

An alternative Gondwana: Biota links South America, New Zealand and Australia

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Ever since Eduard Suess first theorized its existence in an effort to explain the distributions of *Glossopteris*, Gondwana has been a biological or paleontological phenomenon. Today, it remains an elegant symbol of the intricate relationship between geological and biological history. Some early 20th century paleontologists, such as Hermann von Ihering, believed that “only the *history of life* on the Earth enables one to grasp the geographical transformations of the past” (Ihering in Wegener 1966, vii, original italics). Ihering’s sentiments are echoed by Léon Croizat’s “Earth and life evolve together” (Croizat 1964, p. iv), which transformed 20th century biogeography. Gondwana was discovered by biogeographers, biologists and paleontologists, who identified repeated distributions across impermeable barriers such as oceans and mountain chains. Land bridges became an all-purpose, theoretical “escape clause” to explain trans-Atlantic distributions of terrestrial and freshwater organisms.

Throughout most of the twentieth century, geologists dominated the study of Earth history, which in turn, rigidly molded our views of historical biogeography. Geologists looked at the surface of the Earth from a static perspective. The Earth provided an inert and ever-stationary landscape over which life randomly dispersed. The hypothesis of a planet Earth that did nothing more than rotate and tumble around the sun was not open to any further speculation. The end of the apparent battle between Vulcanists and Neptunists saw an end to geologists at war (see Hallam 1983). Geology today, as then, is a highly organized discipline that frowns upon unconventional interpretations, especially those supported by non-geological evidence. Perhaps this is why biogeographers, a highly disorganized, multidisciplinary group of biologists and geographers, continue to challenge geological interpretations of the Earth. Taxic distributions do not match current palaeoreconstructions of the Earth. Geologists may dismiss this simply as *ad hoc* dispersal, flora and fauna trekking across the globe in a random manner. So great is this belief that many biologists, not accustomed to challenging geological hypotheses, quickly

accept this view of the world.

Despite the conventional interpretations, there are indeed patterns: the same, repeated distributions exhibited by a great number of unrelated organisms. It is these patterns that caught the attention of Alfred Wegener, Alexander Du Toit and Dwight Taylor. Many like Wegener did not see such patterns as evidence that would necessarily engage the geological establishment at the time. Instead they sought geological or geophysical evidence, which at the time was difficult to come by or required equipment that was not available or was financially crippling. The reconstructions of a large landmass called Gondwana that existed 65 million years ago was dismissed universally as unrealistic. Ironically enough, when the static Earth view was overthrown, it was that same reconstruction that would immediately become accepted as “the model” for geology. Why would a reconstruction that was ridiculed for over 100 years suddenly be accepted without question? Where were the alternatives? Why has everyone favored that particular continental drift reconstruction? The answer lies in our world view.

Everyone who owns a map of the world will see Africa placed proudly in the middle and Alaska and eastern Russia framing the world on each side (Figure 1). Australia is usually crammed in at the bottom right with New Zealand in tow. The single largest part of the Earth, the Pacific ocean, is mercilessly cut in half, reducing it both in apparent size and relevance. There are few large countries in the middle of the Pacific. This was the map that Wegener and many other scientists grew up with, and it is from this map that Gondwana, in its present reconstruction, was conceived. East Africa was placed against the west coast of South America. Madagascar was connected to India to form Sclater’s (1864) Lemuria. Land bridges literally paved the way in reconstructing Gondwana by indicating the most parsimonious routes that a land mass could take. But what if we were to take a different look at the world –by using a map which has the Solomon Islands placed at its centre?

Unlike most other global maps, Figure 2 features a

whole Pacific. Larger nations have been inconveniently placed to either side of the Pacific and Indian oceans. The Americas are squeezed to one side and Europe and Africa have been pushed to the other. In the middle is the big blue Pacific Ocean with a date line straight down its middle. If we are fortunate to own a geological map with the same projection we see that the Australian plate is immense, with its eastern edge extending well beyond New Zealand (Figure 3). Wegener did not own such a map but certainly should have been aware of the taxic distributional patterns across the Pacific. Many Australian and New Zealand taxa share close relationships to South American taxa. Many Southeast Asian taxa exhibit a close relationship with Mesoamerican taxa, and North East Asian taxa appear closely allied with Western North American taxa. Had Wegener and others used a Pacific-centered map they may have also seen that the Australian and Asian continents fit neatly into the continental margins of South and North America, respectively. If such maps had been conventional, perhaps a different reconstruction of Gondwana would have resulted, one that had no

