

pictures of pollen and seed morphology and accompanying text would be more meaningful if augmented with a simple table outlining morphological variation for each genus. A table summarizing the key morphological characteristics of the higher groups (subtribes, tribes) would be most helpful. The dense discussion of taxa excluded from *Rondeletieae* s.l. would be much clearer with a table showing their current assignment and noting the key characters involved. Future volumes should also address the author's criteria for circumscription and ranking at the genus level. This is particularly crucial with regard to the many monotypic genera (six of the ten treated here) and for resolution of the "*Rondeletia* complex" (which includes almost half of the species in *Rondeletieae* s.l.). I'd also like to see a more explicit discussion of biogeographical patterns, especially for genera such as *Chimarrhis*, with a broad neotropical distribution.

One must, when reviewing systematic research, avoid being caught in a sort of "Catch-22" or "chicken-and-the-egg" dilemma of alpha versus beta taxonomy: when detailed descriptive information is lacking, higher level analyses are impossible; *but* the primary descriptive work is difficult to approach when supergeneric structure is lacking. The need for basic description of little-known species, particularly when human activity threatens them with extinction, is well recognized. Thirteen of these 39 species are rare, and many are in danger of extinction. These genera can be especially difficult groups to study, due to their tiny flowers and fruits (often 2–4 mm long), their patchy rain forest distributions, and the paucity of herbarium material. This volume furnishes basic information on nomenclature, taxonomy, known distributions and natural history, providing a foundation for further phylogenetic investigations and conservation efforts. It is a substantial contribution to our understanding of these little known and biologically interesting groups of neotropical plants. It will certainly be a useful reference for neotropical taxonomists and for researchers in the Rubiaceae.

## References

- Delprete P. G. (1996) Evaluation of the tribes Chiococceae, Condamineae, and Catesbaeeae (Rubiaceae) based on morphological characters. *Opera. Bot. Belg.* 7: 165–192.
- Lincoln R., Boxshall G., Clark. P. (1998) A dictionary of ecology, evolution and systematics, 2nd edn. Cambridge University Press, Cambridge.

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**Scotland, R., Pennington, R. T. (eds.): Homology and Systematics: Coding Characters for Phylogenetic Analysis.** (Systematics Association Special Volume 58). 53 figs., 40 tabs., 8 photographs, 6 appendices, VII, 232 pp. Taylor & Francis, London, 2000. Hardcover US \$ 110.95. ISBN 0-7484-0920-3.

Lincoln Constance (1964) has characterized plant systematics as an unending synthesis that involves not only new forms of data and approaches to data analysis but also arguments about values. In 1964, the value of phylogeny as a goal in systematics was highly contentious – Constance (p. 262) noted "it is fashionable to deplore and disparage the construction of evolutionary models, especially phylogenetic trees." Curiously, Constance made no reference to homology in his vision of the unending synthesis. Since that time, we have been deluged with papers on homology. The recent attention to homology in the systematic synthesis appears largely to be a consequence of the adoption of phylogeny reconstruction as a major goal in systematics. Numerical taxonomy (Sneath and Sokal 1973) and cladistic analysis – particularly Hennig's (1966) distinction between plesiomorphic and apomorphic character states – require systematists to declare explicit hypotheses of homology in the form of a character matrix. *Homology and Systematics: Coding Characters for Phylogenetic Analysis*, a volume based on

papers presented at a Systematics Association symposium in 1997, arises from this concern with the character matrix. Pennington tells us in his introduction to the volume that the “problem tackled . . . relates to the fact that the outcome of phylogenetic analyses relies upon the constituent parts of a data-matrix” (p. 1).

