, most of the meeting was allocated to symposia: Phylogenetic Packages for Microcomputers, Multistate Characters in Cladistic Analysis, Botanical Cladistics, and Primate Phylogeny. One day of contributed papers was scheduled.

The symposium on cladistic software featured five speakers. Wayne Maddison ("MacClade: A graphic and interactive program for analyzing character evolution . . .") introduced the next version of MacClade (2.0, co-authored with David Maddison), which runs only on Apple MacIntosh microcomputers. Unlike all other phylogenetic packages, his program is not designed primarily to find parsimonious trees (although it includes a local branch-swapping Wagner parsimony algorithm), but rather to enable the investigator to manipulate trees, and to investigate character evolution as constrained by a specified taxon cladogram.

This program makes heavy use of the MacIntosh's screen-oriented, mouse-enabled mode of interaction. One can rearrange the cladogram at will, and the program automatically optimizes the data set on the new tree, and displays tree statistics (length, consistency index), the tree, and/or the data matrix in a variety of output styles. The program maps selected characters on the tree, and specifies ambiguous and unambiguous character states at nodes. The program currently handles a maximum of 80 taxa and 200 characters, 10-state integer characters, missing data, polymorphisms, and unordered, irreversible, or ordered (nonlinear as well as linear) character-state trees. As always, the logic of transformational hypotheses is still the user's responsibility. Plans are afoot to allow character-state trees that include closed loops (and hence provide more than one way to arrive at a given state), as well as asymmetrically weighted bidirectional changes on character-state trees. For all the people who tire of running analyses, watching them crash, re-running analyses, coding user-input trees, re-running analyses, mapping output back onto results, re-running analyses, re-coding transformations, re-running analyses, and generally exploring what some optimum actually implies—this program is the first to address their needs efficiently. MacClade is the spreadsheet of phylogenetic packages: the cladogram provides the formula, and the bottom-line implications of a particular character, coding change, parsimony criterion, or branch swap, are instantly displayed. The MacIntosh's attention to graphic style means that results can be output directly to a laser printer.

David Swofford ("PAUP: A computer program for phylogenetic analysis under parsimony") talked about his new version (3.0) of micro PAUP. While the previous release of PAUP was a modified version of the mainframe program, the new version will be completely re-written. Both the old and the new version of PAUP are traditional phylogenetic packages, in that a chief purpose is to find shortest-length cladograms.

Exact solutions are possible for up to 20 taxa (in the current version, 2.4.1), but therefore, global branch-swapping and hard work are the only recourse. The new version will have no intrinsic limits on the size of the data set. It will include other parsimony criteria (e.g., Dollo), an option that merges fully bifurcating trees that become identical when zero-length branches are collapsed (rather than outputting them all, as did earlier versions), and will automatically code character-state trees, if a matrix of the step lengths of character state transitions is supplied. This last feature is a major novelty, like the closed-loop character-state trees mentioned above, because the matrix need not be symmetric. One can specify, for example, 3 steps for an A to C change, but 1 step for a C to A change; possible uses include ontogenetic truncations, or gain versus loss of complex characters. The new version will also include a monitor of progress, so one can tell whether the program is hung up, or merely thinking, and it will not require a math coprocessor chip.

Steve Farris ("HENNIG-86: An MSDOS program for phylogenetic analysis . . .") spoke briefly about his microcomputer package, HENNIG-86, but as it is not finished yet, he mentioned only a fast, small, efficient, non-branch-swapping Wagner parsimony algorithm called SHEN. Instead he concentrated on a proposed improvement over both the ancestor function (Farris, 1970) and nested parentheses style of tree input. His new method, supported by HENNIG-86, uses five symbols to group taxa and to describe tree structure. Input trees will be easier to code, easier to read and proof, and polychotomies are allowed. HENNIG-86, like the more recent versions of PHYSYS, also accepts alphanumeric names for characters. Like PAUP 3.0, HENNIG-86 will not require a math coprocessor chip.