Panthalassa, a pre-Pacific super-ocean stuck between the east coast of Australia and western coast of South America, but instead expanded the current Indian Ocean between the Western Australian coast, eastern Africa, Madagascar and India –situated like a giant Tethys or “Lemurian” Ocean (Figure 4). Such an alternate Gondwana has rarely been considered despite the hoariness and notoriety of trans-Pacific disjunctions. Instead, land bridges, island hopping, seamount hopping, and long distance dispersal have long been favored as explanations for such problematic distributions. Viewing the world from a Pacific perspective 100 years ago may well have started wide-ranging endorsement for this alternative Gondwana –a reconstruction that would not be suggested until the 1970s (see Carey 1976).

The difference between the speculative and the confirmed in plate tectonics

One of the most significant scientific advances in the



Fig. 1. World map centred on the Atlantic Ocean.



Fig. 2. Alternative map featuring a whole Pacific Ocean.

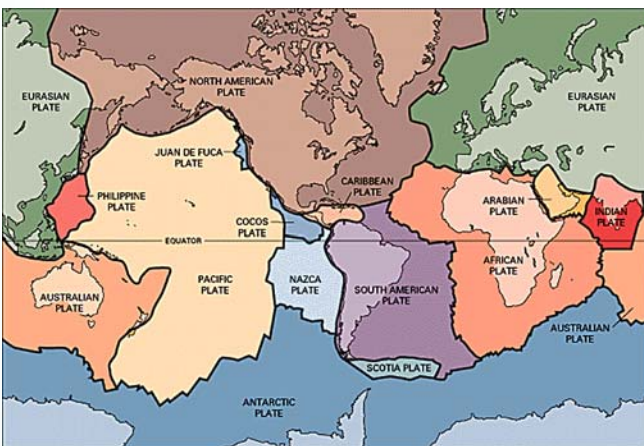


Fig. 3. Map of the tectonic plates of the world.



Fig. 4. Alternative reconstruction of the paleocontinent Gondwana.

twentieth century was the theorization and empirical validation of plate tectonics. Evidence supporting plate tectonics includes geodetic data (GPS, VLBI, etc.) that have confirmed motion of plates, matching most plate tectonic predictions to a high degree of accuracy; seismic tomography showing cool, dense slabs penetrating as much as 660 km into the Earth at trenches; magnetic anomaly data and confirmation of seafloor spreading, etc. Researchers have also gathered a considerable amount of evidence supporting numerous aspects of the theoretical paleomap of Pangaea first put forth by Wegener (1912). This includes matching continental outlines and geological ties linking regions across the Atlantic and Indian Oceans, juvenile age (<200 ma) of the Atlantic and Indian seafloor; identical or closely related, poor-dispersing taxa, both fossil and extant, linking South Africa with South America and India with Madagascar. This latter evidence provides the simplest and most compelling case for Pangaea/Gondwana, and its probity seems even more obvious today than when Wegener first highlighted it nearly a century ago. For example, the fit of South America into Africa and the fossil taxa that these regions share—like the small aquatic reptile *Mesosaurus*—usually appear in the introductions to the subject of plate tectonics in grade-school text books.

Still, a few aspects of the classical Pangaeon/Gondwanan reconstructions have not enjoyed similar empirical support and have been repeatedly scrutinized and challenged. For example, the classical depictions of Pangaea (e.g., Barron et al. 1981) show the Southern Asian regions of Lhasa, Qiangtang, Sibumasu, Tarim, West Burma, North China, South China, and Indochina as part of Laurasia, separated from the Gondwanan regions of India and Australia by a wide Tethys Ocean. A few researchers, however, have challenged this depiction, noting both geological and biogeographical links that would seem to contradict the view of such a vast separation (Shields 1979; Carey 1988, pp. 158-161). Since that time, it has now become conventional that these presumed Laurasian regions actually began in the Paleozoic as northern Gondwanan terranes, juxtaposed with India and Australia. Thus, while a few biogeographers noted that many of the closely-related and apparently trans-Tethys taxa shared by these regions (trilobites, brachiopods, corals and stromatoporoids, nautiloids, gastropods, conodonts, etc.) would have had a difficult time crossing the full extent of an ocean, it has become widely accepted that these taxa did not in fact cross an ocean (e.g., Metcalfe 1998 and references therein). Likewise, Briggs (2003) has also recently challenged the convention view of Late Cretaceous India as an isolated micro-continent in the middle of the vast Tethys Ocean due to poor-dispersing taxa shared by India, Madagascar and Southern Asia. These taxa include iguanid

