FORUM

Into the storm: A personal retrospective on panbiogeography, Part II

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PART II: UNITED STATES OF AMERICA

My initial exposure to panbiogeography occurred at the time when an important debate was taking place over the methodological and conceptual relationships between panbiogeography and vicariance biogeography[1]. A key figure in this debate was Gary Nelson at the American Museum of Natural History who co-authored the controversial Croizat et al. (1974) paper along with Donn Rosen. This publication was widely seen as summarizing panbiogeography and its synonymy with vicariance biogeography, but Croizat (1982) later disavowed the relationship and Craw (1982) contrasted the two methodologies.

The Croizat et al. (1974) article was preceded by a manuscript written by Croizat that was submitted to *Systematic Zoology*. After the article was rejected by all the reviewers, Nelson offered to help revise the paper as a co-author (later with the inclusion of Donn Rosen). Substantial changes were made that focused on vicariance rather than panbiogeographic approaches (Llorente et al. 2000). Gary had understood that these changes were acceptable to Croizat, but he did not know that Croizat was seriously ill at the time and unable to properly assess the changes (Michael Heads, personal communication). Mike was able to obtain a copy of Croizat's manuscript during a visit to Coro, and we attempted to have it published in *Systematic Zoology* to allow readers the opportunity to see the differences for themselves and give some insight into why Croizat might later express misgivings. As one of the reviewers, Gary did not object to publication, but another reviewer was strongly opposed and the editor decided not to accept the article as it may be seen as an indication that the co-authors had done something wrong.

During the emerging debate over vicariance and panbiogeography, Gary was corresponding with Robin and Michael and he was also the external reviewer for Ian Henderson's PhD thesis (that included a panbiogeographic approach to caddis fly biogeography in New Zealand). Having moved to Vermont in 1988 I took the opportunity to meet with Nelson to talk about biogeography. At our first meeting I promptly launched into the nature of differences between Croizat's manuscript and the published paper. In those days I tended to be rather blunt and my

[1] This account is accurate to the best of my ability and memory. But I emphasize that it is a personal perspective and I acknowledge that the events described here may be seen differently from other perspectives. I also may have failed to include other significant events or individuals and for any such oversight I apologize in advance.

sledgehammer approach would probably have offended just about anyone else. But Gary took it all in stride and he responded with the argument that there were differences between our copy and the one he received from Croizat. Although we did not resolve our differences, I found Gary to be a refreshing change from most established biogeographers I had previously met in New Zealand. Being deeply interested in the nature of biogeography he was not bothered by different points of view and he was familiar with Croizat's work. I remained in regular contact with Gary and he continued to offer his hospitality during subsequent visits. Discussions continued to be interesting, stimulating, and always refreshing (and sometimes caused me to reflect on my own assumptions). In contrast, a meeting with Norman Platnick pretty much ended when he said my views on his understanding of ocean basin homology made him angry.

In 1983 I began a corresponding with David Hull. At a time when most people were dismissing Croizat out of hand, David was communicating with Robin and Michael and even willing to discuss the subject with naive newcomers such as myself. In hindsight this is perhaps not too surprising as Croizat was said to be a principal reason for David writing the book *Science as a Process* (Hull 1988), although much of the book focused on cladistic debates in the United States. David provided me with measured advice, support and critique. He expressed concern about our outspoken support for Croizat with the warning that it might be better to say nothing until tenure was obtained. He may have been correct, but if one does not speak out, will one ever? So I did not follow his advice to my cost. I have since told university graduate students that they should never question anything in science beyond the boundaries set by their advisors and leaders in their field – if they wanted to build a successful career.

In 1989 David invited me to visit Northwestern University and present a seminar to the Department of Philosophy. The audience was small and David found that he was unable to attend as he had overlooked a scheduling conflict with a philosophy conference being held at the same time in Chicago. Subsequent contact with David was intermittent and I last heard from him in 1997, although I also wrote to him until 2000. A few years later Hull (2008) published a chapter on panbiogeography in which he argued that vicariance biogeography won and panbiogeography lost. He criticized panbiogeographers for never publishing a condensed account even though he cited Craw et al (1999). But it remained an unresolved puzzle as to why he did not discuss the expanding interest in panbiogeography in Latin American countries. It was as if events outside the United States were not central to his conception of scientific progress in this field.