Norman Platnick ("An empirical comparison of microcomputer parsimony programs") presented the results of his benchmark comparison of programs for IBM PC-style machines. Because HENNIG-86 was incomplete, he was forced to limit the study to PHYLIP 2.8 and 2.9 (by J. Felsenstein), PAUP 2.4.0 and 2.4.1, and SHEN. One may hope that he will update his tests to include the programs previewed at these meetings: PAUP 3.0 and HENNIG-86. He ran the same 25 data sets as Luckow and Pimentel (1985), but included 10 more that had missing data (a problem not all packages could handle in 1982) and 10 others with weighted characters. Detailed comparisons were presented in 14 tables, which I won't bother to summarize here, except to say that run times varied from 7 seconds (7 taxa, 16 characters) to about 21 hours (36 taxa, 77 characters). Obviously, mainframe computers are still desirable for large or complex data sets, but mainframe programs will probably lag behind micro versions in terms of innovations. Basically, PAUP is the most deluxe and most powerful package currently available, but it only runs on IBM compatible systems. PHYLIP will run on virtually anything (the "Volkswagen" of packages, according to its author), but trades power and efficiency for that portability. PAUP generally gets results quicker, sometimes dramatically so as compared to PHYLIP. It seems to find shorter trees more easily than PHYLIP. Bill Fink (1986) came to similar conclusions. With its 24 distinct programs, PHYLIP is certainly a more diverse package than PAUP, and it sometimes works startlingly well, but on the whole it is trickier to get quality results, and more time-consuming to use. PHYLIP is free, but PAUP costs \$50.00. No word yet on the cost of HENNIG-86.

Compared to MacClade, even PAUP is clunky, because the ROM features of the MacIntosh surpass those in IBM-style machines. On the other hand, Swofford announced an intention to provide PAUP for the MacIntosh, which would make IBM hardware a distant second choice. All micro packages are trending toward increased flexibility in data format, and increased tolerance of simultaneously active software. As yet, no program allows one to change, add, or delete a character or taxon without resubmitting the data set for analysis, but MacClade is close. At the similar symposium held at the Society for the Study of Evolution meeting in New Hampshire, the major programmers

(except Farris, who was absent) decided to agree on a single, nested parentheses-style format for input trees. If Farris's innovations in tree-coding prove to be an improvement, one may nevertheless hope that other programmers will support his notation, even if only as an option.

Finally, most programmers are paying greater attention to publication-quality output, whether via laser printer or plotter. None has yet solved the difficult problem of plotting characters on trees, possibly beatifying the discouraging proliferation of naked cladograms. Another trend on the software level may reflect an emerging cladistic consensus about data and algorithms—the micro packages favor, in various ways, integer coding and Wagner parsimony. It may be of interest to note that Felsenstein (who was invited, but was not able to participate in the Hennig Society symposium) has distributed about 600 copies of PHYLIP (main and micro), Swofford about 250 copies of PAUP (main and micro), and Maddison about 100 copies of MacClade; the population of numerical cladists is probably a fairly large proportion of active taxonomists.

William Day ("The myth of optimality in phylogenetic inference") reviewed why NP-complete optimization problems are difficult, and noted that he has shown that most problems in phylogenetic inference (9 of 10 he mentioned, including compatibility analysis) fall into the same category, as identified by, among others, Foulds and Graham (1982). Computer folks regard an algorithm for solving NP-complete problems as efficient if they can do it in "polynomial" time (he didn't say what order polynomial, though), and as inefficient if they do it only in "exponential" time. No polynomial-time algorithms exist for any NP-complete problem, but if anyone finds one, probably all NP-complete problems will succumb to the same approach. Day said that many very, very rich organizations (the military-industrial complex?) containing many very, very intelligent people have been working on NP-complete problems for a very, very long time, without being able to show either that efficient search algorithms are possible, or that they are impossible. I guess that means that either good or bad news is very, very unlikely anytime soon.

The afternoon session focused on the analysis of multistate characters. Unfortunately, the symposium organizer and kick-off speaker, Mary Micevich, could not attend. Scott Miller ("An experimental approach to multistate characters") presented one of the rare autochthonous examples of transformation series analysis on morphological data, showing that the method can suggest shorter, more consilient transformational hypotheses, which an author can either accept or reject (Scott had no objections to the proposed emendations of his coding scheme). Overall tree-length obviously decreases, because the original character-state trees (tree innards, not termini) are recoded to reduce homoplasy.

