Biogeography and Scientific Revolutions

Dennis McCarthy

Buffalo Museum of Science, Buffalo, USA

As our past disputes over evolution and continental drift make clear: those who underestimate the probative value of distributional evidence are likely to end up on the wrong side of science history. It appears that biogeography, which has served as the focal point of two recent scientific revolutions, is about to usher in a third.

Currently, a significant number of distributional facts, particularly involving oceanic disjunctions of poor-dispersing taxa, are in direct conflict with conventional palaeomaps of the Mesozoic Pacific and Tethys. Many researchers have dealt with these inconsistencies by ignoring basic biogeographical realities and positing radical cross-ocean dispersal hypotheses to explain the problematic disjunctions.

The Revolutionaries

The five revolutionaries (see inset), a group which could also include T. H., Huxley (evolution), Alexander du Toit (continental drift), and Leon Croizat (vicariance), all helped raze conventional assumptions in geology, biology and psychology -- yet, as noted, each of them, like Huxley, du Toit, and Croizat, also happened to be biogeographers. The question is, 'Why would so many revolutionaries in so many disparate fields of thought all be specialists in the little known field of biogeography?'

One possible reason is that biogeography is the science of adventurers. During an interview about his book, *Consilience*, E.O. Wilson once told me he suspected that those who followed the consilient view of the sciences and the sociobiological view of human nature and culture would be more likely, on average, to favor certain outdoorsy activities like rock climbing and kayaking. His implication, perhaps, was that a love of nature combined with a certain fearlessness or, at least, moxie might be helpful in rejecting religious and academic dogma for the steelier, realistic views of life. Adventurousness may also be a trait commonly shared by scientific revolutionaries. Wegener, while studying meteorology, took up hot air ballooning and in 1906 broke the world record for most time aloft, more than 52 hours. In 1912, while on an expedition in Greenland, he and his team barely survived what was at that time the longest crossing of an ice cap. The 'father of continental drift' would ultimately die on an expedition in Greenland in 1930. Alfred Russel Wallace spent a number of years along the Amazon and was one of the first Europeans to explore Rio Negro. In 1852, on his trip back to England from South America, his ship caught fire and sank, stranding Wallace and his shipmates in cramped and leaky lifeboats until their rescue ten days later. Undaunted, Wallace would later travel to Indonesia and become one of the first Europeans to live in New Guinea for an extended period of time. Darwin's five year jaunt

around-the-world, with a stop in Galapagos is well known and needs little elaboration here. Du Toit, like Wallace and Darwin, studied extensively throughout South America. He also helped map the Cape of Good Hope and spent time in the other Gondwanan continents, India and Australia.

The writings of these revolutionaries, like their life histories, advertise their Magellanic nature. Wallace's *On the Law Which Has Regulated the Introduction of New Species*, Darwin's *The Origin of Species*, Wegener's *The Origin of Continents and Oceans*, du Toit's *Our Wandering Continents*, do not smell of the class room; they smell of swamps, jungles, rivers, and beaches. Such risk-takers are not likely to be awed by professors or cowed by textbooks. There is not a schoolmarm among them.

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But innovative and accurate theories require more than just chutzpah; they depend on an agile and unbiased mind encountering a store of telling facts that entail an often simple yet unconventional conclusion. And this is what truly makes the study of biogeography so important. It is likely that, excepting the principle of material causality, no other known tenet or group of facts has proved more fruitful to the intellectual progress of the human race than the distributional patterns of plants and animals. Wegener, du Toit, Darwin, and Wallace were not simply biogeographers by hobby; they repeatedly used the implications of distributional facts to govern their earth-changing conclusions. Their method was so successful because it was so utterly biogeographical. They did not use orthodox assumptions to explain distributions; they used distributions to test orthodox assumptions.

In a letter to J.D. Hooker in 1845, Darwin described biogeography as the key to unlocking the mystery of speciation, referring to 'geographical distribution' as 'that grand subject, that almost keystone of the laws of creation.' Fourteen years later, he would publish *The Origin of Species* with two chapters devoted to 'Geographical Distribution.' In them, Darwin notes that frogs, toads, and newts are almost completely absent from oceanic islands - places where they would be expected to thrive. These distributions, as Darwin pointed out, are inconsistent with the 'theory of independent creation', that is, the idea that species could be independently created in two or more vastly separated regions. Instead, this biogeographical evidence supported the viewpoint of common descent. Frogs, toads, and newts are all descended from a mainland ancestor and have not been able to reach remote oceanic islands.