With all the international attention given to the panbiogeographic work, it is all too easy to forget that Croizat was also a student of botanical structure and function (e.g. Croizat 1961). Croizat developed a comprehensive synthesis of plant morphology addressing every aspect of morphology (Heads 1984) and proposed models of morphogenesis that differed radically from established textbook models of plant evolution, including the composite origins of flower and leaf, and deconstruction of leaf, stem, root as fundamental units of plant morphology. Croizat's botanical thoughts were widely ignored even as many botanists individually propounded views that were similar or in agreement (Heads 1984). I was therefore fortunate to now be near Rolf Sattler, a botanical morphologist at McGill University and one of the few botanical researchers who had taken Croizat's *Principia* seriously. Over the next few years until his retirement, I would periodically meet to talk about his work and Croizat's morphogenetics. I found Rolf to be kind and compassionate individual who understood the traditional resistance to Croizat's botany and biogeography.

In the late 1980's and early 1990's the future of New Zealand panbiogeography looked bleak, but there were emerging hints of increased international interest. Patricia Gentilli at the Smithsonian Institution told me about Juan Morrone who was very interested in Croizat's work and took it seriously. I began corresponding with Juan and he came to Vermont in 1993 to discuss Croizat's work. Although I now recall little of the conversation details, I do remember how delightful it was to discuss panbiogeographic methods and concepts with someone directly interested in their application. We have since then stayed in contact as he and his colleagues have generated numerous publications that applied panbiogeographic methods (sometimes along with other approaches).

In 1990 I contacted the editor of *Annual Review of Ecology and Systematics* about publishing a review article, but the editors said that panbiogeography was already covered by Craw's (1988) book chapter published two years earlier. I then approached the Oxford University Press and I was pleasantly surprised to receive a positive response and by 1991 a book contract was signed. I knew this project was going to be challenging as Robin, Michael, and I were scattered across the globe and lacked committed institutional recognition or resources. Finalization of the manuscript took almost eight years. A thoughtful anonymous reviewer drew attention to some significant deficiencies and a substantially new manuscript was organized by Robin. Subsequent book reviews were predictably variable, although far less negative and scathing compared with earlier reviews of the special issues in *Tuatara* and the *New Zealand Journal of Zoology*. The first printing sold out.

Robin Craw and Michael Heads had established the first sustained panbiogeographic research program since Croizat, although there were earlier biologists who also recognized or applied his work (Grehan 1990). During preparation of the 1990 special issue on panbiogeography, Robin drew my attention to Dwight Taylor as apparently the first person to publish articles adopting Croizat's panbiogeography (Grehan 2007). In the process of contacting Dwight, his colleague Jane Gray (a paleobotanist at the University of Oregon) also put me in touch with New Zealander Lucy Cranwell who had made positive references to Croizat's work during the 1960's. I wrote to Lucy (now in Tucson, Arizona) in September 1996 and my wife Claudia and I remained in contact with her until she passed away in June 2000. Lucy described herself as 'Hookerian' rather than 'Darwinian' and she was intrigued to hear about the continuing interest in Croizat's work. By the time Claudia and I were able to visit, she was too ill to receive visitors and sadly, she passed away not long after. At that time I also learned of the tragic death of Pilar Franco-Rosselli who was then among the very few active supporters of panbiogeography (Franco-Rosselli & Berg 1997). Her loss, along with that of Lucy, was a deep reminder of the fragility of life and they will always be missed.

While working on the panbiogeography book, my attention was drawn to the Galapagos problem. This archipelago had iconic status in evolutionary biology because of Darwin's visit and its contribution to his understanding about evolution. Ironically, it was the biogeography – the way organisms were distributed – that opened his eyes to the possibility of evolution. Darwin's model of chance dispersal was never seriously questioned by proponents of the Modern Synthesis who ignored Croizat's alternative biogeographic model and prediction of a major tectonic feature at the Galapagos. Ernst Mayr declared that there was no geological evidence for any former land connections involving the Galapagos and since Croizat was wrong about the Galapagos he could not be right about anything else. Mayr (as with most traditional biogeographers, even today) could not accept the possibility that biogeography might be able to reliably predict geology, or provide evidence of former geographies where geological evidence may no longer exist. Ironically, even while Ernst was using geology to refute Croizat, geological research was generating evidence more in accordance with Croizat's predications than the prevailing 'oceanic island' model. Building upon the outline in Craw et al. (1999), I compiled further biogeographic and geological evidence on the evolution of the Galapagos. The published paper (Grehan 2001) did not seem to receive any serious attention, perhaps because about this time Darwinian biogeographers were increasingly accepting the authority of molecular clock theory to preclude origins that might otherwise be linked to earlier geological events.