lizards, boid snakes, crocodylians, two families of frogs, a mammal, freshwater ostracods, and charophyte algae (see McCarthy 2005 and references therein.) Once again, another hypothetical oceanic gap between a number of closely-related fossil taxa has been removed from paleomaps.

These recent shifts in paleomaps should give biogeographers pause whenever they are confronted with paleo-oceanic disjunctions, particularly involving terrestrial or shallow marine taxa. It may also be beneficial for researchers to understand precisely why paleomaps are still subject to extreme theoretical shifts in the locations and extent of marine gaps—despite the overall success of plate tectonics.

As shown earlier, evidence for certain aspects of Pangaea—like the connection of South America and Africa—follows from independent analyses of a number of facts from a number of disciplines. This is positive, existing evidence from biogeography and geology that all support the same conclusion. Theories regarding the extent and location of ancient seafloor, however, have the peculiar problem that no seafloor in the world is older than 200 ma, and the majority of it formed in the last 60 ma. Thus, the extent and placement of most Early Tertiary or Mesozoic marine gaps is merely speculative. For example, Briggs has no theoretical concerns in shrinking the Late Cretaceous Tethys gap between northern India and southern Asia because all of the Tethys has been subducted anyway. Certainly, we have marine deposits throughout northern India and southern Asia, requiring the existence of an epicontinental Tethys seaway throughout much of the Mesozoic. But evidence confirming the actual extent or duration of the north-south oceanic gap between Gondwanan and Laurasian regions simply does not exist. Biogeographical patterns, at this point, can be used to test various theories of the extent, timing, and location of marine gaps.

This conservative approach to paleomaps, in which an effort is made to distinguish between the speculative and the implied, is used here with respect to Southern Trans-Pacific distributions. This will ensure that we do not dismiss repeated examples of patterns of disjunctions, all strongly supporting vicariance, simply because such a conclusion conflicts with certain conventional paleocartographic assumptions about the location and extent of ancient and now-vanished seafloor.

The biotic links among Australia, New Zealand, and South America

Southerly trans-Pacific disjunctions are among the most conspicuous and notorious of all known distributional patterns. In *The theory of island biogeography*, Mac-

Arthur and Wilson (1967) provided four examples of major questions typically considered by biogeographers. One of the four was: "How can we account for the phylogenetic similarities of the biotas of southern South America and New Zealand?" (MacArthur and Wilson 1967, p. 5). In a now classic paper on biogeography, Lars Brundin stated that "Among the problems raised by the distribution of plants and animals in the southern hemisphere, there is none which takes a more central position and is more stimulating to the imagination than the problem of transantarctic [trans-Pacific] relationships" (Brundin 1966, p. 46). Brundin speculated that by 1966 the vast literature on the subject of southern disjunctions "would probably by far exceed 1000 titles" (Brundin 1966, p. 49).

Significant studies of trans-Pacific disjunctions had already begun by the middle of the nineteenth century, and Joseph Hooker, focusing on plants, was perhaps the first to rule out dispersal:

"Enough is here given to show that many of the peculiarities of each of the three great areas of land in the southern latitudes are representative ones, effecting a botanical relationship as strong as that which prevails throughout the lands within the Arctic and Northern Temperate zones, and which is not to be accounted for by any theory of transport or variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes" (Hooker 1853-55, p. xxxvi).

Brundin (1966) also quoted this remarkable description of Southern Hemisphere vicariance and recounted many of Hooker's figures on trans-Pacific flora. For example, Hooker counted 76 genera shared by South America and New Zealand, 17 of which did not live in Australia. Padding Hooker's list, Brundin added trans-Pacific disjuncts from the Diptera, among which Brundin estimated the existence of no fewer than 50 trans-Pacific groups that implied direct land connections. Brundin, writing at the advent of the continental drift revolution, used the distributions to argue for Antarctica as a migration route, hence the phrase "transantarctic distributions".