Likewise, all mammals, except bats, are absent from remote oceanic islands. As Darwin wrote:

'Why, it may be asked, has the supposed creative force produced bats and no other mammals on remote islands? On my view this question can easily be answered; for no terrestrial mammal can be transported across a wide space of sea, but bats can fly across.'

Darwin also pointed out that the endemic inhabitants from islands are nearly always most closely related to taxa from the nearest continental source:

'The inhabitants of the Cape de Verde Islands are related to those of Africa, like those of the Galapagos to America. I believe this grand fact can receive no sort of explanation on the ordinary view of independent creation; whereas on the view here maintained, it is obvious that the Galapagos Islands would be likely to receive colonists, whether by occasional means of transport or by formerly continuous land, from America; and the Cape de Verde Islands from Africa; and that such colonists would be liable to modifications; the principle of inheritance still betraying their original birthplace.'

Like Darwin, Wallace (1855) also used distributional patterns to help mould the theory of evolution and challenge conventional assumptions in biology. *On the Law Which Has Regulated the Introduction of New Species*, Wallace's rudimentary prologue to his evolutionary view, is first and foremost a biogeographical paper. In it, Wallace puts forth arguments that read much like the work of Croizat, anticipating Croizat's dictum that life and Earth evolve together:

'Of late years, however, a great light has been thrown upon the subject by geological investigations, which have shown that the present state of the earth, and the organisms now inhabiting it, are but the last stage of a long and uninterrupted series of changes which it has undergone, and consequently, that to endeavour to explain and account for its present condition without any reference to those changes (as has frequently been done) must lead to very imperfect and erroneous conclusions.

'The facts proved by geology are briefly these: -- That during an immense, but unknown period, the surface of the earth has undergone successive changes … That all these operations have been more or less continuous, but unequal in their progress, and during the whole series the organic life of the earth has undergone a corresponding alteration.'

After this passage, Wallace lists a series of observations from 'Organic Geography and Geology' such as the fact that families tend to be more widespread than genera, which in turn are more widespread than species, which are often limited to a particular geographic region. He also noted that the most closely related species are nearly always found in adjoining regions. These and other biogeographical and biogeological observations led Wallace to conclude that:

'Every species has come into existence coincident both in space and time with a pre-existing closely allied species'.

Three years later, in 1858, Wallace would pen his famous letter to Charles Darwin: *On the Tendency of Varieties to Depart Indefinitely From the Original Type*, where he clearly identifies the struggle for survival as a mechanism for evolutionary change. (Wallace disliked the phrase 'natural selection' because he believed it anthropomorphized Nature.) Wallace's intellectual progression is quite clear. His vast knowledge of biogeography led him directly to a biogeographical principle regarding speciation, which in turn, led him to the theory of evolution.

The recent rebellion in geology, which finally resulted in widespread acceptance of the pre-Jurassic closure of the Atlantic and Indian oceans, is no less indebted to biogeography. Suess named Gondwana after a region in India where the southern fossil flora *Glossopteris* is found, underscoring that Gondwana was, at bottom, a biogeographical concept. As with *The Origin of Species*, Wegener's *The Origin of Continents and Oceans* also contains a chapter on geographical distributions. Wegener's arguments need little elaboration here as they appear in most popular works and middle school text books on plate tectonics. For example, a Google search shows that 832 webpages that refer to 'plate tectonics' also refer to '*Glossopteris*.' 485 webpages refer to both 'Plate tectonics' and '*Mesosaurus*'. The webpages are mostly educational primers on 'Geology Basics' or 'The Story of Plate Tectonics' and discuss the fact that the trans-oceanic disjunctions of these fossil taxa helped confirm that the oceans between the Gondwanan continents were closed because these taxa were unable to cross oceans.

In the middle of the twentieth century, those geologists and biogeographers like G.G. Simpson (1940, 1943) who fought to maintain the orthodox view of continental stabilism put forth explanations for the disjunctions that included trans-oceanic rafting of vertebrates and a convenient pattern of fossil absences. In response, Alexander du Toit (1944) wrote the paper, Tertiary mammals and continental drift. A rejoinder to George G. Simpson, with quotes that remain relevant today:

'The notion of random, and sometimes two-way, 'rafting' across the wide oceans ... evinces, however, a weakening of the scientific outlook, if not a confession of doubt from the viewpoint of organic evolution…'.