For the better part of the next decade my primary interests were absorbed by another topic, although one not entirely detached from biogeographic considerations. This occurred by accident when browsing a used book store in the outskirts of Pittsburgh with Claudia. She found a book called *The Red Ape* written by Jeffrey Schwartz (1987) and she thought it would be of interest to me because it was about orangutans and human evolution and I had expressed interest in the biogeography of this subject. Claudia was not impressed when I did not immediately express enthusiasm for the orangutan topic, but she decided that we should get it anyway. It just goes to show how thick I can be at times; as demonstrated not long after when we listened to a lecture on primate classification by Alan Walker at The Pennsylvania State University. Alan said that everyone accepted the chimpanzee as our nearest living relative other than a lunatic fringe (actual words) who thought it was the orangutan. If only Alan had not used the phrase 'lunatic fringe'. This was a term that had also been used against Croizat. And why Walker bothered to mention the orangutan at all I have never been able to understand.

I knew I had to read *The Red Ape*. Within its pages I found a solidly presented cladistic argument that made me wonder what could be so wrong to justify the nature of Alan's rejection. I asked Alan but received no reply. This was a harbinger of things to come. My previous experience with attitudes towards Croizat's work paled in comparison with the amount of scorn, some in professional publications, that was placed on both Schwartz and the orangutan theory. At least this time I was more aware of how much emotion could drive science. I quickly found that opponents could give me no more than rhetorical objections or assertions (such as – the evidence is wrong), and one prominent primatologist even expressed considerable outrage when I included the topic in an exhibit on human evolution at the Buffalo Museum of Science.

Behind the intensity of rejection was another surprisingly simple epistemological boundary between what was considered 'internal' and true, and 'external' and false. Along with the technological revolution in DNA base-pair sequence comparisons that allowed rapid phylogenetic analyses, there had developed an almost universal view in primate studies that 'genetic' DNA similarities provided the ultimate and only reliable evidence for reconstructing evolutionary relationships. Morphological evidence was 'traditional' and by implication dated and redundant. There was no room to consider the possibility that morphological evidence (which is, ironically, also genetic) could also represent a potential falsifier of molecular evidence.

In January of 2002 I contacted Jeff, who found to be very forthcoming about explaining his arguments and supporting his evidence (in contrast to his detractors). I learned that we both shared skepticism about Darwinian claims for the prominence of natural selection and Jeff also had no prejudice against panbiogeographic methodology. From these discussions I reviewed the documented evidence and established to my satisfaction that there were indeed many more derived features shared between humans and orangutans than humans and the African apes (Grehan 2006).

Jeff and I then entered into a collaboration to test the morphological evidence through systematics analysis. The result overwhelmingly (I use that term here because molecular studies also invoke its implied authority) supported the human-orangutan relationship and this was further emphasized by fossil hominids that also feature several specialized orangutan features not found in humans (i.e. they represented primitive retentions from the common human-orangutan ancestor). A common response from opponents was that the biogeography did not make sense because hominids evolved in Africa whereas orangutans evolved in East Asia - as if somehow this should not happen. Of course any practicing biogeographer knows that the nearest relative does not need to have an adjacent distribution and such disjunctions are more the rule than the exception. We knew that if we attempted to publish the orangutan evidence in a primate or human evolution journal we would have likely run into a solid wall of conservative prejudice similar to that confronting panbiogeography half a century earlier. We decided that it was better to submit the paper to the *Journal of Biogeography* because of the combined systematic and biogeographic analysis. As it was, the journal editors had to work at finding reviewers willing to review the paper. In the end they were able to find two reviewers and even then it took three revisions before the paper was finally accepted (Grehan & Schwartz 2009).

We were fortunate that the *Journal of Biogeography* editors were willing to consider a paper that was not only eccentric to popular belief, but also presented views about which they themselves had reservations. Although the paper resulted in two published responses from molecular theorists, it had no noticeable impact on the general science of human origins period. Subsequent publications continued the pretense that a viable alternative did not exist. During development of the paper I did come across several primatologists and paleoanthropologists who expressed sympathy or agreement with the orangutan theory (Grehan 2006) including some who did not want to be publically identified. One person who worked for an orangutan conservation organization said that they would probably lose their employment if they did! The paper also received expressions of support from cladistic theorists such as Malte Ebach, Gary Nelson, Chris Humphries, and David Williams with respect to the argument that molecular sequence methods could be cladistically problematic.

The high point of my biogeographic career was an invitation from Jorge de Carvalho to present a paper for the *Neotropical Biogeography Symposium* coordinated by Dalton S. Amorim at the twenty-seventh edition of the Brazilian Congress of Zoology in Curitiba, Parana in February, 2008. The Congress was attended by more than 4,000 people and approximately 800 people attended the first day of the biogeography symposium (Löwenberg-Neto & Haseyama 2009). It was an amazing experience. For the first time I found myself in an environment where panbiogeography was considered a respectable research program. I was fortunate to be able to meet a number of prominent and active biogeographers, including Juan Morrone who I had not seen since our first meeting 15 years earlier. This was the first time I attended a biogeographic conference in almost exactly two decades (the last being the panbiogeography symposium in New Zealand). I did not know audience expectations in advance so I focused primarily on outlining some of the general principles, concepts, and history of panbiogeography. But my greatest enjoyment was the opportunity to meet so many interesting and active researchers in the field of biogeography. I was later kindly invited to contribute a chapter on panbiogeography for the student textbook *Biogeografia da América do Sul* (de Carvalho & Almeida 2010).