A number of recent papers that have also focused on southern trans-Pacific disjunctions have only strengthened the trans-Pacific bond. Sequeira and Farrell (2001) provided a table of twenty-four disjunct groups of Gondwanan insects at various taxonomic levels, from family to genus. All twenty-four live in both Australia and Central/South America, and twenty of the twenty-four live exclusively in these Gondwanan regions. The other four also live in South Africa. This should seem remarkable given that in conventional reconstructions Australia and South America are on opposite sides of Gondwana with South Africa in between them.

Heads (1999) provided a detailed analysis of the multiple trans-Pacific disjunctions among the plant-genus *Abrotanella* and its relatives, concluding that vicariance was the only reasonable explanation for the distribution and that the sister taxa linked a number of trans-Pacific regions, including northern New Guinea-western USA-Chile, East Tasmania-Chile, and Stewart Island-southern Chile. Cranston and Edward (1999) studied two sister group relationships among the insect genus *Botryocladus* (Diptera: Chironomidae), linking Tasmania to Chile. They also concluded the distributions supported vicariance. Shields (1998) studied Triassic fossil flora from Argentina and Queensland, Australia, noting the regions share so many identical or closely related fossil plants that the distributions are most reasonably explained by vicariance.

Other taxa linking Australia with South America include meiolaniid turtles and monotreme mammals. Other taxa linking New Zealand with South America include the lichen *Fuscopannaria subimixta*, the evergreen *Laurelia novae-zelandiae* (New Zealand) and its Chilean sister, *Laureliopsis philippiana*, and the flat oyster *Ostrea chilensis*. New Zealand's lizard-like Tuatara is a living fossil, an example of the last remaining sphenodon—and its most recent fossil relatives are the Late Cretaceous sphenodontians of Patagonia (Apesteguia and Novas 2003). The freshwater fish, *Galaxias*, and the beech-like trees, *Nothofagus*, both boast multiple trans-Pacific sisters linking all three regions—South America, New Zealand and Australia. McCarthy (2003) noted many of these distributions conformed to a very precise pattern, linking specific regions of Eastern Australia and New Zealand with specific regions of South America, again implicating vicariance.

More recent studies have likewise strengthened the biotic bonds across the Southern Pacific. Giribet and Edgecombe (2006), for example, constructed a cladogram for the stone centipede *Paralamyctes* using morphological and molecular data. They noted that *Paralamyctes* was a great candidate for cladistic analyses because it occurs on all Gondwanan continents except Antarctica, has limited dispersal capability, and has very narrow distributional limits. Because of the centipede's distribution, Giribet and Edgecombe employed narrow areas of endemism, or "microareas," such as Chile and North New South Wales—rather than the broader continental regions typically used. Their analysis uncovered a repeated pattern of southern South America (Australia, New Zealand) in their subtrees. Relevant to the discussion here, Giribet and Edgecombe concluded:

"The microarea approach does not prohibit 'reassembling' continental areas to explore alternative patterns. For example, it remains possible to retrieve a repeated pattern of (southern South America (Australia + New Zealand)) in our subtrees..., corresponding

to the so-called 'plant southern pattern' of Sanmartín and Ronquist (2004)" (Giribet and Edgecombe 2006, p. 76).

Sanmartín and Ronquist (2004) used parsimony-based tree fitting in conjunction with permutation tests in order to uncover biogeographical patterns among Gondwanan taxa in what they described as "the largest biogeographic analysis of the Southern Hemisphere attempted so far," involving 54 animal and 19 plant phylogenies (1393 terminals). Significantly, they overcame sampling bias by providing results in terms of a ratio of dispersal events "that we would have seen if all areas had been equally well represented in the data set" (Sanmartín and Ronquist 2004, p. 230). Figure 5, from Sanmartín and Ronquist (2004), display their results, detailing frequencies and directions of dispersal (as inferred by Tree-fitter) of terrestrial plants and animals superimposed on PT polar views of the Southern Hemisphere in the Late Cretaceous-Early Tertiary. The frequencies are proportional to arrow thickness. Note that the large arrows pointing into Antarctica (from South America and Australia) indicate taxa that have moved between South America and Australia. Antarctica was not part of the analysis, as "none of the studied groups are now present there". The arrows pointing to Antarctica merely reflect the theoretical assumption of Sanmartín and Ronquist that all the taxa shared by Australia and South America had to move through Antarctica. Also, while the one Antarctic arrow appears to be pointing from Western Australia, Australia is treated as a single biogeographic unit, and the arrow is not meant to designate any particular part of Australia. Many of the Australian taxa in the data set of Sanmartín and Ronquist were referenced by McCarthy (2003), and all of those taxa occur in eastern Australia.