'To argue that such southern disjunctive distribution is due to colonisation from the north through forms not yet discovered in the Holarctic region, is neither scientific nor fair...'.

Wegener and du Toit, of course, have now been vindicated - and Simpson-like arguments often become the first examples in which young students learn that mainstream scientists are not always objective. Historical lessons about the stabilist hypotheses of cross-ocean rafting or convenient fossil absences help underscore the rationalizations that scientists are willing to fashion in defense of orthodoxy. Yet, as will be shown, these same arguments are resurfacing today.

The return of radical dispersalism and the subordination of distributional evidence

In defending the view of continental stabilism, Dr. Rollin T. Chamberlin of the University of Chicago once wrote:

'Wegener's hypothesis in general is of the footloose type, in that it takes considerable liberty with our globe, and is less bound by restrictions or tied down by awkward, ugly facts than most of its rival theories.'

What is ironic about Chamberlin's statement is that the exact opposite was the case. It was Chamberlin's views that were speculative while it was Wegener and du Toit who were confining themselves to facts. Chamberlin's assumption that continents were ever-stationary, no matter how firmly believed by experts of that time, was still an assumption. In contrast, we know precisely where certain taxa reside, and we know precisely how they move. We know that remote oceanic islands like Hawaii, Pitcairn, and Easter Island lack native terrestrial vertebrates. All these facts confirm that while terrestrial vertebrates may often cross narrow marine barriers to proximal islands, they clearly cannot cross the full extent of an ocean. The geological assumption that created an oceanic separation

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between so many poor-dispersers was wrong.

Despite the efficacy of distributional analyses in past scientific revolutions, a number of researchers have abandoned this glorious tradition of biogeography and now use everything *except* distributional facts when fashioning distributional explanations. The result is a recent spate of hypotheses of cross-ocean rafting events of terrestrial vertebrates and patterns of convenient fossil absences - all of which are required to maintain fashionable geological and molecular-clock assumptions.

The biogeographical controversy today, mostly involving the question of vicariance across the Pacific, is between 1. researchers who agree that many distributions are the result of long distance, trans-marine colonization but who accept that certain distributional (and biophysical) facts provide compelling evidence for vicariance and, 2. radical dispersalists who, like their counterparts from the middle of the 20th century, believe that distributional facts should always be subordinate to geological (and now molecular) assumptions. The methodology of the latter mainly consists of looking at conventional paleomaps for the time period of diversification that has been inferred from fossil data and/or the most recent molecular analyses. If the paleomap places an ocean between the sister taxa, then the conclusion is an ancestor crossed it. This assumption is maintained regardless of the immobility of the taxon, its absence from all oceanic islands, the vastness of the alleged barrier, or the repetition and the precision of the distributional patterns. In other words, biogeographical facts, no matter how compelling or well known, are deemed irrelevant.

The banded igauna is is only found on Tonga and the Fiji Islands. How did it get there?

In one of the many recent papers that adopted this anti-distributional methodology, de Queiroz (2005) ended up advocating jump-dispersal of monkeys, cichlids, and geckos across the full extent of an ocean. De Queiroz dismissed concerns regarding the uncertainty in molecular dating techniques with the assurance that 'conservative choices can be made in such analyses'. But were all of the choices that he referenced really conservative?

De Queiroz supported the claim of trans-Atlantic rafting of New World monkeys with a reference to the molecular analyses of Schrago and Russo (2003), who calibrate their molecular clock on an assumed Cercopithecoid-Hominoid split at 25 mya and calculate the divergence of New and Old World monkeys at 35 mya. Arnason *et al*. (1998, 2000) however note that even the traditionally assumed divergence at 30 mya for the Cercopithecoid-Hominoid lines is far too recent, for it suggests a diversification of Equidae and Rhinocerotidae at 28 mya , cetacean origin at 30 mya, and Eutheria origin at 80 mya. Each of these times significantly post-dates the earliest fossils of these groups: ~48 mya, 50 mya, and more than 120 mya, respectively. Arnason *et al.* (1998, 2000) instead calculate that the Cercopithecoid-Hominoid divergence took place >45 mya and calculate the split between the New and Old World Monkeys at 60 - 70 mya. At this time, the oceanic barrier was merely a narrow seaway, and the Falkland plateau may have been particularly close.

