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PHYLOGENETIC ANALYSIS OF MORPHOLOGICAL DATA (TWO VOLUMES)

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MARTÍN D. EZCURRA

CONICET-Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Sección Paleontología de Vertebrados, Ángel Gallardo 470 (C1405DJR), Ciudad Autónoma de Buenos Aires, Argentina.

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OSTEOLOGY AND DEVELOPMENT OF THE ANURAN *AVITABATRACHUS*

Re-examination of the type skeleton of the pipimorph frog *Avitabatrachus uliana* from the Candeleros Formation of northwestern Patagonia

A NEW TURTLE FROM THE UPPER CRETACEOUS OF PATAGONIA

The new fossil has a unique combination of characters, suggesting an unrecognized lineage of southern turtles

SYSTEMATICS OF MIOCENE SLOTH *EUCHOLOEOPS*

Analysis of *Eucholoeops* remains previously assigned to *E. fronto*, *E. lafonei*, and *E. externus* suggests their reassignment to *E. ingens*

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Phylogenetic trees are hypotheses of interrelationships among taxa and explain the sequence of evolutionary transformation of characters (either phenotypic and/or genotypic). As a result, phylogenetic analyses and their resultant trees are key in modern Paleontology and Biology to study the evolution of species. During most of the last century, evolutionary trees depicted ancestor-descendant sequences. They were built using non-numerical methods, with subjective criteria dependent on each researcher's understanding of the evolution of the group. The irruption of numerical methods and optimality criteria based on maximum parsimony (and probabilistic methods) after 1950 provided a more objective methodology to build phylogenetic trees and an explicit way of hypothesis testing and reproducibility, satisfying key principles of the Popperian theory (Farris, 1983).

Phylogenetic analyses have become a standard method in modern Paleontology, mainly in Vertebrate Paleontology. This proliferation of phylogenetic analyses has been prompted by the appearance of computational programs that allowed easier handling of larger taxon-character data matrices. Multiple research projects have been and are focused on studying the phylogenetic relationships of fossil organisms. Still, it is also extremely common that these analyses are included to complement other main goals, such as the description of new species. Despite their frequent usage, I have noticed pervasive problems when conducting phylogenetic analyses, particularly in decisions when building the character lists of the data matrices and choosing tree search parameters. Indeed, a substantial number of phylogenetic analyses that I have peer-reviewed in the last 15 years failed to find the optimal trees or comprehensively explore the tree-space as a result of wrong decisions at the time of setting tree search parameters (*e.g.*, a low number of replications that would result in a low sample of optimal hits, stagnancy in regional optima because of the impossibility of overcome suboptimal valleys). I think that

this problem is a consequence of the lack of a deeper understanding of the modern phylogenetic methodology, and it is generated by a combination of factors, including an underestimation of its complexity and, more importantly, the lack of a bibliography addressing the topic in both an accessible and comprehensive way. Fortunately, the latter gap is filled with the publication of "Phylogenetic Analysis of Morphological Data", a recently published two-volume book by Pablo A. Goloboff. In addition, this book is focused on phylogenetic analyses based on morphological data, and, as a result, paleontologists will find its content particularly useful.

The author, Pablo A. Goloboff, is a world-leading expert in phylogenetic analysis theory and is one of the authors of the most frequently used computer program to run such analyses: TNT ("Tree analysis using New Technology"). Goloboff is the author of more than a hundred peer-reviewed papers; the vast majority focused on empiric cases and/or the theory behind phylogenetic analyses. In particular, his first paper introducing TNT to the scientific community (Goloboff *et al.*, 2008) has been quoted more than 5,000 times. During the last three decades, he has also dictated multiple post-grade courses in Argentina and overseas about phylogenetic analyses and the usage of TNT. Thus, it isn't easy to think of a person more appropriate to write this kind of contribution.