The figures are significant because they display in a visually intuitive way the ease of dispersal (or range expansion) between many pairs of Gondwanan regions. And as is clear from a glance, New Zealand, Australia, and South America share more ancestral taxa than any other pairs of Gondwanan regions studied by Sanmartín and Ronquist. For example, although Madagascar was directly attached to Africa in the Early Cretaceous and has never been separated by more than 400 km from its continental neighbor, plants and animals have managed to move with a greater facility between New Zealand and South America than between Madagascar and Africa. Or to put it another way, even though New Zealand and South America have allegedly never been connected and are currently separated by the most significant oceanic barrier on the globe, the plants and animals of New Zealand more closely resemble that of South America than Madagascan taxa resemble that of Africa. Unflappable is the biogeographer who is not astounded by that fact.

Thus, the mystery that Hooker faced in the middle of the nineteenth century still taunts us today: What is the explanation for these trans-Pacific biotic links?

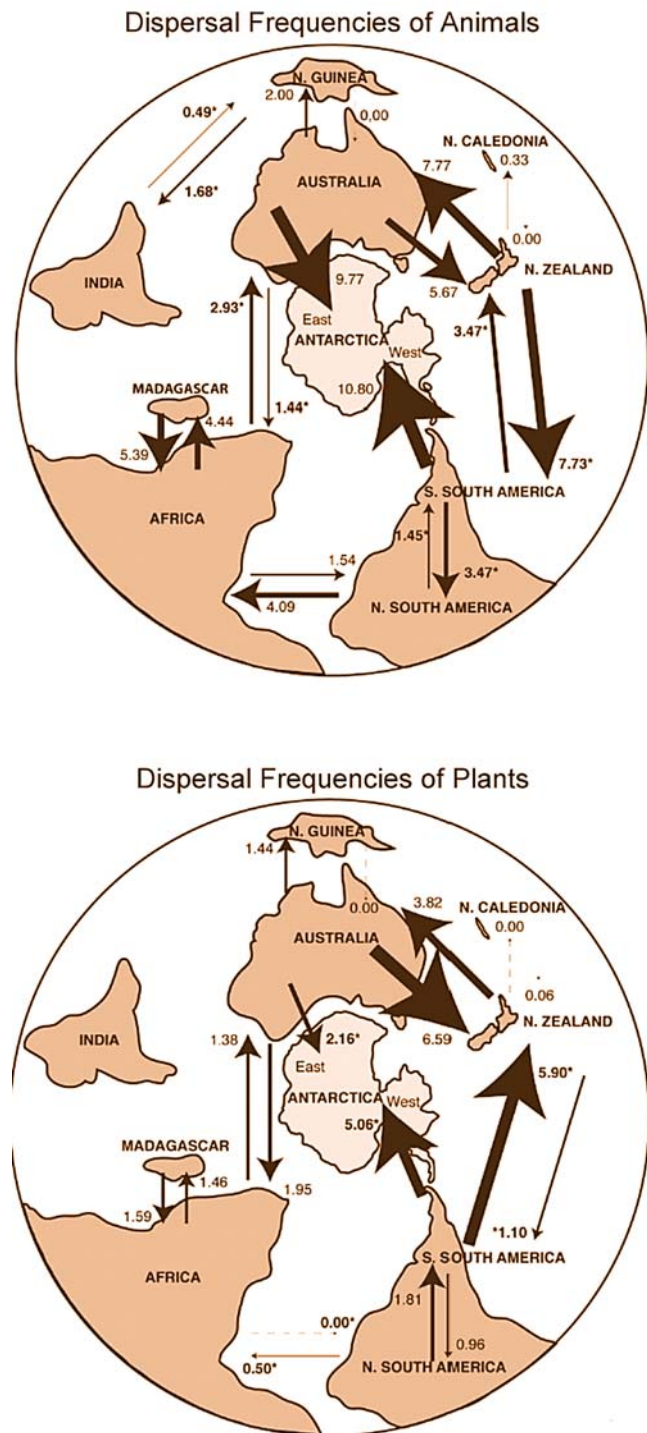


Fig. 5. Maps from Sanmartín and Ronquist (2004, figs. 9, 10), illustrating the frequency and direction of dispersal of terrestrial animals and plants in the southern hemisphere.

