



<http://researchspace.auckland.ac.nz>

ResearchSpace@Auckland

Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- Any use you make of these documents or images must be for research or private study purposes only, and you may not make them available to any other person.
- Authors control the copyright of their thesis. You will recognise the author's right to be identified as the author of this thesis, and due acknowledgement will be made to the author where appropriate.
- You will obtain the author's permission before publishing any material from their thesis.

To request permissions please use the Feedback form on our webpage.

<http://researchspace.auckland.ac.nz/feedback>

General copyright and disclaimer

In addition to the above conditions, authors give their consent for the digital copy of their work to be used subject to the conditions specified on the Library Thesis Consent Form.

*Panbiogeography:
A Cladistic Approach*

Roderic D. M. Page

Department of Zoology

University of Auckland

*Thesis submitted in partial requirement for the degree of
Doctor of Philosophy in Zoology. 1990.*

This thesis is set in 12 pt Palatino. Text was prepared using Microsoft Word 5.0 on a IBM XT compatible microcomputer, and printed on an Apple LaserWriter Plus laser printer at the Department of Zoology, University of Auckland.

Apparently several cladists regard their dendrograms as final scientific achievements, but what precisely must the taxonomists do with them — frame them to hang them on the wall? [A. D. Meeuse]

Contents

	Acknowledgments	x
	Abstract	xii
1.	Introduction	
	A Guide to the Thesis	1-2
	Prospect	1-5
	References	1-7
2.	New Zealand and the New Biogeography	
	Of Flies and Phylogenetics	2-3
	Croizat and the Poverty of Biogeography	2-6
	The New York School	2-9
	The False Opposition Between	
	"Vicariance" and "Dispersal"	2-12
	New Developments in New Zealand	2-13
	Geology and Geomorphology	2-16
	Prospect	2-20
	Acknowledgments	2-20
	References	2-21
3.	Tracks and Trees in the Antipodes:	
	A Reply to Humphries and Seberg	
	Tracks and Spanning trees	3-3
	Tracks and Parsimony	3-4
	Croizat Did Draw Minimal	
	Spanning Trees	3-6

Relationships or Proximity?	3-8
Cliques and Component Analysis	3-9
Nelson's Consensus Method	
Is a Clique Method	3-10
A Worked Example	3-11
The Relationship Between	
Biogeography and Systematics	3-15
The <i>Ficus</i> Example	3-17
A Cladistic Version	3-18
Coevolution as a	
Model for Biogeography	3-19
An Alternative View	3-21
Conclusion	3-22
Acknowledgments	3-23
References	3-24
4. Quantitative Cladistic Biogeography:	
Constructing and Comparing Area Cladograms	
Constructing Area Cladograms	4-2
The Problem	4-3
Confusion about	
Components and Consensus	4-5
Missing Areas	4-6
Widespread Taxa	4-6
Do Assumptions 1 and 2	
Discard Evidence from Characters?	4-8
Redundant Distributions	4-10
Algorithms	4-11
Measures of Fit	4-12
Comparing Area Cladograms	4-14

Pairwise Tree Similarity	4-14
Generalizing Pairwise Distances	4-15
Comparing Multiple Equally	
Parsimonious Area Cladograms	4-17
Statistical Test	4-18
Why Biogeography Needs Statistics	4-18
Null Hypotheses	4-19
Test Protocol	4-20
General Area Cladograms	4-22
Implementation and Applications	4-23
Discussion	4-26
Acknowledgments	4-27
References	4-28
Appendix	4-34
Algorithm for Assumption 1	4-34
Algorithm for Assumption 2	4-37
5. Comments on Component-Compatibility in	
Historical Biogeography	
The Rationale for Assumption 2	5-2
Implementing Assumptions 1 and 2	5-7
Constructing Area Cladograms	5-8
<i>Xiphophorus</i> as an Example	5-9
PAUP and "Nelson's Problem"	5-13
Explaining the "Unexplained Jumps"	5-15
Platnick's Reanalysis of	
Rosen's Data	5-16
A Statistical Digression	5-17
What is Nelson's Consensus Method?	5-20
Summary	5-23