Richard Holmquist ("The effect of restricted transition/transversion ratios and spatially nonuniform base substitution on pathways of DNA evolution") spoke on methods of constraining analysis of human and mitochondrial DNA sequence data by specifying transversion/transition probability ratios, and unequal nucleotide representation. He couched his discussion in an analogy to traffic problems in California; I found it hard to understand what he was saying about DNA evolution. He reported that the observed ratios of nucleotides are different from the distribution that would have been produced by presumed transition/transversion probabilities. On that basis he suggested that strict parsimony procedures should be modified by the use of physical chemical evidence to weight transformational hypotheses. However, his comments on human genome evolution seemed questionable, because his analysis was a two-taxon statement, with polarity assumed, not really argued or justified by, for example, reference to outgroups molecular data.

Charlie Mitter ("Close encounters with an ocular micrometer") spoke on the use of quantitative characters, and outlined problems in converting such data to discrete states. Some methods tend to produce autapomorphic and hence consistent states which,

however, contain little systematic information. He presented a combined data set dominated by qualitative characters which had a consistency of 0.48 among themselves; the gap-coded quantitative characters had a consistency of 0.40 among themselves; the same set recoded as continuous variates had a consistency of 0.14. However, only continuous scoring defined the groups which were well-defended by the qualitative characters. He reflected that the evolutionary interpretation (e.g., tempo of change, developmental thresholds for the appearance of a gap) of quantitative data is obscure. Imposing gaps without an underlying biological rationale is not obviously the best thing to do.

Dick Pimentel ("The properties of data for cladistic analysis") concluded the symposium by reiterating the close relationship between transformational hypotheses and the coding of multistate characters. He illustrated several common ways to misrepresent the relationship, and made a general plea for logic when coding multistate trees. Despite an affection for morphometrics, he agreed with Mitter that quantitative data generally made results murky, and extended the pessimism to multivariate statistics as well.

In comparing the morning and afternoon sessions, I was impressed that programmers have fully caught up with theorists by enabling previously unavailable ways to code character-state trees. Such notions as closed loops, asymmetric transition matrices, or close control of relative probability of reversion within single character-state trees are finally being offered by programmers. The multistate character symposium did not rise to the importance of its topic. This is the third time the Hennig Society has sponsored a symposium on character analysis, and each time the result has been less than invigorating. Beyond Mickevich's paper on transformation-series analysis (Mickevich, 1982), the field of character analysis has seen no major new ideas in at least a decade. To be sure, part of that time theorists were waiting for programmers to implement such classic options as Dollo's Law, Camin-Sokal "parsimony," polymorphisms, and partial or complete reversibility. However, it seems that the theory hasn't advanced as the programs caught up.

Some impediments are obvious. From an analytical point of view, the difference between state and character has never been clear, nor even the difference between character and taxon, analogously viewed. These are not merely definitional problems, and the current discussion has not really clarified the issue (Ghiselin, 1984; Colless, 1985; Duarte Rodrigues, 1986). The fundamental block seems to be an adequate treatment of transformation. On the one hand, it is unclear whether states, characters, taxa, or all three transform. On the other, the hierarchical structure in the data renders it unclear to what extent levels are different and require different styles of analysis. I don't know if systematists should worry about symmetry in their theory, but as it stands, cladistics is asymmetric in its treatment of taxa and characters. For example, we use recursive algorithms to identify the shortest taxon tree, but character trees are usually invariant in taxon analysis. Even the few algorithms that recursively search for shortest character-state trees accept the boundaries of characters and the existence of character states as inviolate user input. Cladograms are effects of character-state trees, which are themselves effects of definitions of states, and states are effects of transformational hypotheses. The set of perceived "states" seems to result from the traditional perception of the comparative anatomy of the group being studied, and that varies widely even between relatively closely related groups. Thus the theory is fundamentally heuristic, and perhaps it should not be surprising that advances emanate from a fundamentally heuristic source—programmers. The symposium did illustrate the breadth of the field—from nucleotide coding mutations where possibilities and probabilities can be strictly limited, to moth genitalia, where the same concepts are highly indefinite. Procedures for analyzing characters are obviously in need of comprehensive review.