Biogeography, despite what recent anti-vicariance papers attempt to imply, is by no means mute on this subject. Monkeys do not occur on any oceanic island (Mittermeier *et al*. 1999). So if they do have the ability to raft across oceans, it is apparently a talent they do not like to flaunt. Moreover, while a great number of primate species have colonized the continental islands of Indonesia (Borneo alone boasts 12 different species), they have been unable to cross the relatively narrow marine gap to New Guinea or Australia (Brandon-Jones 1998). In fact, other than the macaques of Sulawesi and Lesser Sunda Islands and the leaf monkeys of Lombok (likely introduced by humans), none of the Indonesian non-human primate species have been able to conquer the narrow Bali-Lombok strait (<40 km) of Wallace's Line (Brandon-Jones 1998).

Far from being the most 'conservative' option, the late date and trans-Atlantic rafting hypothesis of monkeys is actually the most fantastic. It is a deliberate theoretical preference, described as fact, that conflicts with the known distribution patterns of monkeys and would require one of the most extraordinary dispersal hypotheses in the history of terrestrial mammals. Moreover, the assumption of this miraculous rafting event is then used as supporting evidence for dispersal miracles in general.

Another example of a 'conservative' assumption is that the vicariance hypothesis requires origin for freshwater cichlids prior to or during the Early Cretaceous while fossil and molecular clock evidence requires a Cenozoic origin. Each of these is disputable, if not dubious.

First, while the strip of Early-Cretaceous seafloor between Madagascar and Africa does require their separation at that time, the lack of similarly-aged Indian Ocean seafloor north of this strip *does not* suggest that *India* was also similarly separated from either Africa or South Asia. In fact, Briggs (2003a), who de Queiroz references for his conclusions about cichlids, has himself challenged this conventional view, concluding that Cretaceous Indo-Madagascar biogeography demands that 'the depiction of India in late Cretaceous as an isolated continent is in error'. Briggs instead shrinks the hypothetical Cretaceous Tethys gap by assuming a larger Indian continent that was greatly shortened during Himalayan orogenesis. In this way, 'India, during its northward journey, remained close to Africa and Madagascar even as it began to contact Eurasia'. In fact, as little to no ocean floor currently exists that could have separated India from Asia and Africa during the Late Cretaceous, there is no geological reason to assume significant Late Cretaceous separation of these regions at all.

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Second, as Sparks and Smith (2005) argue: 'the discovery of these Eocene fossil cichlids not only effectively doubled the age of the family (Murray 2000), indicating that 'as time goes on' the chance of such finds does not necessarily become 'less probable,' but also that these fossil cichlids represent derived African lineages (Murray 2001; Sparks 2004), suggesting a significantly older origin for the family'.

Third, the molecular clock analysis of Vences *et al*. (2001), which is at odds with the analysis of Kumazawa *et al.* (2000), has been challenged by Chakrabarty (2004) because it relies on cichlids of the East African Lakes for calibration. As Chakrabarty writes, '[The] wide estimates of ages for the lakes, and the fact that the lineages within the lakes may not be the same age as the lakes themselves (Meyer *et al*. 1991; Nishida 1991), make this molecular clock calibration suspect'. Chakrabarty concludes from his review of phylogenetic analyses that vicariance is 'the only explanation'.

Both the geological assumption of a wide Late Cretaceous Tethys and the molecular-clock and fossil-based assumptions of the late timing of the divergence would have to be true in order to necessitate a cross-ocean dispersal event of cichlids. But while each of these assumptions has been recently challenged (and in my view the notion of a wide Late Cretaceous Tethys has been all but refuted), the following distributional and biophysical facts about cichlids, all underscored by Sparks and Smith (2005), remain:

1. The only study done on saltwater tolerance of Malagasy cichlids confirmed that their exposure to saltwater was 100% fatal after 12 hours (Riseng 1997).

2. Cichlids have been unable to reach any oceanic island and have a predominantly Gondwanan distribution, showing the precise sister relationships predicted by vicariance: Africa-South America and India-Madagascar. The dispersal hypothesis requires freshwater cichlids to have negotiated thousands of kilometers of open ocean between India and Madagascar without colonizing any other island or, for that matter, crossing the Mozambique Channel to Africa. Apparently, these taxa like to confine their oceanic jaunts between regions that were once connected.

In both analyses involving monkeys and cichlids, the molecular and geological assumptions required for long distance dispersal have been independently challenged while the distributional evidence remains unambiguous. Thus, what was true in the middle of the 20th century is still true today, radical dispersalist hypotheses result from the elevation of disputed non-biogeographical assumptions and theory over uncontroversial biogeographical facts.