Robert Scotland and Toby Pennington, the editors of *Homology and Systematics*, are interested in the role of homology in preliminary character analysis, in which characters and character states are delimited. Indeed, the volume is perhaps less about homology as a concept than about the practical decisions we make in constructing a character matrix. Peter Stevens, in one of the more readable and interesting papers in the volume, tells us that he “finds the word [homology] so ambiguous that it is best replaced by the synonyms of its particular usages” (p. 83). Stevens’s choice to avoid homology demonstrates clearly one state of contemporary systematics: there is little, if any, agreement on the conceptualization or even definition of homology (Donoghue 1992). Homology seems a visage – once alive as a morphological concept – being reformed in many ways by many hands for reincarnation. Many of us have approached this dilemma by offering alternative forms for homology. For example, de Pinna (1991) has distinguished between primary homology (hypotheses of correspondence based on similarity criteria, such as those proposed by Remane [1952]) and secondary homology (inferences of character state transformation based on cladograms). Discussions of secondary or phylogenetic homology are largely absent from the volume, although articles by Hawkins and Weston touch on those issues. Instead, most of the authors in this volume value homology as it concerns the practical implications of the question “what is a character?”

The volume makes it clear that, as Constance noted, arguments about values will accompany discussions of data analysis and, perhaps, will make synthesis in systematics difficult. In the opening chapter, Brower

devotes much of his discussion to establishing that “construction of natural classifications is an empirical, nominalist operation.” He continues, “I will criticize as superfluous to the success of the systematic endeavor both the reliance on assumptions that evolution has occurred and the popular belief that clades are explained by the process of phylogeny” (p. 10). This point of view is reflected in his discussion of the practical side of character delimitation. For example, Brower suggests that, because true state transformations are unknowable, more agnostic coding methods are preferred.

Whether or not we agree with this point of view, we appreciate that the acceptability of evolution as background knowledge affects our practical decisions in character coding. This dependent relationship between character coding and philosophy is clear in the final two chapters of the volume, in which Scotland explains and argues for the use of Three Taxon Statement (TTS) analysis (Ch. 8) and Williams and Siebert further refine TTS (Ch. 9). TTS analysis is a logically consistent method for discovering relationships among taxa based solely on shared presence of characters, avoiding assumptions of transformations. Under TTS, a data matrix is constructed using a conception of primary homology that requires features to be identical among study organisms.

Various articles in *Homology and Systematics* are concerned with alternative ways of defining characters and their states. Hawkins outlines alternatives from a survey of recent literature. She regards conventional characters as those in which the states can be proposed as transformations of each other (a point that authors such as Scotland and Williams and Siebert regard as problematic). Among Hawkins’s key points are (1) the rejection of nominal variable coding (Pimentel and Riggins [1987]; also known as presence/absence coding [Pleijel 1995]) because it violates the character state transformation assumptions that underlie comparative biology and (2) the inclusion of inapplicable data categories in multistate characters as a common but substantial deviation

from conventional coding. Forey and Kitching examine options for coding multistate characters, concluding that so-called Sankoff coding (the composite coding of Hawkins) is the most satisfactory way to handle complex attributes that require multiple states. Peter Stevens explores how the representation of continuous data affects the delimitation of character states which, in turn, affects the outcome of the phylogenetic analysis. Williams and Siebert examine the effects of alternative matrix constructions for TTS analysis.

Articles in the volume compare the decisions made in the construction of morphological and molecular character matrices. Stevens observes that the identification of characters is readily accomplished with morphological data but is difficult with molecular data, whereas the process of character state definition is unambiguous with molecular data but very difficult with morphological data. Ward Wheeler's article recalls Stevens's observation that molecular characters tend to be settled much later than morphological characters in the construction of matrices because molecular sequence characters are usually identified during alignment. Rather than considering this problematic, Wheeler further postpones the delimitation of characters by combining alignment with tree inference. Although the direct connection to homology assessment is not clearly made, the method is interesting in that it is a departure from the sequential assessment of primary and then secondary homology.

Reciprocal illumination has been important in deductions about homology, at least in theory. In the early phase of cladistics when most characters applied were morphological, reciprocal illumination may have been most important when we were testing our initial decisions about primary homology, making trees, and examining congruence among characters. Reciprocal illumination has become much more important as alternative data sets have become available for given groups of taxa. Paula Rudall demonstrates how incongruence between cladograms based on morphological and molecular data have led to the

reexamination and discovery of new morphological characters, using a case study in monocots.