The third symposium concerned botanical cladistics, organized by Kevin Nixon. By

and large this meant straightforward cladistics done on plants, a long-awaited breakthrough. For years the botanical community as a whole claimed it couldn't be done, but this symposium amply disproved that assertion. The first paper, "Gametophyte development in the Mniaceae (Musci) and its phylogenetic implications," by Steve Churchill and Brent Mishler, claimed that the modular nature of plant construction required a different method to analyze ontogeny, and that the de-differentiation in *Tortula* in particular falsified Nelson's Rule (Nelson, 1978). I wish the authors had explained more about their insights into plant ontogeny; I'm not sure why a modular plant is different from a metameric animal. D. W. Stevenson ("The challenge of finding outgroups within and outside Cycadales") reported a possibly vicariant pattern in Mexican species of *Ceratozamia*, but ultimately could not confirm it due to ambiguity in outgroup relations. Jorge Crisci ("A cladistic analysis of the genus *Cyttaria* (Fungi: Ascomyctina)") conducted a vicariant analysis on the distribution of that parasite on *Nothofagus*, but his results were also ambiguous to some extent because of questions about appropriate outgroups. Kevin Nixon ("Fagaceae: character analysis and generic delimitation") documented the polyphyletic nature of Fagaceae (*Nothofagus* is closer to Betulaceae than to Fagaceae), and reported some fascinating observations about cupule teratology; if neoteny is a problem for ontogenetic analysis, is teratology any easier? Bill Crepet ("Phylogenetic and biogeographic implications of fossil North American Fagaceae") showed that the distribution of extinct Fagaceae was considerably different from that of the modern taxa, and thus that vicariant analysis would be erroneous or incomplete if it ignored distributions of fossils. He dwelt at length on the biogeographic significance of a paraphyletic taxon *Trigonobalanus*. Finally, Chris Humphries and Pauline Ladiges ("Biogeography of western Australian Eucalyptus") presented a progress report on their work on eucalypts along the southwest Australian coast. For once in the largely stillborn history of cladistic biogeography, the investigators have done both their cladistic and geological homework, and the organisms have cooperated by displaying reasonably consilient features. The result was a richly detailed hypothesis describing the common history of eucalypts and southwestern Australia. This work will probably join the few classic demonstrations of the vicariant method. It illustrated particularly well the forbidding amount of preliminary analysis, and preliminary successes, necessary before a reasonably detailed biogeographic history can be forthcoming.

Sunday afternoon was devoted to primate phylogeny (J. Wible and H. H. Covert, "Primates as a monophyletic group"; J. Schwartz and I. Tattersall, "Tarsiers, adapids, and the reality of Strepsirhini"; P. Schmid, "Haplorhine phylogeny and tarsier relationships"; A. Rosenberger, "Cranial morphology and interrelationships of the platyrrhine primates"; T. Harrison, "Catarrhine phylogeny"; E. Delson and E. Strasser, "Cladistic analysis of cercopithecoid relationships"; P. Andrews and L. Martin, "Phylogenetic analysis of extant and extinct hominoids"; B. A. Wood and B. Chamberlain, "Early hominoid phylogeny"; N. Bonde, "Ancestors, species, subspecies; in phylogenetic analysis of hominids, and the classification of "*Homo erectus*.""). The symposium was organized by Fred Grine to focus on the order as a whole, and was the first of an anticipated series through which the Hennig Society might encourage application of cladistic techniques to various groups. For various reasons, primatology seemed to be a difficult field with which to start, not least of which is the atmosphere of evolutionary omniscience in which speculations about the ancestors and near relatives of man are often couched. Cladists, of course, are no strangers to overbearing omniscience of various kinds even within their own sociological set, but as a group they don't tolerate evolutionary narratives well; accordingly it was a lively afternoon. Also, the phylogeny of primates seems comparatively well-known, both in terms of taxa and character systems. Although no one agreed about the position of tarsiers, they did agree in large part about the rest of the cladogram, which was based on apparently well-known

