**BOOK REVIEW**

# HOW REPORTS OF THE DEMISE OF GONDWANA ARE GREATLY EXAGGERATED

## *The Monkey's Voyage: How Improbable Journeys Shaped the History of Life.* Alan de Queiroz. 2014. New York: Basic Books, 370p.

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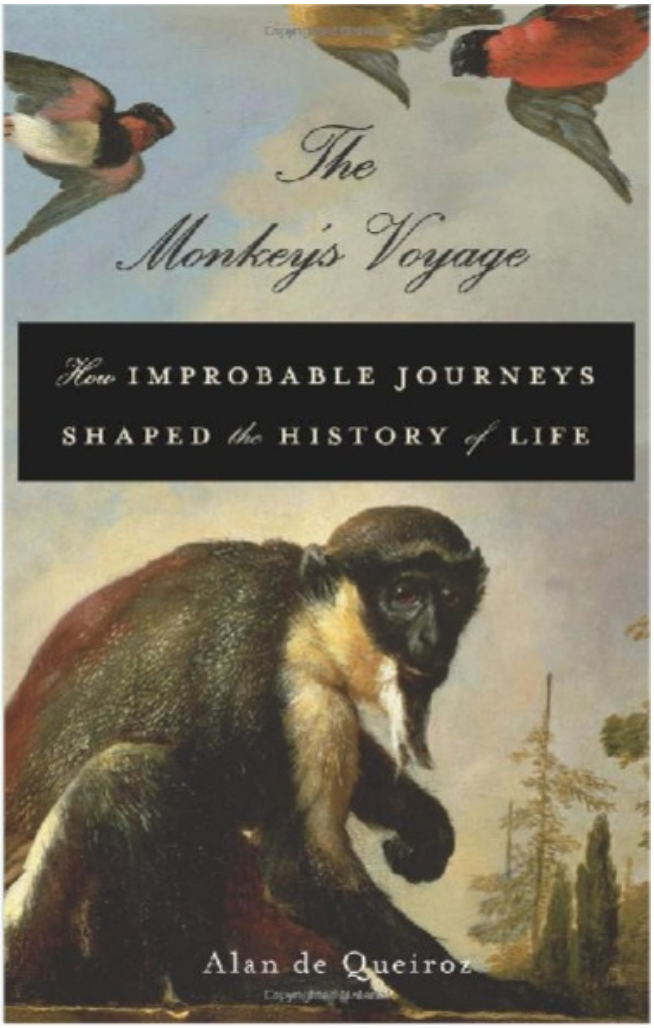
In the last 50 years, biogeography has gone through at least two paradigm shifts, which have resulted in very different views of how to explain disjunct distributions of plants and animals. At the beginning of the 1960's the dominant view was still that long distance dispersal was the only way a species, or genus, or family could find itself on, for example, both sides of the Pacific Ocean. The literature of biogeography was full of scenarios on how otherwise delicate living things could fly, float, hitchhike, or swim over long distances across various barriers. Since the idea of continental drift had yet to take hold, almost everyone bought into, or at least tolerated, the cascades of ad hoc hypotheses that were necessary to explain disjunct distributions. As the works of Wegener, Croizat, Hennig and Brundin became better known and studied, complex, evidence-free scenarios of long distance dispersal could in many cases be eliminated from biogeographical research. Following a period of *Sturm und Drang* (in English: *Storm and Stress*), when debates over scientific etiquette were almost as heated as debates over the new theories, a new paradigm called vicariance biogeography gradually supplanted long distance dispersalism as the preferred organizing theme in biogeography. Making a perhaps over-broad generalization, vicariance biogeography emphasizes continental drift and other geological events as responsible for the widely disjunct ranges found in modern plants



and animals.

Beginning in 2005, a new group of challengers has entered the biogeographical lists. This group, which might be called the "Goodbye Gondwana" (McGlone 2005) school, cites a host of recent molecular dating studies that show, or purport to show, that most species with highly disjunct ranges are too young to have been affected by the breakup of Gondwana. *The Monkey's Voyage* by Alan de Queiroz is an engaging account of the development and controversies of biogeography over the last fifty years. De Queiroz argues that it really was long distance dispersal of the Matthew/Simpson/ Darlington variety that has shaped Southern Hemisphere biotas, not continental drift. He presents himself and his fellow "Goodbyegondwanists" as former vicariance biogeographers convinced by the weight of evidence that most plants and animals that appear to have distributions influenced by Gondwanian continental drift actually originated long after the southern continents drifted apart.

*The Monkey's Voyage* is divided into four sections of between two and four chapters each. Between each chapter is a short account of a case of long distance travel by a plant or animal. The first section, "Earth and Life", is an account of the history of biogeography from Darwin and Wallace to recent arguments over the origin of the New Zealand biota. De Queiroz, perhaps channeling the late David Hull, gives us a mixture of history of science and pop psychology in recounting the New York School, the revolutionary contributions of Lars Brundin, the validation of plate tectonics, and the emergence of vicariance biogeography. This section is as much a propaganda document as a chronicle of events: when Michael Heads, Gareth Nelson and Leon Croizat are placed in a chapter entitled "Over the Edge of Reason", it kind of gives away de Queiroz' game. Nelson and Heads are cited throughout the book for their disparaging comments about molecular dating, until they seem to be the latter-day Cicero and Cato the Younger, forever trying to revive the ancient virtues of parsimony and Popperism and railing against the oncoming tide of likelihoodism and Molecular Elegance.

