



Book review

Foundations of phylogenetic systematics

Foundations of Phylogenetic Systematics. By Johann-Wolfgang Wägele. Translated from the German second edition by C. Stefen, J.-W. Wägele, and revised by B. Sinclair. Verlag Dr Friedrich Pfeil, München Hardcover, ISBN 3 89937 056 2, 2005, € 45.00, 365 pp.

“Foundations of Phylogenetic Systematics” (FPS), Johann-Wolfgang Wägele’s updated translation of an earlier German version (Wägele, 2001), has several unifying objectives, namely “to present a comparison and synthesis of the methodological procedure of Hennigian phylogenetic systematics with new numerical methods, to depict what these methods have in common and where they differ, and to search for a common theoretical basis” (p. 9). FPS manages to allocate roughly equal space to analyses of morphological and molecular data, and is therefore more balanced in its representation of systematic practice than competing texts (e.g., Schuh, 2000; Felsenstein, 2004). The frequent discussions of well illustrated, real-life examples produce a welcome biological feel. Yet FPS also demonstrates how difficult it is to write a textbook that endorses a wide range of phylogenetic methods while maintaining a strict conceptual approach.

The text is finely divided into 15 sections plus references and an index. The 10 longer chapters have up to four levels of subheadings, whereas the remaining chapters (7, 9, 11, 13 and 15) amount to a total of only 10 pages and will receive little attention hereafter.

Chapter 1 introduces the philosophical conceptions relevant to the systematic endeavor. Topics such as the role of language, the limits of cognition, signal versus noise, the origin and testing of hypotheses, and probability and parsimony are treated in a fairly original fashion. The author distinguishes between the processes of classification (based on predicators) and systematization (based on proper names; Ax, 1987), borrowing many elements from Mahner and Bunge’s (1997) biophilosophy. Important new terms are defined in separate boxes throughout the text (there is no glossary at the end). The phenomenological method is introduced as that “which tries to avoid the use of axioms or first assumptions in order to study first of all what can be seen or experienced in nature or society” (p. 40).

Chapter 2 examines the subjects of systematics, organizing them into material things (e.g., organisms, struc-

tures, molecules), processes (e.g., inheritance, mutation, selection), and constructs (e.g., taxa, homologies, phylogenies). Wägele regards assessments of the plausibility of evolutionary processes as an important component of phylogenetic analyses. He discusses several existing species concepts, favoring a phylogenetic concept where a species is “a group of ancestors and their descendants, which diverge irreversibly from other such groups along the time axis” (p. 56). The difficulty to predict the fate of lineages is a practical limitation this concept shares with the evolutionary species concept (e.g., Wiley and Mayden, 2000). The section ends with an engaging synthesis of evolutionary processes and rates.

Chapter 3 explores the nature of phylogenetic graphs, even though the reader has yet to learn about the kinds of evidence and analyses used for tree generation. Consequently, passages on monophyly, character polarity, and consensus methods appear out of sequence, and a discussion of stem lineages and crown groups remains incomplete without providing a practical means for inferring such entities.

Chapters 4 and 5 turn to the issues of phylogenetic evidence and character analysis. Sections on similarity and homology are insightful and rich in examples. Under the term “phenomenological character analysis”, Wägele advocates a very thorough a priori examination of potential homologies. This approach is rooted in sense cognition yet also involves assessments of the probability of structural identity and transformation in relation to perceived character complexity. The author argues in favor of differential weighting—either directly or through partitioning of several detail homologies within a larger frame homology—in order to represent the unequal phylogenetic quality of strong versus weak characters. Additional criteria for homology assessment are compatibility (ground pattern similarity) and, to a lesser extent, congruence (in an inferred topology). Remane’s (1952) homology criteria are competently applied to modern case studies including common problems of sequence alignment. Wägele again favors an a priori determination of character polarity and criticizes the practice of polarizing characters by means of outgroup selection. He provides a detailed procedure for recognizing ancestral ground patterns using a variety of criteria, e.g., ontogeny, paleontology, and asymmetrical split-supporting patterns in aligned sequences.

