Erratum


Indentation of block quotes was omitted from this review. The corrected review is reproduced below. The publisher apologizes for the error.


This book aims to revitalize panbiogeography with the cladistic results of molecular systematics (p. vii):

Molecular analysis has revealed an intricate, orderly, geographic pattern in most groups examined .... This molecular/geographic structure has often been described as “surprising” .... The discovery of this structure has been one of the most exciting developments in molecular biology, and it has intriguing, far-reaching implications for evolutionary studies in general.

There are 10 chapters, most about 50 pages long, the last two shorter. The first two set out the logic relevant to Evolution in Space (Chapter 1) and Evolution in Time (Chapter 2). Next, are chapters on Evolution and Biogeography of Primates: A New Model Based on Molecular Phylogenetics, Vicariance, and Plate Tectonics (Chapter 3), Biogeography of New World Monkeys (Chapter 4), and Primates in Africa and Asia (Chapter 5). The book then shifts to Biogeography of the Central Pacific: Endemism, Vicariance, and Plate Tectonics (Chapter 6), Biogeography of the Hawaiian Islands: The Global Context (Chapter 7), and Distribution within the Hawaiian Islands (Chapter 8), followed by Biogeography of Pantropical and Global Groups (Chapter 9). There are 103 figures, mostly original maps showing the logic or interpretation of many case studies. The last chapter is a coda on CODA—a critique of the Center of Origin/Dispersal/Adaptation model of interpretation: Evolution in Space, Time, and Form: Beyond Centers of Origin, Dispersal, and Adaptation (Chapter 10). There is a 3-page glossary of geological terms, a 75-page bibliography with 1200 items, and a 27-page index. Perusing the imperfect index, prepared by the press with no author input, one might erroneously conclude that Ernst Mayr is the most cited author and Michael Heads is one of the least—a single 1-page entry. There is a more informative list of the book’s citations available from the author.

Heads succeeds in fitting all these attractive subjects into a coherent and even compelling whole. His writing guides the reader to crisp understanding entirely worthy of the past, and of a growing presence, and on into the future. How does he accomplish this marvel?

In Chapter 1, in a section headed “The Four Processes Proposed in Biogeography and the Two That Are Accepted Here,” the logic is simply stated (p. 11):

Four key processes have been proposed in biogeography. As discussed above, differentiation (e.g., speciation) can be due to vicariance of a widespread ancestor or to founder dispersal from a center of origin. In addition, two overlapping sister clades can be explained as the result of range expansion (by normal ecological dispersal, simple physical movement) or by sympatric differentiation.

Of the four processes just cited, vicariance and normal ecological dispersal are accepted as important by all authors. They are the two processes that are accepted in this book as explaining distributions.

The time dimension (Chapter 2) is more problematic (p. 97, 59):

The molecular phylogenies and the beautiful distributions of the clades they reveal are the raw material for this book. Sampling is improving all the time, and the only real problems with the molecular work are the interpretations of evolution in space (reading the sequence of nodes as a dispersal sequence) and time (calibrating the nodes with fossil or island age and assuming that branch length reflects age).

Differentiation in morphology and molecules occurs over space and through time. Spatial variation can be observed directly; establishing the age of a clade is more difficult.

The difficulty is 2-fold: the first is that (p. 60) “a model of how evolution proceeds—for example, whether it is
clock-like or not—has to be adopted.” Historically, Heads sees that “The Biogeography of Hutton and Chapman Was Replaced with the Evolutionary Clock of Matthew, Mayr, and the Modern Synthesis.” His summary (p. 64):

To summarize, at all biogeographic breaks, for example, the Atlantic Ocean, different pairs of clades show differing degrees of divergence. There are two possible explanations:

- Evolution is clock-like and the different pairs split at different times.
- Evolution is not clock-like and the different pairs split at the same time. Degree of difference is related to prior genome architecture, not to time.

If the first option is correct, a general vicariance event cannot explain any biogeographic pattern; distribution patterns must all be pseudopatterns and the result is chance coincidence.

Here I am reminded of a scientific meeting in London (5 September 2001; published by Donoghue and Smith 2003). Francisco Ayala presented a paper on “Molecular clocks: whence and whither?” An audience member then asked: “Francisco, is there a molecular clock?” He gave a complex reply. The same member asked again: “Francisco, is there a molecular clock?” This time he gave a one-word answer: “No.”

Heads gives the same answer but proceeds with the second difficulty, “Calibrating the Evolutionary Clock” (p. 67):

Apart from cross-calibrating from another node with a known age, there are only three ways to date evolutionary development:

- Use the oldest fossil of a group. But this only gives a minimum age for the group.
- Use the age of the island or the strata that a group is endemic to. But young islands and strata often have old taxa.
- Correlate the geographic distribution of a group with associated tectonic events. But tectonic features can be reactivated at different times.

All three methods are flawed, but the first two have serious, inherent limitations, while the third suggests possible lines of research.

He nevertheless achieves a simplification (p. 71):

The method of dating used in this book does not assume an evolutionary clock, even a relaxed one. Instead it fits multiple tectonic events (rather than multiple fossils) to a phylogeny. This indicates a chronology in which rates can show extreme changes within and among lineages and genes at different times and places.