Acknowledgments	5-24
References	5-25
Appendix	5-29
Nelson Consensus Tree	5-29
Algorithm	5-30
6. Component Analysis: A Valiant Failure?	
Making Area Cladograms	6-2
Wiley's Critique of Component Analysis	6-4
What is Component Analysis?	6-5
Missing Areas	6-6
Widespread Taxa	6-8
Wagner Parsimony in Biogeography	6-11
The Difference between	
Rules and Algorithms	6-11
Homoplasy in Wagner Trees	6-13
Mapping Trees — an Alternative	
Parsimony Criterion	6-16
Mapping Between Trees	6-17
Assumptions 1 and 2	6-20
Widespread Taxa	6-20
Redundant Distributions	6-23
Implementation and Application	6-25
Summary	6-28
Acknowledgments	6-30
References	6-31
7. COMPONENT: A MS DOS Program for Component Analysis	
Motivation	7-1
Features	7-2
Requirements	7-3

	What COMPONENT Doesn't Do — Yet	7-4
8.	Cladistics with Confidence: The Bootstrap Revisited	
	Confidence Intervals for Trees	8-3
	Practical Issues	8-6
	An Example — Kluge's <i>Epicrates</i> Data	8-9
	Congruence	8-10
	Confidence Intervals	8-13
	Summary	8-18
	References	8-19
9.	Temporal Congruence and Cladistic Analysis of Biogeography and Cospeciation	
	Temporal Congruence	9-4
	Materials and Methods	9-6
	Overview	9-6
	Data	9-7
	Parsimony	9-7
	Test for a Molecular Clock	9-10
	Phylogenetic Inference with a Clock	9-12
	Component Analysis	9-13
	Results	9-15
	Is There a Clock?	9-15
	Phylogenetic Estimates	9-20
	Component Analysis	9-24
	Discussion	9-34
	Limitations of the Analysis	9-34
	Temporal Congruence	9-36
	Acknowledgments	9-37
	References	9-38
	Appendix 9.1	9-43

Appendix 9.2 9-45

Appendices

- I. COMPONENT User's Manual
 - II. Graphs and Generalized Tracks: Quantifying Croizat's Panbiogeography.
-

Acknowledgments

Brian McArdle happily took me on as a student, although he freely admitted his ignorance of cladistics. It has become clear over the last four years that his ignorance was rather less than he thought, while my ignorance was much greater than I had ever imagined. I thank Brian for giving me both the freedom and the facilities to follow whatever line of enquiry I chose.

Robin Craw's 1978 essay "Two biogeographical frameworks: Implications for the biogeography of New Zealand" in *Tuatara* first kindled my interest in biogeography. I thank Robin for his interest in this work, and for some astute advice. I spent many a long lunchtime in the Senior Common Room discussing biology and evolution with Russell Gray. The time was well spent, and I thank Russell for challenging a closet empiricist to think about process and theory. Professor Pat Bergquist gave Russell and I the opportunity to teach an MSc course in systematics and biogeography for two years. That experience was invaluable, and I thank the students who took the course — although I fear I learnt more than they did.

The single most important event during my studies was my trip to the United States. I am indebted to Joel Cracraft for the invitation to attend the symposium on biogeography held at New Orleans, and I thank him and Dave Ritchie of Tony's Britannia Ltd for the financial assistance that made my attendance possible. Contacts made on that trip have been invaluable. I especially thank Gary Nelson and Norman Platnick for their continued interest in my work. The editorial staff and reviewers of the journals *Cladistics*

and *Systematic Zoology* improved much of the content of this thesis: in particular I thank Jim Carpenter and Robert Zink.

Abstract

This thesis develops a quantitative cladistic approach to panbiogeography. Algorithms for constructing and comparing area cladograms are developed and implemented in a computer program. Examples of the use of this software are described.

The principle results of this thesis are:

- (1) The description of algorithms for implementing Nelson and Platnick's (1981) methods for constructing area cladograms. These algorithms have been incorporated into a computer program.
- (2) Zandee and Roos' (1987) methods based on "component-compatibility" are shown to be flawed.
- (3) Recent criticisms of Nelson and Platnick's methods by E. O. Wiley are rebutted.
- (4) A quantitative reanalysis of Hafner and Nadler's (1988) allozyme data for gophers and their parasitic lice illustrates the utility of information on timing of speciation events in interpreting apparent incongruence between host and parasite cladograms.

In addition the thesis contains a survey of some current themes in biogeography, a reply to criticisms of my earlier work on track analysis, and an application of bootstrap and consensus methods to place confidence limits on estimates of cladograms.