The book is divided into two volumes: "*From observations to optimal phylogenetic trees*" and "*Refining phylogenetic analyses*", respectively. The first volume begins with an introduction to phylogenetics, explaining its most basic concepts, such as logical aspects, tree terminology, parsimony, synapomorphy, and optimality criterion. This first chapter ends with the basic notions of implementing parsimony analyses in the software TNT. Chapter 2 tackles the explanation of the key concepts of homology and characters (*e.g.*, character independency, choice, and settings, discrete and continuous characters). Thus, this chapter is of paramount

importance to anyone that wants to get involved in phylogenetic analyses based on morphological data. Chapter 3 deals with character optimization, starting with a historical account and afterward discussing the concepts of additive characters, ambiguity, polymorphisms, missing entries, inapplicable characters, and synapomorphies, among others. This chapter finishes with a description of the implementation of these concepts in TNT. Chapter 4 discusses the debated topic of models and assumptions related to phylogenetic analyses based on morphological data. This chapter describes the basic notions of model-based (Maximum Likelihood and Bayesian inference) and parsimony-based analyses, with a conclusion of the strengths and weaknesses of these methods to reconstruct phylogenetic relationships using morphological data. Finally, this volume finishes with a fifth chapter describing the strategies and algorithms to find the most parsimonious trees in great de-

tail. Chapter 5 ends with an account of the general settings and the implementation of the tree-search algorithms in TNT.

The second volume of "*Phylogenetic Analysis of Morphological Data*" starts with Chapter 6, which focuses on describing consensus methods. Subsequently, this chapter describes and discusses the most commonly used tree comparison metrics (e.g., Robinson-Foulds distances, rearrangement distances, distortion coefficient). Finally, Chapter 6 tackles how TNT implements consensus methods, tree comparisons, topologically unstable taxa identification, supertrees, and tree distance measures. Chapter 7 deals with character weighting (homoplasy penalization), a strongly debated topic and target of subjective opinions grounded on long-standing misinterpretations of the logical bases of parsimony, which are particularly pervasive among paleontologists. The core of this chapter is the description