data sets, and to which rather little was added in the course of the afternoon. The topics which might have aroused a Hennigian audience—cladistic method or theory, new character systems, novel results based on re-analysis of existing data, or perhaps incon-sistent but separately strong data sets, were not forthcoming. The symposium was interesting as a demonstration of the extent to which cladistic methods have been adopted in the heartland of adaptationist narration—human evolution. The jargon has arrived—synapomorphy, plesiomorphic, outgroup, etc., but much of the methodological rigor seems still to be in transit. For example, a regrettable number of the talks failed to display any data set, and instead intensively described the set of characters supporting the favored tree. Many also avoided discussion of homoplasy or character sampling, and displayed denuded cladograms without data, while concentrating on the reconstruction of “morphotypes” (features of imaginary ancestors at cladistic nodes) as an analog to synapomorphy schemes. The modern discussion of equivocal assignation of states to nodes (Mad-dison et al., 1982), quantitative analysis using explicit methods (Sokal and Sneath, 1963); Farris et al., 1970), and the useful distinction between cladograms and trees (Platnick, 1977) informed only a few of the talks. One speaker was contemptuous of quantitative analysis of data in general, a surprisingly reactionary stance. The difference between evolutionary scenarios and cladograms was often unclear, chiefly because the graphic presentation of scenarios had changed: gracefully curving but amputated tree limbs posed coyly in space are “out,” and severely functional, unambiguously connected, stick-like figures indistinguishable from cladograms are “in.” However, I thought I recognized the same old crone, even in her new designer clothes. Perhaps the guts of the analyses were left out to save time. It may also be that the low diversity of the order (a couple hundred extant species), or the relatively immense number of prior descriptive studies, permits workers to omit mention of sampling problems. If not, misunderstood cladistics may have emerged from its shadowy lair in grant proposals (if I can spell “synapomorphy” can I have the money?) to reveal itself as largely the same as old evolutionary systematics. Several of the speakers (Wible and Covert, for example) did present and analyze data quantitatively, but to me they seemed the exception, not the trend. To cap it all, throughout the symposium participants disputed a revealing controversy: can character transformations or weighting be inferred from their ecological, functional, or evolutionary importance, and do these considerations supercede morphology, ontogeny, and character concordance as criteria of homology? Most cladists would fear circularity, and instead suggest the analysis of real features on real specimens, as far as possible with process theory in abeyance, and only then evaluate the results in terms of whatever process theory is deemed to apply. It would seem obvious that the fruitful interplay of prediction and test is more assured with the latter procedure than the former, but this symposium showed that the argument is still very controversial among primatologists.

The symposium did allude to two issues of some methodological interest. Bernard Wood used phenetics to group specimens into species, and then used cladistics to diagnose and group species. If the species rank is defined as the point at which hierarchically biased analyses break down (or when reticulation becomes paramount, see below), this might make sense. Second, Niels Bonde defended specification of ancestral taxa because such identifications could be disproven by finding autapomorphies—well and good. He also took a very strict definition of fossil species—they must be distinct taxa that overlap in time and space. Taxa that don't show evidence of distinction in sympatry are to be regarded as the same species, implying, I gather, synonymy for many extinct hominoid taxa.

The best day of the meetings was probably Monday, the day for contributed papers. Mike Donoghue (“Cladistic analysis and the species problem”) argued that cladistics doesn't resolve groups when reticulation is rampant, and that reticulation is interbreeding. The flip side of interbreeding, reproductive isolation, always defines species