Pacific biogeography

Nowhere is the practice of subordination of biogeographical evidence more common than along the Pacific margins. As recently noted, a myriad of trans-Pacific disjunct taxa, both fossil and extant, link narrowly defined systems of sister areas on opposite sides of the Pacific, with each particular region from Tierra del Fuego to Canada showing a clear biological link to a corresponding Western Pacific region from Stewart Island to Japan (McCarthy 2003). A few examples of disjunct sister taxa from New Zealand and South Chile include: the flat oyster, *Ostrea chilensis*, which does not have an extended pelagic phase (O'Foighil *et al*. 1999), and the plant genus *Abrotanella*, which lacks the typical method of dispersal in the family, the pappus (Heads 1999). The most recent fossil relatives of the only living sphenodon, New Zealand's lizard-like, Tuatara are the Late Cretaceous sphenodontians of Patagonia (Apesteguia and Novas, 2003). Further north, the freshwater-restricted sisters, *Brachygalaxias* and *Galaxiella*, are limited to south-central Chile, Tasmania, and Southwestern Australia (Waters et al, 2000). The neotropical sun bittern (*Eurypyga helias*) is the closest relative of the flightless kagu of New Caledonia and two extinct flightless species (*Apterornis*) from New Zealand (Cracraft 2001). Fiji's banded iguana *Brachylophus* is sister to the Californian iguanid *Dipsosaurus* (Sites *et al.* 1996) and iguanas occur nowhere else in the Central or West Pacific. This is just a small sampling of hundreds of narrow-range, poor-dispersing trans-Pacific disjunctions that do not appear on any intervening oceanic island and strictly adhere to a common distributional pattern (McCarthy 2003).

To focus on a single example: the disjunction of the Fijian banded iguana and its Californian sister requires, according to conventional paleomaps, an 8000 - 12000 km rafting trip, mostly over hypothetical (i.e., currently non-existent) seafloor. This is more than three times longer than the now forsaken trans-Atlantic rafting trips put forth to save continental stabilism. This hypothetical trip would be the greatest oceanic jaunt of any taxon in the history of terrestrial vertebrates - and by far. Yet the banded iguana is restricted to Fiji-Tonga and appears on no other oceanic islands. Given that so many other taxa share the same tropical Western America - Western Pacific distribution, it is difficult to imagine a stronger biogeographical argument for vicariance. If a cross-Panthalassa rafting hypothesis does not strain credulity, then what dispersal hypothesis would?

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Rafting vertebrates and distributional evidence

As stated earlier, many of the trans-Pacific disjunct taxa, like the banded iguana, the flat oyster *Ostrea chilensis*, the flightless kagu, the Tuatara, the plant genus *Abrotanella*, etc., are restricted to a very narrow Western Pacific range and absent from all other oceanic islands. Not only do the biophysical limitations of these taxa imply that they cannot cross the full extent of oceans, but their absence from all other purely oceanic islands confirms their difficulty with wide marine gaps. The importance of such evidence today is not simply ignored but openly challenged by those who support miraculous dispersal events.

Recently, a paper submitted to a biogeographical journal noted the absence of a variety of alleged trans-oceanic dispersers from oceanic islands - and the reviewer, who suggested rejection, challenged the significance of such absences with the comment: ‘Biogeography is not about things that haven't happened’. More than 140 years after Darwin first explained the theoretical significance of the absence of terrestrial mammals and amphibians from remote oceanic islands, modern 'biogeographers' are now contending that their subject is not concerned with such matters. Likewise, more than 60 years after du Toit challenged the hypothesis of cross-Atlantic rafting, which was used to rescue the hypothesis of a wide Mesozoic Atlantic, biogeographers are now positing rafting events across a gap nearly three times wider in order to rescue the hypothesis of a wide Mesozoic Pacific.