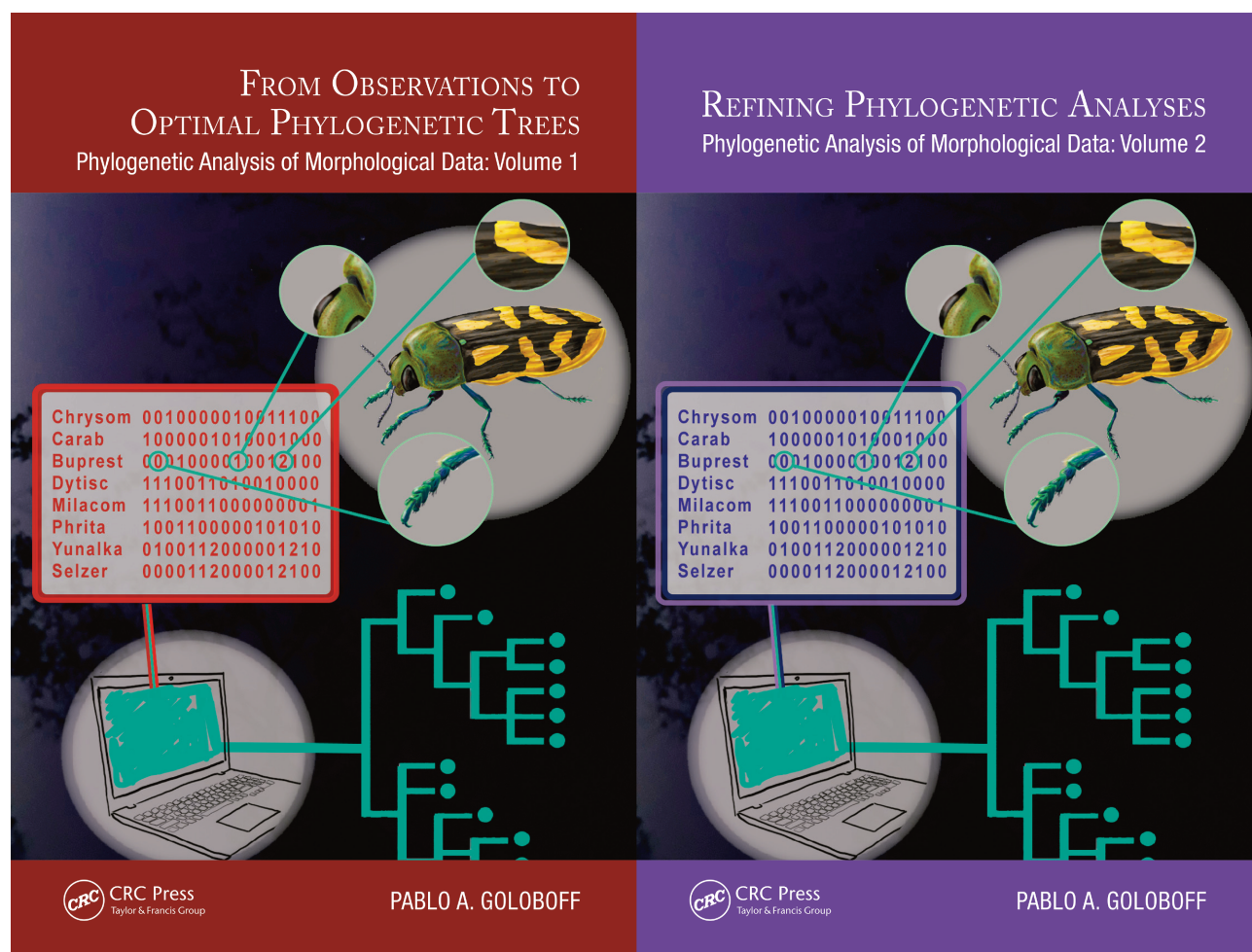


Figure 1. Covers of the two volumes of the book "Phylogenetic Analysis of Morphological Data" by Dr. Pablo A. Goloboff. CRC Press.

and discussion of the implied weighting method, which was developed during the 1990s by the author himself. Goloboff also uses this chapter to discuss a series of papers that have evaluated the performance of equal and implied weighting parsimony versus model-based analyses using simulated datasets. The author strongly advocates that implied weighting outperforms both equal weighting and model-based analyses. Finally, Chapter 7 describes the implementation of implied and extended implied weighting in TNT. Chapter 8 deals with the methodologies more commonly used to measure branch support in phylogenetic trees: Bremer support and its variants and different resampling methods. This part of the book is particularly relevant for correctly interpreting resampling frequencies in phylogenetic analyses. Finally, as in most other chapters, it finishes by describing the implementation of the branch support analyses in TNT.

Chapter 9 deals with a relatively recent addition to phylogenetic analyses that has continuously gained more popularity in recent years, which is the use of geometric morphometric constellations as continuous characters. This chapter starts with a theoretical discussion of this character type and its application within the parsimony framework, including landmark alignment and optimization issues. Finally, there is a detailed account of how geometric morphometric characters can be imported and analyzed in TNT. Chapter 10, the last chapter of the book, deals with the topic that is probably more unfamiliar to the vast majority of people who work on empirical phylogenetic analyses, which is scripting. Scripting dramatically increases the versatility of a program, allowing the user to manipulate, customize, and automate routines within the software. Chapter 10 begins with the basics of the TNT language, including expressions, operations, loop coding, and variable setting, among others. Subsequently, this chapter deals with more specific scripting issues, such as handling errors, managing

input files, output file formats, tree editing and branch labels, and other plotting facilities available in TNT.

In conclusion, this book has the potential to provide both researchers and students alike with the theoretical bases and tools for the correct building of robust phylogenetic data matrices, their analysis, and subsequent interpretation. Large (> 100 taxa) and continuously growing phylogenetic datasets are becoming more common and a good understanding of the phylogenetic methods is crucial. Analyses using parallel computing in clusters are becoming more useful to avoid long computational times. Unfortunately, this topic and how TNT implements it are addressed only superficially in a few sections of both volumes and the reader should seek for this information in recently published papers written by Goloboff and colleagues (*e.g.*, Morales & Goloboff, 2023). All in all, I think that "*Phylogenetic Analysis of Morphological Data*" will become quickly in a 'must-read' reference to any person interested in phylogenetics, mainly those that have to work with morphological data, including paleontologists.

Martín D. Ezcurra
CONICET-Museo Argentino de Ciencias Naturales
"Bernardino Rivadavia"
Sección Paleontología de Vertebrados
Ángel Gallardo 470 (C1405DJR)
Ciudad Autónoma de Buenos Aires, Argentina
martindezcurra@yahoo.com.ar

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