BOOK REVIEW

Molecular Panbiogeography of the Tropics by Michael Heads, a post-review

Molecular Panbiogeography of the Tropics. M. Heads. 2012. University of California Press, Berkeley, 565 pp.

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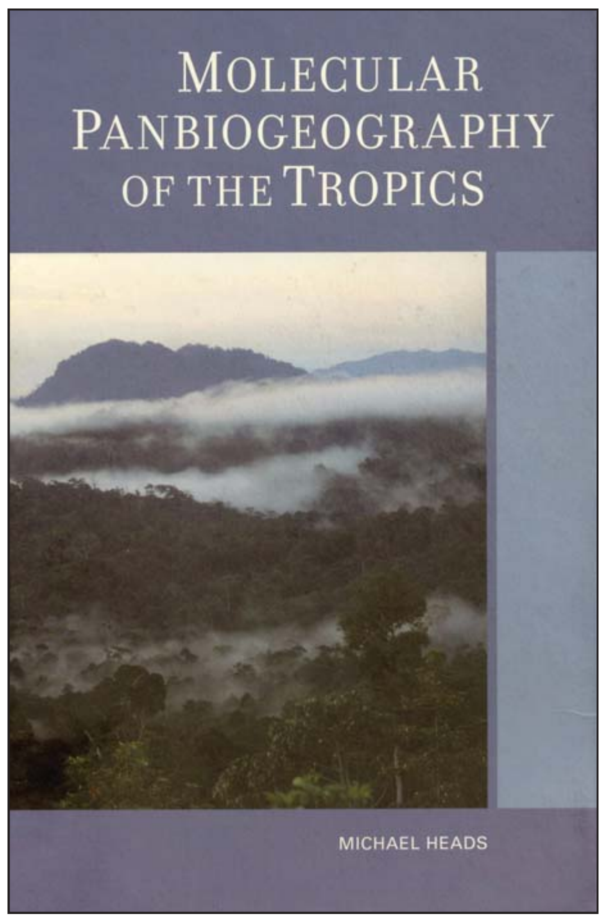
In 2012 I saw the first notices for Michael Heads' new book and, being familiar with his earlier thoughts and commentaries on the use and misuse of molecular phylogenetics, I suspected that we were in for a *royal donnybrook* in the systematics and biogeographical literature. I purchased the book and a lot of popcorn, and sat back to await developments.

In this short note a year later, I review some of the reactions to Heads' work as well as a very belated review of some aspects of the book itself. Several reviews of the book have appeared, some positive (Nelson 2013, Morrone & Escalante 2012), others decidedly unfriendly (Holland 2012, Shapiro 2012, O'Grady 2012). To the latter group we might add Walters et al.'s (2013) *Lysenkoist* plea to suppress all panbiogeographic publications, which mentions *Molecular Panbiogeography* but only in passing.

Both Nelson and Morrone and Escalante provide summaries of the book's chapters and general content. In brief, Heads contends that molecular phylogenies (stripped of their dubious clockish speculations) should be correlated with tectonic events for more reliable hypotheses of distribution. The negative reviews repeat the falsehood that Croizat and his followers categorically denied any role for dispersal as a biogeographic mechanism, misrepresent much



of what has been published in panbiogeography since, and studiously (or maybe just ignorantly) ignore the exceptionally active biogeographic workers in Latin America who incorporate panbiogeographic methods into their studies. They do not, however, land any serious blows to *Molecular Panbiogeography per se*, preferring to complain about panbiogeographers in general.

The core of Heads' critique in both *Molecular Panbiogeography* and his other publications is that the molecular clocks are frequently calibrated on the oldest fossil and this is considered the maximum age of a group, while in reality oldest fossils show the minimum age, (until another, older fossil is discovered). Not surprisingly this view is disputed by Holland, Shapiro and Walters et al., but for the most part they limit themselves to *ex cathedra* statements about the superiority of more modern techniques, more abstruse computational algorithms that now (trust us!) eliminate those pesky earlier problems with molecular dating. Shapiro makes a more concerted effort discuss the issue but he begins with a curious statement:

> "If we grant that the oldest fossil representative of a lineage can only give a minimum estimate of the age of the lineage *(which is both obviously and logically true* [emphasis mine])"… (Shapiro 2012).

Now, a methodology that begins by ignoring something obviously and logically true strikes me as a curious way of going about science. Holland (2012, p. 145) states that the "standard interpretation" of the age of fossils of common ancestors is the maximum age — a statement neither obviously nor logically true and somewhat at odds with the influx of "relaxing" algorithms now being used in phylogeographic publications.