as a special case of autapomorphy in general. He considered evolutionary scenarios that would lead to conceptual and nomenclatorial confusion, such as paraphyletic species, but advised marking their names with an asterisk. Mark Norell ("Temporal patterns, taxonomic rates, and phylogenetic hypotheses: The effect of lineages") distinguished between groups (defined by first appearance of apomorphy) and lineages (defined by date of sister taxon), and showed through models as well as real data that estimates of the duration of taxa were different under the different points of view. M. Zandee ("Component compatibility in historical analysis") presented an enigmatic (to me, at any rate) argument for clique analysis of area cladograms. He emphasized a hypothetical data set in which he obtained shorter trees than with parsimony and component analysis. If he did this by ignoring incompatible data (as would clique analysis in general), he would have to justify that known weakness. Stay tuned, I guess. Kevin de Queiros presented the most cosmic talk of the meetings ("What is systematics?"), and concluded that much confusion had arisen from not distinguishing phylogenetics and classification. As one might expect from so broad a topic, it generated a lot of discussion, but the discussion (like the talk) turned mainly on definition of terms and goals. Steve Farris ("Consensus ultrametrics") presented a new method for producing consensus trees among cladograms with different numbers of taxa, involving an ultrametric based on a scaled advancement index for monophyletic groups. He claimed that it will avoid quirky results (such as an unresolved polychotomy because of one aberrant taxon's position in the cladogram), and should reproduce the groups that otherwise discordant cladograms still agree on. Ward Wheeler ("Molecular convergence: Cuckoo clocks and cladograms in ribosomal RNA") presented a lucid analysis of rRNA sequence data, for which he got the award for best student paper, demonstrating that substitution is not clock-like and is physiologically constrained. He further argued that to exclude homoplasy from molecular data is to conclude that holometabolous insects evolved twice. The remaining talks dealt primarily with analyses of particular groups and/or their effects on classification (J. Wolters, "Cladistic analysis of 5S rRNA and 16S rRNA secondary and primary structure . . ."; A. Wyss, "The phylogenetic affinities of the walrus and the monophyly of pinnipeds"; P. Tassy, "The classification of the Proboscidea: How many cladistic classifications"; B. B. Collette and J. Russo, "The stability of classifications and phylogenetic uncertainty: Scombroidei, a case study"; E. S. Gaffney, "A history of classification of turtles"; G. Pereira-Suarez, "Phylogenetic analysis of the fairy shrimp genus *Dendrocephalus*"; and J. Shoshani, "Mammalian phylogeny: Comparison of morphological and molecular results"). P. Tassy had only weak evidence for a particular tree, and had difficulty deciding which nodes of the cladograms should have names. Bruce Collette advised against changing classifications of economically important groups in the face of uncertainty. The speakers used methods ranging from rules of thumb such as "common is primitive," or "it is generally assumed that so-and-so is the outgroup," to the use of Lundberg rooting (Lundberg, 1972) and bootstrap subsampling (Felsenstein, 1985; Penny and Hendy, 1985) to explore the reproducibility of subgroups on a tree.

The meetings this year illustrated several things. People are certainly doing phylogenetics with an increasing variety of taxa and characters, especially molecular ones. Some talks would have been better if they had emphasized the general over the particular, but perhaps that is my personal bias. The majority of papers reported competent analyses of particular groups; the Hennig meetings are still the place to come to see phylogenetic methods applied well. Cladistic theory clearly has been codified. Does the mere sprinkling of theory papers this year reflect that, or possibly the small number of people working in the field? At any rate, the diversity of texts required to explain the theory have yet to be written. The subject therefore remains a largely oral tradition, and the meetings continue to serve their essential purpose as a forum for explication and debate.

The next meeting of the Society will convene in Stockholm at the end of August or beginning of September, 1988, annexed to a Nobel Foundation symposium focusing on theoretical and practical issues in phylogenetics.

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EMBRYOPHYTE SPORE WALLS: ORIGIN, DEVELOPMENT, AND HOMOLOGIES

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The continuing importance of reproductive characters in plant systematics is emphasized in recent phylogenetic classifications (Parenti, 1980; Hill and Crane, 1982; Crane, 1985a, b; Bremer, 1985; Dahlgren and Bremer, 1985; Mishler and Churchill, 1985). As these characters and their interpretations may be drawn from the literature of specialized disciplines, such as palynology, it is often impractical to subject them to critical reassessment in the course of broad synthetic studies. This can lead to the persistence of misinterpretations prevalent within the particular discipline. This paper is concerned with characters relating to the ultrastructural organization of the sporoderm: the wall surrounding the spores or pollen grains (microspores of seed plants; Chaloner, 1970a) of most land plants. Only exceptionally in the recent literature have sporoderm characters