The second section, "Trees and Time", is a review of the development of molecular techniques, in particular molecular clock methods. I began this section with high hopes: as a non-user, I found the descriptions of how molecular methods were developed readable and interesting. Moreover de Queiroz devotes the better part of one of the chapters in this section to a surprisingly forthright review of problems and uncertainties, especially during the early development of clock methods. I was disappointed, however, when he claimed that relaxed clock methods had fixed much of the earlier uncertainty, but gave only a very cursory explanation of exactly what a relaxed clock is. After the good and quite detailed description of Hennig's methodology and a good description of the basics of vicariance biogeography in the previous chapter (in spite of some rather catty

comments about the vicariance biogeographers themselves), and given that relaxed clocks are the basis for de Queiroz' entire thesis in this book, I found the end of this section on molecular techniques strangely thin.

Having established, at least to his own satisfaction, that molecular dating is now robust and precise, de Queiroz proceeds to reinterpret Gondwana almost out of the biogeographical picture. The third section of the book, "The Improbable, the Rare, the Mysterious and the Miraculous" (the title seems to be a sly dig at the anti- dispersalist rhetoric of some pan- and vicariance biogeographers) is a collection of case histories from recent literature that show apparent long distance dispersal by various organisms at times long after they could have been helped by the breakup of Gondwana. In this section, the ad hoc hypotheses and Just-So Stories from the pre-vicariance era make their triumphant reappearance, with relaxed clocks giving them cover. The signature case, and the one that gives its title to the book, is the appearance of New World monkeys. Everyone agrees that they are the sister group of Old World monkeys; the bone of contention is if they separated before or after South America separated from Africa. Molecular dating suggests Africa and South America had pulled apart before the two ancestral monkey clades separated, so this would mean the ancestors of New World monkeys had a long raft ride to get across the Atlantic Ocean to their present address.

But maybe not quite that long: de Queiroz cites some geologic studies that postulate that the Atlantic was not as wide then as it is today and that there is evidence for now vanished islands between the continents. Thus it seems that in the new biogeography, invoking vanished island arcs to aid "long distance" dispersal is allowed — unless you're Michael Heads talking about Pacific island biotas. In *Molecular Panbiogeography of the Tropics*, Heads (2012a) postulated that Pacific atolls and vanished islands along seamounts could account for part of Hawai'i's biodiversity without resorting to long overwater jumps. De Queiroz admits that such island chains were possible but dismisses out of hand their biogeographical role on the grounds that the molecular dates for almost everything in Hawai'i are too recent. As the Atlantic islands apparently were around recently enough to coincide with the molecular dates of New World monkeys, they, of course, are a solid hypothesis. In *The Monkey's Voyage* they are found in the "Improbable" section, whereas Heads' hypotheses are brought up in the "Over the Edge of Reason" chapter.

A second example, from plants, illustrates what De Queiroz considers improbable, mysterious and miraculous dispersal. This is the sundew *Drosera meristocaulis* in the tepuis of Venezuela, and its close relation to a group of Australian sundews. In de Queiroz' telling, this species is a "weird" (p. 153) exception to the rule of a widespread genus of plants with poor dispersal abilities. Interestingly, carnivorous plants were an area of expertise for Croizat (Llorente *et al.* 2000) and the first three chapters

of *Principia Botanica* (Croizat 1961) deals at some length with *Drosera* and related carnivorous plant genera and families. The geographic structure of *Drosera* that de Queiroz mentions in passing is discussed in these pages. Those impressed by the "flight" of *D. meristocaulis* might also pause to wonder why none of the *Droseras* could manage the much shorter jumps from eastern South America to the western or central Andes or to México, or why the widespread species *D. indica* and *D. burmanii*, both "out of Australia" have wide ranges in Asia but *D. indica* reaches Africa while *D. burmannii* is found no further west than Sri Lanka, but a sister species *D. sessifolia* is found in eastern South America. A recent molecular phylogeny of *Drosera* (Brittnacher 2014) confirms much of the geographic structure discussed by Croizat and also shows several other "miraculous jumps" in other species (this web phylogeny predates the *D. meristocaulis* study). While de Queiroz confines himself to speculating about improbable aquatic bird transport only for *D. meristocaulis*, the web phylogeny has to invoke imaginary flocks of ducks going every which way to account for the disjunctions in their phylogram.

Or maybe there is a simpler explanation: relaxed clocks are still not the infallible dating methods their proponents claim.