Head's overall point is that dynamic tectonic processes give more believable calibrations than statistical manipulations of hypothesized rates of nucleotide sequence change. His discussion of the distribution of New World primates shows how their current distribution correlates with past tectonic events. This leads to a pair of interesting conclusions: the western parts of Ecuador and Colombia are biogeographically more similar to Central America than to the rest of South America; and, New World primates probably arose from mangrove inhabiting ancestors. On the first point, to Head's examples from monkeys we can add the two species of tapirs (*Tapirus*, Kricher 2011, p. 69) and at least one genus of mayflies (*Ulmeritoides*, Leptophlebiidae; Salles & Domínguez 2012). In the latter case, a species of *Ulmeritoides* belonging to the Central American clade has recently been found in western Ecuador (Flowers, *unpublished data*). Together these suggest a biogeographic region that includes Lower Central America and extends along the Pacific coast to roughly the present-day city of Guayaquil, Ecuador.

Three chapters of *Molecular Panbiogeography* are devoted to an analysis of distributions of the biota of Central Pacific, especially the Hawaiian Islands, and, not surprisingly, this has drawn much of the ire of the dispersalists. Heads points to numerous cases of putative poor dispersers with widely disjunct distributions that might better be explained by shorter hops along emergent islands of the past. Heads' discussion of alternative geological mechanisms seems mostly speculative, if plausible, and it is here that Holland and O'Grady aim their most vigorous blows. Holland, a "traditional biogeographer"—I'm sure he would not object to that term— working in Hawai'i, is on his home turf and so might be expected to have the advantage in this particular debate. Yet where Heads gives many specific examples of what he considers problematic distributions, Holland's review lets all of Heads specific claims pass without comment. O'Grady, who has likewise published on Hawaiian distributions, gives a more thorough critique of the panbiogeography approach, focusing on the lack of geological evidence for former Pacific islands in the vicinity of Hawai'i. He also provides a good list of references on the topic and points to a couple of gaps in Heads' own review of the literature. Yet O'Grady also leaves un-explained the numerous examples of disjunct distributions found around the Pacific, since it seems that some sort of "synthetic, well-supported" something has or will settle all doubts . So, while we may not be convinced by Heads' appeals to theoretical past tectonic activity, we are still left with the original problematic distributions that "traditional biogeography" still doesn't explain very well.

Similar instances of apparently damning critiques of panbiogeography that on inspection fizzle away to trivial quibbles can be found in Walters et al. (2013). On the issue of the age of the New Zealand biota, Walters et al. claim that the young ages they favor "have been quantified in internally consistent analyses that are also consistent with fossil evidence". But the proper dating of fossil evidence is exactly the bone of contention between panbiogeographers and dispersalists in general, and between Heads and his critics in particular. Until that issue is settled (and it has NOT been settled), "internally consistent" could merely mean that the analyses are all wrong by the same amount.

Shapiro, in his review, states that "the number of phylogeographic papers is now in the thousands and many are in first-rate journals", while panbiogeographers inhabit "an unproductive backwater". However even this is apparently too much to bear for Walters and his compatriots of the "New Zealand sank with all hands" modern school of biogeography. Discovering that 24 articles using panbiogeography have been published in the last 2 years, they seem to fear an imminent hijacking of evolutionary science by the renegades unless right-thinking editors put the hammer down. Cue the ghost of Lysenko.

Ironically, one point where I must part company with Heads is in his rather uncritical *acceptance* of molecular phylogenies as inevitably superior to morphological phylogenies.

The problem Heads sees is one of interpretation: morphologists are too attached to center-of-origin and other New Synthesis concepts, which leads to pedestrian and/or incorrect conclusions. On the other hand, the clade structure of molecular phylogenies is taken to be correct without question. Hence, a molecular study suggesting that both mulberries and blackberries belong in the Rosales, despite their morphological floral differences, means that all our basic ideas of what is a flower and what is an inflorescence now have to be reworked. While this may be true, the same reworking can be prescribed for some of the basic ideas of molecular biology as well (Gissis & Jablonka 2011). Heads also believes that molecular taxonomy is less prone to discordant phylogenies due to taxonomists cherry -picking their character sets. However, Mooi & Gill (2010) cite molecular studies in fishes where researchers using the same methods on very similar (although not identical) pools of species come up with discordant cladograms. Regarding one set of studies, they state:

> "These apomorphy-free trees that contradict strong morphological evidence are cases where we actually know less about the included taxa than we did before the study commenced." (p. 35)

The point here is not that Mooi & Gill are dead right or that the molecular workers they are discussing (and by extension, Heads) are dead wrong. Rather it is that both nucleotide sequences and morphological structures can give important information, and both can mislead the investigator if adopted uncritically.

Let's be honest. Heads and his fellow panbiogeographers have something they want to prove. So do the dispersalists. If panbiogeographers have gone out on a limb trying to prove the relevance of past tectonic activities, dispersalists have constructed their own limb called Goodbye Gondwana, and are not eager to have any molecular panbiogeographer saw it off under them. Both sides have accused the other of *cherry-picking* data that works to their own advantage, and to some extent each side may have a point. And now both sides can claim that molecular biology (through carefully selected examples) supports their respective positions. At the moment we still lack the information and/or the technology to finally settle the debate. It may be that we can never settle it. If a reader is turned off by all the controversy, he or she can skip over it and still find much to ponder and many new ideas on tropical biogeography to explore in *A Molecular Panbiogeography of the Tropics*.

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