The points and counter-points of this debate have not changed much since the nineteenth century. The evolutionary assumption of common descent, like the hypothesis of vicariance, predicts that certain continental poor dispersing taxa will be absent from oceanic islands. Both theories require very clear distributional patterns, particularly involving poor-dispersers. Contrariwise, neither the theory of independent creation nor the theory that all these disjunct vertebrates are capable of oceanic jump-dispersal, offers a rational explanation for this pattern of island truancy. The aforementioned reviewer who rejected this argument claimed that absence is only partly due to dispersal ability and ‘that all sorts of other factors are involved, involving an amalgam of geology, climate, evolution, ecology, and history’. This is precisely the counter-argument Darwin anticipated from those favoring independent creation, which is why he was careful to note that such absences from oceanic islands ‘cannot be accounted for by their physical conditions; indeed it seems that islands are peculiarly well fitted for these animals’. And Darwin is still correct. The most likely reason for the distributional pattern of monkeys and banded iguanas is *not* because of a conspiracy of local environmental circumstances that has somehow prevented long-term colonization of every other oceanic island in the world. The most reasonable explanation probably has to do with the fact that monkeys and banded iguanas drown -- so they cannot reasonably be expected to cross the full extent of an ocean. Analogous arguments hold for cichlids, *Ostrea chilensis*, *Abrotanella*, etc. Quite simply, the reason why all these taxa *appear* both biophysically and distributionally to be isolated by wide marine gaps is because they are, in fact, isolated by wide marine gaps. It's not a coincidence.

Du Toit also seemed aware of the connection between the debate over vicariance and Darwin's past arguments against special creation, which is likely why he contended that the hypothesis of rafting across the wide oceans, i.e., the rejection of vicariance, 'evinces … a weakening of the scientific outlook, if not a confession of doubt from the viewpoint of organic evolution.' In other words, supposing that the trans-Atlantic fossil sister taxa were always disjunct re-opens the door to theorists of special creation who had argued precisely the same thing.

McDowall (2004) challenged the seeming triviality that taxa that can cross the full extent of an ocean are likely to be wide ranging and found on other oceanic islands, by referencing a single counter-example: a diadromous fish that had merely crossed the Tasman Sea to New Zealand and had also colonized 'islands to the north.' This taxon, however, is not relevant to the claim that numerous taxa can traverse the full breadth of the ocean yet remain restricted to only two narrow regions.

This 'cross-Pacific dispersal/wide ranging' dispute need not foster endless debate amongst the litigants, for, in the end, empirical evidence raps the gavel. Kingston *et al.* (2003) have recently provided a comprehensive analysis of range data for each of the 114 species of flora on Pitcairn. Since Pitcairn is a juvenile oceanic island group that formed in the middle of the ocean, long-distance trans-marine dispersal is required for all inhabitants. According to Kingston *et al.* (2003): 'The flora of the Pitcairn Islands is derived from the flora of other island groups in the south-eastern Polynesian region, notably those of the Austral, Society and Cook Islands. Species with a Pacific-wide distribution dominate the overall Pitcairn group flora'. They also note that Pitcairn, unlike New Zealand, *did not exclusively share any plant with South America*. Instead, all plants that had colonized both Pitcairn and South America had also managed to disperse across the full breadth of the Pacific. For example, *Asplenium obtusatum* G. Forst, found in both Pitcairn and South America, also occurs in Easter Island, Polynesia, New Zealand, and Australia. None of the 114 species were poor dispersers. None were born of narrow range ancestors that appear in only one other distant continental region.

This empirically confirms that which had otherwise seemed self-evident: Taxa that are able to colonize the remoter regions of the Pacific can annex nearer regions too. Often, the nearer regions are used as stepping stones. A handful of exceptions may exist, but one should not mingle exceptions with the overwhelming rule.

The following table comprises the terrestrial vertebrates and freshwater fish that are currently assumed to have crossed the full extent (more than 3000 km) of an ocean barrier. When different analyses have provided different dispersal dates, the most recent one was chosen (Table 1).

Taxon	Regions	Earliest assumed date of divergence	Reference
Tarentola geckos	Africa and Cuba	23 ma	de Quieroz (2005)
Monkeys (Platyrrhini)	Africa and South America	35 ma	de Quieroz (2005)
Caviomorph rodents	Africa and South America	35-31 ma	de Quieroz, (2005)
Cichlids	Africa and South America	41-58 ma	de Quieroz (2005); Vences *et al.* (2001)
Cichlids	India and Madagscar	25-29 ma	de Quieroz (2005); Vences *et al.* (2001)
Aplocheiloid killifishes	Africa and South America	Early to Mid Tertiary	Briggs (2003b)
Aplocheiloid killifishes	India and Madagscar	Early to Mid Tertiary	Briggs (2003b)
Boine snakes	South America and Madagascar and East Asia	Paleocene or earlier	Vences *et al.* (2001)
Iguanines	South America and Madagacar	Cenozoic	Vences *et al.* (2001)
Podocnemine turtles	South America and Madagascar (and perhaps Africa)	Cenozoic	Vences *et al.* (2001)
Agamid lizards	Australasia and South East Asia (across the Tethys)	30 ma	Hugall and Lee (2004)
Banded iguana	California and Fiji	Eocene (?)	Sites *et al.* (1996)

Table 1. Distribution ranges of taxa.