Solutions

Essentially *all* researchers who have provided wide-ranging biogeographical analyses of South America-Australia/New Zealand have concluded that many of the biotic links among the regions are indicative of vicariance (Hooker 1853-55; Croizat 1964; Brundin 1964; Matile 1990; Crisci et al. 1991; Shields 1998; Heads 1999; Glasby 1999; Cracraft 2001; Cranston 2003; McCarthy 2003, 2005). Even Sanmartín and Ronquist (2004), who posit long distance dispersal for the biogeographical pattern displayed by plants, agree that the animal links are best explained by vicariance. Apparently, the only disagreement involves the question of the vicariant event, that is, the researchers disagree about the geological cause that led to the disjunctions.

Matile (1990), Shields (1998), Glasby (1999), Glasby and Álvarez (1999), Cranston (2003) and McCarthy (2003, 2005) agree that the most parsimonious explanation for these distributions is a past juxtaposition of the vicariant regions, New Zealand, Australia and South America. Followers of panbiogeography (Croizat 1964; Heads 1999) appear to support something not too dissimilar –the juxtaposition, at the very least, of the disjunct terranes upon which the taxa are found and a Mesozoic (or at the very least a late) birth of the Pacific.

This conclusion is consistent with all other analyses of similar biogeographical patterns across other marine barriers. In fact, in nearly every other case, when researchers conclude that the great number of biotic ties currently shared by pairs of trans-oceanic regions is the result of vicariance, they invariably mean that these currently separated regions used to be juxtaposed. All geologists and biogeographers now agree that the fossil taxa shared by South America and Africa, on opposite sides of the Atlantic, or shared by India and Madagascar, separated by the Indian Ocean, are evidence the regions were once united. As noted earlier, since the paper by Metcalfe (1998), it is now convention that the fossil taxa shared by East Asian regions and Australia in the Paleozoic, classically depicted as separated by a vast Tethys, are evidence that the regions were together. Moreover, Briggs (2003) has now argued that in the Late Cretaceous India and South Asia, classically depicted as being separated by a vast Tethys, were actually in proximity –a view that is likely to become convention soon. As shown, the South Pacific regions Australia, New Zealand and South America flaunt an even greater number of trans-oceanic disjunctions of poor dispersing taxa, providing even more compelling evidence for juxtaposition. The researchers who have closed the gap between these trans-Pacific regions use the same arguments and follow the same line of reasoning as those who have closed the trans-Atlantic, trans-Indian, and trans-Tethys disjunctions.

Those committed to conventional paleomaps, however, must seek alternative explanations, which is to say, they must make an arbitrary distinction between vicariant signals across the Pacific and those across other oceans. For the plant ties, for example, Sanmartín and Ronquist suggest long-distance, trans-Pacific “concordant dispersal,” perhaps using Antarctica as a stepping stone. This theory of coordinated-jump-dispersal across the full breadth of an ocean, first employed by followers of continental fixity to explain the trans-Atlantic and trans-Indian Ocean disjunctions, has a conspicuous problem (Figure 6). New Zealand is currently 8000 km away from South America and 2700 km away from Antarctica at its closest point. Australia is another 2000 km west of New Zealand. (For the sake of comparison, the distance across the Atlantic between Brazil and West Africa is 3000 km). Yet despite these great distances, a great number of the taxa alleged to have jump-dispersed the Pacific are restricted to a very narrow range of regions and are absent from all other Southern Pacific Ocean islands and other nearby conti-