In the staid world of contemporary plant morphology, Rolf Sattler can sometimes seem a terrorist. Peter Weston suggests in *Homology and Systematics* that Sattler seeks to "refute the basis of classical plant morphology and to replace it with a better alternative" (p. 132). Sattler's alternative emphasizes "process morphology"—the idea that similarities in developmental processes are key to hypotheses of homology—and "complementarity" (Rutishauser and Sattler 1985), recognizing that structures can have various homologies or partial homologies under different conceptualizations of development and form. Sattler wants a morphology that is not influenced by evolutionary concepts. Weston suggests that this goal permits Sattler to make inappropriate comparisons and criticisms. For example, it permits Sattler to critique stem and leaf categories by comparing typical stems and leaves with liverwort thalli, which were present long before stems or leaves evolved in the sporophyte generation of the land plant life cycle. Weston considers Sattler's process morphology to be no less idealistic than the classical morphology that Sattler finds untenable. Although Sattler's process morphology has been subject largely to benign neglect, it preceded plant developmental genetics in bringing homeosis to the attention of evolutionary morphologists. Morphologists may also find that developmental genetics will soon conceive a nearly Sattlerian sense of partial homology. Sattler's approach to homology and morphology offer little to cladistics because of its avoidance of characters and its hierarchical naiveté, but Weston suggests that we should take from Sattler a broadened outlook on how we reconstruct morphological diversity using cladograms.

Hawkins and others call for a theoretical framework that will inform character conceptualization and suggest that until it is achieved there will be inconsistency in character construction. We do not find a good

indication of how to formulate a theory of characters in this volume, although that is not the objective of *Homology and Systematics*. Articles in the volume, especially those of Brower, Hawkins, and Stevens, touch on what we regard as the phenomenology of characters—a philosophy based in an approach that includes assessing primary homology, examining congruence among characters, and reciprocal illumination. Although it may be outside the scope of this book, we wonder whether a theory of morphological characters can truly advance without input from developmental genetics, developmental morphology, and morphological evolution. Unfortunately, *Homology and Systematics* does not take us to a significantly more synthetic understanding of morphological characters because of its rather narrow range of articles, many of which reject the notion that evolutionary information can inform our understanding of characters.

If the objective of *Homology and Systematics* is not to formulate a theory of characters, it is also not about homology. In *Homology and Systematics*, homology is more an underlying motive—or a even a caution. For example, we take two basic points from the volume: different coding methods imply quite different notions of homology and inconsistent coding methods produce inconsistent cladograms. These are important points, and they call for all of us to be far more explicit about our hypotheses of primary homology and careful in our design of characters. We suggest those points also call for us to substantiate our character state delimitations with more extensive, detailed descriptions of our study organisms and their variations.

It is ironic that the recent impetus for focusing attention on the role of homology in character coding may be due to widespread use of phylogenetic methods because many authors in this volume are among those who have come to argue against phylogeny as a valuable goal in systematics. Thus, *Homology and Systematics* is concerned narrowly with primary homology – hypotheses of correspondence that can be

formulated without reference to evolutionary concepts. In regard to primary homology, the volume offers few insights; indeed, Brower suggests that the “basic process of recognizing homologous features has not changed for 200 years or more, and although we now have more precise analytical tools and a wider range of characters to sample, there is nothing fundamentally different about the way we infer the pattern of the Natural System from the way it was inferred by our predecessors” (p. 19). We might prefer to think more innovatively about primary homology as well as more broadly about the reach of homology in systematics. For example, we wonder whether developmental genetics offers not just new characters for homology assessment, but perhaps also new criteria that can be applied to formulating hypotheses of primary homology. We also wonder whether inferences of secondary homology based, for example, on studies of ontogenetic evolution or patterns of homoplasy, could be valuable in assessing primary homology in subsequent studies. However, we agree with the authors in *Homology and Systematics* that the construction of character matrices is a fundamental problem in systematics, and let us hope that this volume stimulates further work on this and the other fascinating aspects of homology that have broad ramifications throughout systematics.