The preceding distributional hypotheses, as well as the evidence provided by oceanic islands, suggest a series of distributional patterns that require explanation:

Even accepting molecular clock

assumptions that provide the most recent dates of divergence, no terrestrial vertebrate has managed to cross an ocean (>3000 km) in the last 20 my - despite numerous alleged trans-oceanic dispersals prior to that.

No terrestrial vertebrate has managed to disperse to a juvenile (pre-Eocene) oceanic island more than 2000 km from a source (perhaps no more than 1500 km).

All of the seafloor barriers crossed by the taxa comprise crust that is almost all less than 83 my. The majority of the crust of these seafloor barriers is less than 40 my.

Every pair of regions (destination and source) are ancient regions that have recently been claimed to have been in proximity in the Late Cretaceous for geological reasons, including Africa-India-Madagascar (Briggs, 2003a), Fiji - Neotropics (McCarthy, 2003), Australasia - Southeast Asia (McCarthy, 2005).

The most likely explanation for these distributional facts is *not* that pre-Miocene vertebrates were better rafters and preferred to jump-disperse between ancient regions that were once in proximity. A more reasonable explanation is that the papers disputing the geological palaeomaps and molecular clock assumptions are, in fact, correct.

Geology, a speculative science

In a paper published posthumously, the Australian botanist L.A.S. Johnson (1998) introduced his historical analysis of Proteaceae biogeography with an interesting admission regarding his first views on the subject: ‘Unfortunately, at the time we wrote this paper [on Proteaceae], we were misled by conservative geologists who had not got around to accepting continental drift, and our phytogeographic understanding was much distorted by this’. Yet even after the recent triumph of vicariance over the dominant stabilist paradigm in geology, some still tend to elevate geological speculation over basic distributional realities. Implicit in papers that indulge in extravagant dispersalism and a plethora of just-right fossil absences is the notion that the basic principles of biogeography are wispy and yielding while geophysical theories are made of sterner stuff. Such papers appear to extend the legend that planetary scientists work in a field devoid of speculation, the belief that when a biogeographer and geologist confront each other on a narrow path, the biogeographer must step aside. But the question Wegener and du Toit may well have asked half a century ago is still apropos today: Does any scientist, from any field, really believe that we know more about the formation and inner workings of planets than about the locations, habits, relationships, and biomechanics of plants and animals -- about taxa that we have watched and held and explored inside and out?

The fact of the matter is geology, geophysics, and planetary science are, by no means, settled subjects. Recently in the 125th Anniversary edition of journal *Science* (Vol. 309 [5731], 2005) a list of ‘125 Questions: What don't we know?’ was put forth. Two of those questions were ‘How do planets form?’ and ‘How does Earth's interior work?’ Forty years ago the discovery of seafloor spreading revolutionized geological theory, revitalizing the long-rejected theory of continental drift. But even over the last decade, many long standing geological assumptions have been falsified, requiring drastic alterations to orthodox views. Recent paleomagnetic studies of the Detroit seamount have falsified the long-accepted view, taught to a generation of grammar school students, that the Emperor-Hawaii seamount trend was the result of Pacific plate motion over a stationary hotspot (Wilson 1963). The Detroit seamount was actually determined to have a paleolatitude nearly 20 degrees north of conventional expectations (Tarduno *et al*. 2003; Sager 2002), revealing that hot spots are not really ‘fixed’. Palaeostratigraphic, Palaeomagnetic and palaeobiogeographical data have also refuted the view of an oceanic (Tethyan) separation of South Asia and East Asia from India and Australia, respectively, in the Palaeozoic. Instead, the classic plate tectonic view of Pangaea has now been abandoned - and all of southern Laurasia, including South and North China are now placed adjacent to the Eastern Gondwana continents India and Australia during that time. Likewise, the long standing view of India as an isolated microcontinent in the middle of the Tethys in the Late Cretaceous has been rejected by Briggs (2003a) because of the oceanic gap this would place between a variety of terrestrial vertebrates. Briggs instead adopts an inflated-India (narrower Tethys) hypothesis which allows Africa, Asia, India, and Madagascar to remain in proximity in the Late Cretaceous. Also, the extreme Tethys gap between Australia and Southeast Asia in the Late Cretaceous has also been recently challenged due to biogeographical and geological reasons (McCarthy 2005). Palaeomaps, it seems, are like the weather: If you don't like the alleged size or placement of a pre-Cenozoic ocean, just wait a while. It will change.