De Queiroz and others (e.g. Waters *et al*. 2013) try to project an aura of inevitability to the new young dates coming out of many relaxed clock labs. However, why we should uncritically accept these results is never really addressed. De Queiroz does go over in some detail some of the earlier and now discredited methodology (which assumed a rigid clockishness in DNA) but assures us that we can now trust relaxed clocks. Of course, not all molecular clock studies have come up with suspiciously young dates, and it is interesting that De Queiroz suddenly becomes more critical of molecular studies when they fail to back up the "Goodbyegondwana" party line. For example, he hails the study by Sanmartín and Ronquist (2004) as one of the most important papers on biogeography in the last 20 years. This study showed a lack of correlation between branching patterns of plant clades and the breakup sequence of Gondwana, which leads de Queiroz to gleefully pass along a remark that the paper "signals the last great gasp of the vicariance paradigm" (p. 165). However, when de Queiroz discusses the other part of Sanmartín and Ronquist's paper—where they found *positive* correlation between animal branching patterns and gondwanian fragmentation—then suddenly he discerns all kinds of problems with their methodology: not enough widespread groups, wrong methodology, no dates— none of which seemed to bother him in the plant part of the study when the results were supporting the Goodbyegondwanist position.

Molecular biogeographical studies nowadays involve some variation of [Maximum Likelihood + BEAST = divergence date] Maximum likelihood algorithms are used to produce an initial cladogram or cladograms of the organisms being studied, and then BEAST or some similar

program is used to estimate times of divergence. At both stages the outcomes depend heavily on what models of molecular evolution, and what date calibrations the investigator feeds into the programs.

Heads (2012b) has examined a number of studies using relaxed clock methods and concludes many are still conflating minimum (fossil) ages with maximum ages, although most authors now loudly proclaim they are doing no such thing. How so? By putting probability estimates on Bayesian priors (such as exponential priors) that bias the estimate of the age of a clade heavily toward the known but minimum fossil age.

The problem of the "new" biogeography does not stop with relaxed clock methods *per se*. De Queiroz briefly alludes to “statistical methods largely taking over from the non-statistical approaches of the die-hard cladists” (p. 276). While not going into details, he is evidently referring to the switch from parsimony to maximum likelihood algorithms as the method of choice in phylogenetic studies. Wheeler (2012) explains the difference as follows:

> “Unlike minimization-based parsimony, ML (maximum likelihood) methods require explicit models of character evolution (as opposed to edit cost regimes) and edge parameters (branch lengths; parsimony requires none) to determine tree optimality. [page numbers not available in the Kindle edition]”

Since ML methods are the favored algorithms for producing the trees on which relaxed clock programs operate, the question of what models are input at the beginning by the investigator becomes very important to the dates that come out at the end. Farris (1999) disputes the claim that ML methods give greater statistical consistency than parsimony methods, and in the process notes that some ML models have been adopted more for ease of calculations that for accuracy or realism. Indeed, he has recently critiqued a paper, co-authored by Kevin de Queiroz, (brother of Alan de Queiroz ), for supporting use of “unrealistic” models as background knowledge (in ML) while objecting to the realism of a parsimony–related model (Farris 2008). Whatever one thinks of the specific issues raised in these exchanges, it seems evident that the entire process of inferring these young relaxed dates is every bit as open to uncertainty and bias as the vicariance methods the Goodbyegondwanists criticize.

Love it or hate it, parsimony has been discussed and dissected in the literature since it first appeared. It has a basically simple fundamental premise and arguments both for and against this algorithm are usually straightforward. But parsimony’s favored replacement

> “casts aside as obsolete methodologies that are clearly understood and philosophically justified in favour of statistical approaches that it does not even bother to explain completely or intelligibly. (Indeed, to judge from the available literature, it may not be possible to do so.)” (Brower 2014, p. 110).

The fourth section, “Transformations”, contains two chapters; in “the Structure of Biogeographic ‘Revolutions’” de Queiroz seems to be channeling Hull once again with sociological explanations of why so many of us fell for the “prettyness” of vicariance biogeography in the face of what de Queiroz claims is scant evidence. However, one could play this game in reverse and harp on the plethora of subjective ways results of maximum likelihood and relaxed clocks might be knowingly or unknowingly “tweaked”. One might also note sociological effects of the belief that molecular methods are by definition superior to morphological studies, and the infatuation of administrators and funding agencies for the high-techiness, lucrative indirect cost markups, and impact factor inflation of molecular studies over the “old-fashioned” work of organismal phylogenetics (Boero 2010).

In the final chapter de Queiroz presents his own idea of a new paradigm for biogeography, where Gondwana isn’t exactly denied but rendered irrelevant by repeated recent invasions. Those perpetually dazzled by anything molecular and high tech will enjoy de Queiroz’ entertaining writing and accept his new biogeography without troubling themselves about the algorithm behind the curtain. However, *The Monkey’s Voyage* for all of its forceful argumentation and interesting anecdotes still does not, in my opinion, make the case that molecular dates trump traditional biogeographic evidence. Wheeler (2012), who has written perhaps the most balanced treatment of the new systematic techniques, closes with a cautionary note about molecular dates:

> “… can hypotheses be falsified with “molecular” dates? Are these estimates sufficiently precise to adjudicate between biogeographic or other scenarios? This does not appear to be the case at present, but time will tell.”

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