Chapter 6 presents an overview of phylogeny reconstruction methods using parsimony. Here and in various other sections of the text, the author takes a critical stance towards “phenetic cladistics”, where assessments of character quality are presumably superficial and congruence is the only criterion for recognizing homology. He continues with a summary of alternative methods of character coding, weighting procedures, tree statistics and measures of support. His favored Hennigian phylogenetic cladistics is contrasted with phenetic cladistics, with the principal difference being an a priori versus a posteriori assessment of character quality. This is followed by a useful discussion of frequent problems in aligning and analyzing DNA sequences with parsimony, namely, differential indel weighting and solutions to long branch phenomena. Spectral analysis (e.g., Wägele and Rödding, 1998) is recommended as a means to evaluate the information content of aligned sequences prior to tree construction. The combination or partitioning of multiple character matrices is contingent upon perceived signal quality and strength.

Chapter 8 deals with model-dependent methods for tree reconstruction. The emphasis is on the conceptual level, with the more technical aspects reserved for the appendix (chapter 14). Wägele offers a hierarchical summary of likelihood models and their respective assumptions, then proceeds to distance methods, and finally reviews Bayesian inference. Chapter 10 illustrates how information external to an analysis (biogeographical patterns, fossils, evolutionary considerations, etc.) can be subjoined to test the plausibility of a particular reconstruction. Chapter 12 gives a critical synopsis of modern alternative views on classification. Lastly, the Appendix presents a more detailed description of the algorithmic workings of likelihood models, parsimony searches, distance methods, and other fairly recent developments such as optimization alignment. This leads into a single page (chapter 15) with links to relevant websites and software applications.

Even though FPS is broad in its treatment of tree building methods, well written, and nicely illustrated, I would hesitate to recommend it as an introductory text for students of systematics (as the title may suggest). Above all, the author’s phenomenological approach seems idiosyncratic; it is employed to push an agenda that is too particular to serve a wider audience. I suppose that phenomenology is invoked in part to stress the importance of careful and critical observations of potential homologies. Indeed, the strongest sections are those that review issues of information quality, homology assessment, coding, and weighting in light of plausible evolutionary considerations. While I happen to agree with many of Wägele’s recommendations, his approach throughout is highly inductive and therefore rarely limited just to sense perception. This is exemplified by his criteria for selecting reliable characters

(p. 102), which depend fundamentally on assessments of character transformations according to their perceived evolutionary rate, complexity, adaptive value, independence, phylogenetic sequence of appearance, etc. Following such rules is useful and may even be necessary, but it surely does make one look at “phenomena” differently, weighing them up or down according to inferences about the relative likelihood of particular evolutionary processes. In the end, the author’s conceptual stance and his recommendations for practice are a poor match. This is also evident in the sections on model-dependent approaches, where references to phenomenology are effectively replaced by a discussion of axiomatic assumptions about DNA substitution processes—far removed from the level of immediate sense data. At this point I felt that the distinction between material things, processes, and constructs (see above) was no longer very useful.

Several additional peculiarities of FPS are worth mentioning, though many others cannot be addressed here. Revising the sequence of chapters would produce a more natural unfolding of themes and methods. I missed a section or at least a listing of representative treatments on historical coevolutionary analyses. Applications of phylogenetic results in other biological disciplines (e.g., conservation) are summarized on a single page. There is hardly anything on the history of systematics and its past and continuing challenges. I mention these omissions to underscore that FPS is best understood as food for thought about phylogenetic inference rather than a broad introduction to the field. But then Wägele’s style of writing is too matter-of-fact to defend his stringent and sometimes controversial perspective. This is perhaps most apparent in his repeated criticism of superficial character analyses and the role of the congruence test in “phenetic cladistics” (see also Platnick, 2006; for comment). Certainly, testing for congruence is not circular (p. 218), as it can strengthen as well as weaken hypotheses of homology that were initially proposed without reference to a tree (e.g., Franz, 2005). The purported Central European/American schism feels forced.

In summary, Wägele’s FPS is for the most part an authoritative and engaging read on contemporary methods of phylogenetic inference. Its strongest passages vehemently emphasize the importance of thorough character analyses vis-à-vis assessments of evolutionary probability. FPS is a worthy and affordable addition to the library of any advanced student of systematics.

References

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