But while new discoveries continue to change our views on the formation of planets, continents and oceans, we can at least take comfort in the firmness of very basic biogeo-

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graphical realities, like, for example, that terrestrial vertebrates drown and oceans are vast. This is why past scientific revolutionaries chose to focus on the 'grand subject' of distributions rather than remain faithful to the conventional assumptions of other fields of science.
Biogeography is really where the facts are - indeed the simplest facts of all. Wegener and du Toit faced ridicule for not accepting certain conventional geological assumptions, but no amount of authority can overcome the following elemental fact: Terrestrial vertebrates cannot cross oceans. That is why they do not appear on remote oceanic islands (>2000 km from a source). That is why we know they have not been able to cross an ocean in the last 20 million years. Their difficulty with wide marine gaps was obvious when Darwin used it as evidence for evolution; it was obvious when Wegener and du Toit used it as evidence for a closed Atlantic and Indian Oceans; and it is still obvious today. The 'grand subject' of geographical distributions is once again about to triumph over conventional assumptions in other fields of science.

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Dennis McCarthy will be presenting a talk at the SA Biennial Sympoisum in Cardiff, 2005.

Meeting Report

The Palms: an International Symposium on the Biology of the Palm Family

The Linnean Society, London and the Royal Botanic Gardens, Kew
April 6-8 2005

For an angiosperm family of relatively modest size (2361 species at the last count; Govaerts & Dransfield 2005), the palms appeal to a disproportionately large number of researchers in a plethora of different fields. Explanations for interest in the family are typically wrapped up in brave boasts such as 'palms are second only to the grasses in economic importance', though our legume colleagues might disagree, or the more romantic 'palms are emblematic of the tropics'. Regardless of the factual basis of such rhetoric, there is no doubt that palms have a special appeal that accounts for the impressive turn-out at the recent international symposium on the biology of the family. More than 100 delegates from 22 different countries came to London in April this year for two days of talks at the Linnean Society and a day of workshops and tours at Kew.

In the opening lecture of the structural biology session, Barry Tomlinson (Harvard University) tackled 'the Uniqueness of Palms' head on from the perspective of functional morphology, exploring the opportunities and limitations of arborescent life within monocotyledonous constraints. He highlighted several record-breaking features of the family, some well known, such as the largest leaves and largest seed, and others less widely trumpeted. In particular, Barry detailed the astonishing corollary of a palm's commitment to stem-building by primary growth alone: stem vasculature remains indefinitely functional over very extended periods. Given the exceptionally long life spans of some palm species, up to 720 years in *Livistona eastonii* (Hnatuik 1977) for example, this feature further underlines the record-breaking tendencies of this champion family.

The four talks that followed Tomlinson's further emphasised the remarkable structural properties of palms. Paula Rudall (Royal Botanic Gardens, Kew) approached palm floral morphology within the broader context of monocot flowers, focusing in particular on isolated taxa such as *Nypa* and *Eugeissona*. James Tregear (IRD, Montpellier) followed on with a report of his research group's activities in floral developmental genetics in palm oil; detailed work on MADS box genes suggests that some, but not all elements of the ABC model can by applied to palms. Still within the palm flower, Sophie Nadot (Université Paris-Sud) illustrated the surprising diversity of developmental patterns in monosulcate pollen types in palms. Sandrine Isnard (AMAP, Montpellier) concluded the session with a further ego boost to the palm community with her elegant examination of the outstanding biomechanical strategies of climbing palms, particularly in *Plectocomia*.

The phylogeny and evolution sessions commenced with a review of the palm fossil record by Madeline Harley (Royal Botanic Gardens, Kew). The palms have the richest fossil record in the monocots (sorry, another superlative), but as Madeline showed, this should not be interpreted as evidence for great age. The palms, in fact, do not appear unequivocally until the Santonian/Coniacian boundary in the late Cretaceous, some 40 million years later than the earliest monocot fossil, *Mayoa* attributed to Araceae (Friis *et al*. 2004). Aaron Pan (Southern Methodist University,