Is he correct to jettison, except as minimal age estimates, the accumulating results of molecular dating? And to see their historical development (p. 60) as stemming from William Diller Matthew (1871–1930) and Ernst Mayr (1904–2005)? He does not continue the long-standing dispute over dispersal versus vicariance but rather commits to a consistent mode of interpretation (p. 7):

In the vicariance approach, the focus is on tracing the originary breaks between groups, not on locating a point center of origin within a group. In a dispersal analysis, the first question is: Where is the center of origin? In a vicariance analysis, the first question is: Where is the sister group? The focus is not on the group itself or on details of its internal geographic/phylogenetic structure, but on its geographic and ecological relationship with its sister group and other relatives.

The key word here is “breaks,” a term in recent use particularly in molecular biogeography (p. 7–8):

In this model, a group of organisms originates by the breakdown of a widespread ancestor, not by evolving at a point and spreading out from there. Analysis of any group can start either with a point center of origin or, alternatively, with a widespread ancestor. In the latter model, a group evolves on a broad front over the region it occupies, by “fracturing” with its sisters (vicariance) at phylogenetic and biogeographic breaks or nodes. A node is not a center of origin or an ancestor; it is a break where the distributions of two or more groups meet.

Breaks have always figured in the logic of panbiogeography (Croizat 1956, p. 209):

...let us suppose that we have laid on the table before us a framed piece of glass two feet square, and let us homologize this glass to a whole order of plants or birds. Let us hit this glass a blow in such a manner as but to crack it up. The sectors circumscribed by cracks following the first blow may here be understood to represent families. Continuing, we may crack the glass into genera, species, and subspecies ....

Panbiogeography—the word—originated with Léon Croizat (1894–1982), in a 3-volume work, so entitled, privately published in 1958. He remarked therein (Volume I, p. 139):

...loath as I am to coin neologisms it might perhaps be useful to designate as
For Heads, the correlation with geology allows estimation of absolute age; all other procedures give only minimum ages, and the origin of a group is likely older than any minimum, even by one or two orders of magnitude. He is thus at odds with many modern authors who, in his terms, “transmogrify” an estimate of a minimum age into a maximum and consequently argue that a group is too young to have been influenced by remote geological processes with which it might seem correlated in a causal relation.

Transmogrification—“an error in logic” (p. 68)—if it is a process apt to deceive, or merely self-deceive, then why should it exist at all? Heads quotes Pfeil and Crisp (2008, p. 1630):

> Although all fossil calibrations in principle imply only minimum age, a lack of older fossils that we can confidently use to calibrate phylogenies in current knowledge also sets a boundary on the maximum ages of lineages for which we have evidence.

Heads comments (p. 414):

> This is not logical—a lack of older fossils does not set anything except the minimum age. It seems as if the authors wanted to accept fossil dates as both minimum ages (the logical approach, followed in their initial analysis) and maximum ages (the traditional approach, followed in their biogeographic discussion), but this is not possible.

Physical biogeography—the distribution of life and the historical processes relevant thereto—is complex. The history of its study is consequently littered with simplifying assumptions. Heads accepts the least simplifying, the correlation with geology—that earth and life evolve together—Léon Croizat’s favorite slogan (p. 99):

> Instead of trying to prove or disprove the vicariance/dispersal argument in theory, it may be more productive to see what the results are if different sets of assumptions are tried out in practice. Can dispersal or vicariance provide a coherent scenario for world distribution? Of the two possible options, a dispersal scenario is easy to describe. Any pattern at all can be explained by chance dispersal, and global biogeography would be seen as the result of endless, one-off dispersal events, each one unrelated to any other aspect of biology or geology.

Croizat (1964) once described the method of pani- biogeography (p. vi):

> …it consists of constant, strictly objective comparisons conducted among as many patterns of distribution of plants and animals as possible the world over.

and its results (1964, p. 712):

> The patterns of geographic distribution of plants and animals—whatever their “means” [of dispersal] are absolutely congruent, as a fact of nature, within a minimum of fundamental tracks and centers.

In the old pani-biogeography, key concepts are track and node, a track being a taxon’s distribution (and internal relationships), represented most simply by a line on a map, and a node being an area where several different tracks overlap or intersect. In Heads’ account, matching Croizat’s method and result, there is scarce mention of track (“set of nodes,” p. 408), and a node is only that of a cladogram. Still his account, cloaked in the findings of molecular systematics, continues the spirit of the old and amply confirms Croizat’s prediction (1964, p. xvi): “my work shall live.”

> Of Heads’ many case studies, one of the most interesting is that of the Hawaiian Islands—interesting because it is at odds with ever-prevailing sentiment that, whatever the specifics currently in fashion, the islands, their history, and that of their biota are well understood. His account suggests that there is still much to learn (p. 406):

> Instead of relying on long-distance dispersal with founder effect speciation, the model of Hawaiian biogeography suggested here proposes a major phase of mobilism and range expansion in the Cretaceous, followed by a phase of immobilism and vicariance of metapopulations by tectonic processes. Normal ecological dispersal occurred at all times within each metapopulation.

A reader may stumble over words such as mobilism, immobilism, vicariance, and metapopulation. For this there is no remedy except to become familiar with Heads’ usage. That remedy is easy because the language of the book is clear and concise. It should be widely read, especially by students and journal editors!
REFERENCES


Gareth Nelson, School of Botany, University of Melbourne, Victoria 3010, Australia; E-mail: garethn@unimelb.edu.au.