## References

- Constance L. (1964) Systematic botany – an unending synthesis. *Taxon* 13: 257–273.
- de Pinna M. C. C. (1991) Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7: 367–394.
- Donoghue M. J. (1992) Homology. In: Keller E. F., Lloyd E. A. (eds.) *Keywords in evolutionary biology*. Harvard University Press, Cambridge, pp. 170–179.
- Hennig W. (1966) *Phylogenetic systematics*. University of Illinois Press, Urbana.
- Pimentel R. A., Riggins R. (1987) The nature of cladistic data. *Cladistics* 3: 201–209.
- Pleijel F. (1995) On character coding for phylogeny reconstruction. *Cladistics* 11: 309–315.

- Remane A. (1952) *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Akademische Verlagsgesellschaft, Leipzig.
- Rutishauser R., Sattler R. (1985) Complementarity and heuristic value of contrasting models in structural botany I. General considerations. *Bot. Jahrb. Syst.* 107: 415–455.
- Sneath P. H., Sokal R. R. (1973) *Numerical taxonomy*. W. H. Freeman and Co., San Francisco.

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**Freeman, S., Herron J. C.: Evolutionary Analysis.** 2nd ed. 450 figs., 704 pp. Prentice-Hall, New Jersey, 2001. Hardcover £ 32.99, US \$ 78.67. ISBN 0-13-017291-X.

After the great success of the first edition of *Evolutionary Analysis*, Scott Freeman and John Herron have come back this year with a ‘new look’ edition, not only fully coloured and magnificently illustrated, but also updated with many of the recent discoveries in evolutionary biology.

The book is divided into five parts. The introduction begins by presenting the HIV epidemic as a case study for understanding evolution. With AIDS being such a topical subject nowadays, this gives evolutionary biology a practical dimension, in contrast to the ‘catching butterflies with a net’ view that unfortunately too many people still have about this fundamental science. The title of the book itself, by containing the word ‘Analysis’, announces that not only are theories developed, but that actual ways of testing hypotheses make up the bulk of this book. Evidence for evolution is also presented in the introduction, as I presume, a reply to recent attempts by creationists to discard the teaching of evolution in the USA. This first part ends up with a chapter on Darwinian selection, using among others, the classical example of the radiation of finches in the Galapagos archipelago.

Part two discusses the mechanisms of evolutionary change. Starting at the DNA level, mutation and genetic variation are presented, followed by Mendelian genetics, population biology and quantitative genetics. Fundamental concepts such as genetic drift, effect of migration, non-random mating, linkage, and selection, are all very well explained. A demonstration of inappropriate experimental design and misinterpretation is provided using IQ tests in comparing African Americans and European Americans, thereby didactically dismantling racist theories.

Part three deals with adaptation. The analysis of form and function not only uses the classical example of ‘the giraffe and its long neck’, but also presents some fascinating work on spider mimicry by flies, as well as some exciting plant pollination studies. Sex has its own chapter, going back to the evolutionary laboratory provided by the Galapagos, but again, not forgetting plants with discussions of several cases of sexual selection. Kin selection and social behaviour are, obviously, quasi exempt from plant biology, but are still very interesting in my opinion, describing again several classical examples (e.g. mole rats). A chapter on ageing and life histories finishes this part.

Part four is dedicated to the history of life. It begins with the mechanism of speciation, and describes the wonderful study of Douglas Schemske and co-workers on pollinator shifts in monkey flowers. Then follow well presented chapters on how to reconstruct phylogenies, the origin of life and the Cambrian explosion and beyond, including a few references to the large phylogenies of plants that have been produced, and finally, human evolution. By putting together palaeontology, the latest developments in genetics as well as a good body of experiments and game theories, the authors have achieved in this part in making evolutionary biology one of the most embracing and exciting scientific disciplines.

The last part is entitled “Current Research – A Sampler”. It begins with the presentation of one of the biggest challenges in evolutionary