Panbiogeography appears to have had its widest support in Latin America (Heads 2005). In concert with that development, Michael Heads continued to publish numerous papers that spanned an immense range of subjects and demonstrated the practical efficacy of the panbiogeographic method in action and also demonstrated that the geographic concordance of animal and plant distributions with global and local tectonics was an empirical reality. His *Molecular Panbiogeography* and *Biogeography of Australasia* (Heads 2012, 2014) represent an innovative synthesis of Croizat's approach. His publications also refuted popular claims for molecular clock divergence estimates being able to falsify earlier origins. As Mike has pointed out, a technical advance is not necessarily synonymous with conceptual progress.

Looking back I can see my early expectations for panbiogeography were overly optimistic. I was under the illusion that the empirical achievements of panbiogeography (such as predicting future geological discovery) would count for something in science. But it was as if being 'right' was a dubious quality. Sir Winston Churchill was liked even less by many of his detractors when his warnings about the Nazi threat were confirmed. Nevertheless, over the last three decades panbiogeography has indeed shown growth of interest and application, whether as formal panbiogeographic studies or in relation to other analytical approaches.

In hindsight I am not sure that the combative environment in the early days of panbiogeography in New Zealand could have been avoided. For my part, I was very ignorant of the ways of science and human behavior and I did not understand that pejorative responses are the normal social process of science. Just about any radical proposition will be received this way. I now understand that everyone, including myself, only does the best they can according to their respective viewpoints. Each time some hurdle is overcome another will take its place. In the early days it was either impossible or extremely hard to publish panbiogeography. Now there is far more scope of opportunity, although there remain some publications where the difficulty will always be present or depend on the vagaries of the editor. But again, that is the normal course of science.

When panbiogeography was almost the sole preserve of Leon Croizat, it faced the problem of suppression and was often treated as if it did not exist (Croizat 1984; Colacino &

Grehan 2001). But now, after years of numerous and diverse publications on panbiogeography by many authors in different countries, suppression of panbiogeography has become respectable. Eight prominent researchers recently decided that panbiogeography was such a scientific blight that they publicly rebuked editors and reviewers for allowing publication of panbiogeographic research (Waters et al. 2013). This is a remarkably honest paper. Bigotry and suppression have been part of science for as long as science has existed, but rarely proclaimed publicly since it is not seen to be good form, even if practiced. Of course, if one is not the target of their proposed pogrom then this may all seem rather innocuous. After all, it is always tempting to eliminate an irritant. But if panbiogeography is banned, which aspect of biogeography and systematics will be next? Why not call for a ban on employment of researchers supporting panbiogeography? Why not call for their removal from the institutions of science and eliminate their ability to publish at all? And what about other views these authorities don't like, for example criticism of the molecular clock? Waters et al. (2013) are, in effect, calling for a dictatorship where those who oppose their authority will be denied a voice. Is this to be the future of biogeography?

One of the ironies surrounding publication of Waters et al. (2013) is that their call for suppression was published by *Systematic Biology*. This is a remarkable turnaround for a journal that once led the world in promoting debate at the cutting edge of systematics research, and was one of the few leading journals that would publish articles about panbiogeography. With all but one of the authors being from New Zealand (the other being Australian), the Waters et al. (2012) paper also highlights a curious paradox about New Zealand biogeography. On the one hand it can be innovative and progressive, and on the other, conservative and repressive.

Depending on one's metaphysical perspective, my life in science has either been a series of accidents, or it was supposed to work out that way. Was it inevitable that I would find my way into scientific controversy? I am not sure, as my previous research interests were quite mundane. Either way, I have derived immense benefits as well as disadvantages to my career. I think I was fortunate to be able have the chance to start a career in the United States where I benefited from employers who had not the slightest problem with my heterodox views. I also benefited greatly from colleagues such as John Rawlins and Malte Ebach who provided expertise and support for my efforts to work with systematics and biogeography even though I was never trained in such fields.

I continue to express views that are not always well received, but I endeavor to respect individuals and be tolerant (as much as I can) to responses that may sometimes seem unfair. I have found it important to try not to take any idea so seriously that it interferes with a sense of humor (although sometimes I still fall short of that). Perhaps that is the most important lesson. Life is all too short.

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