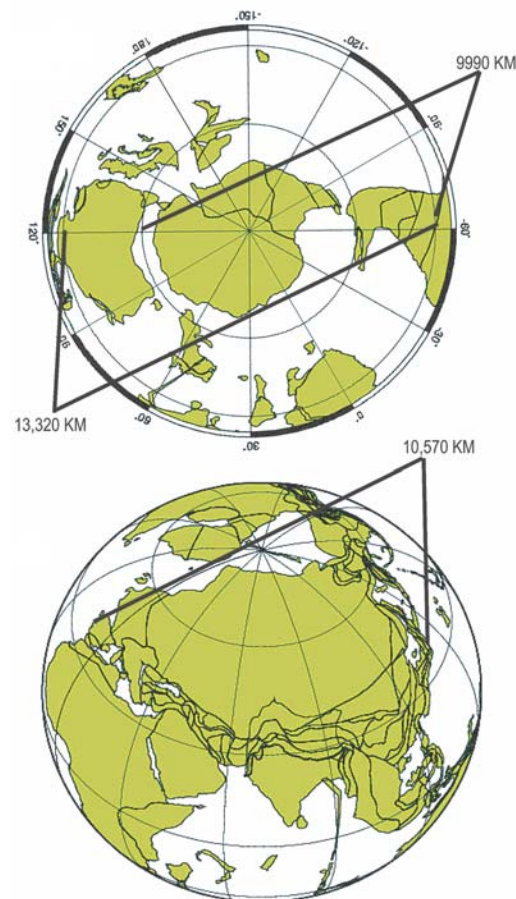


Fig. 6. Distance from South America to Australia in Gondwana and its comparison with the current width of Eurasia.

mental locations. If these taxa can really jump-disperse such vast distances why would they not appear on any other oceanic islands or any other continents?

The common sense notion that taxa that can jump disperse an ocean should be wide ranging often appears in many geological primers that discuss Alfred Wegener's simple argument that a number of trans-Atlantic disjunctions suggest a closed Atlantic Ocean. For example, the following quote appears in a parent/teacher guide for introducing the concepts of plate tectonics on an educational website (Robinson 2005): "Firstly, [Wegener] was able to show that fossils of a small reptile called *Mesosaurus* were found only in South Africa and Brazil. These two places are now separated by the Atlantic Ocean, so how could *Mesosaurus* have lived in both locations? The chance of it crossing the ocean was very small and, if it had been able to cross the sea, why hadn't it been found in other places as well? To Wegener it seemed that the only sensible explanation was that South Africa and Brazil had been joined together at the time when *Mesosaurus* lived" (Robinson 2005, <http://www.geography-site.co.uk/pages/physical/earth/tect.html>).

Another educational website, "Geology Basics" from Carleton College (Daum and Savina 2000), stated this idea more simply:

"While it is remotely possible that *Mesosaurus* could swim the ocean and simply chose to live in eastern South America and west Africa exclusively, it is much more likely that these two areas represent what was a continuous range several hundred million years ago, when the reptile lived and the two continents were joined" (Daum and Savina 2000, http://www.acad.carleton.edu/curricular/GEOL/classes/geo120/geology_basics.htm).

The problem, as noted by these elementary websites, is not simply the assumption that so many poor dispersing taxa have managed to jump disperse an ocean; the major difficulty is that these taxa never ended up anywhere else. And why would this argument be any less compelling for disjunctions across the Pacific than the Atlantic? This question seems particularly troublesome given that the Pacific is nearly three times wider, the Pacific has a far greater number of oceanic islands to support would-be crossers, and trans-Pacific disjunctions involve a far greater number of taxa.

The theory of full ocean jump-dispersal of a wide variety of taxa exclusively located in a very limited number of narrow regions not only wars upon reason, it also conflicts with all known empirical data. The Pitcairn Island group, for example, is only half way across the Pacific. Yet a wide ranging study of all 114 species of flora on the Pitcairn group confirms that it does not exclusively share *any* plant with South America. Or to put it another way, every plant taxon that has managed to disperse between South America and Pitcairn has also managed to colonize other islands significantly

closer –such as Easter Island or the Cook Islands. If a plant taxon can send propagules 4800 km to Pitcairn, it can send significantly more 2400 km, 1200 km, 600 km, etc. New Zealand is 8000 km away from South America. Yet very few of the full-Pacific crossers that have been the subject of such controversy managed to reach anywhere else. Even using Antarctica as a stepping stone would not help resolve this problem as it still requires a number of significant dispersal events.

Moreover, concordant cross-ocean dispersal cannot explain all of the disjuncts, and Sanmartín and Ronquist (2004), like Brundin (1966) and Cracraft (2001), accept that many of the distributions are indicative of vicariance (Sanmartín and Ronquist specifically posit vicariance for animals.) But as noted conventional paleomaps demand that these researchers interpret the vicariant signal in a unique manner. Noting the current paleomaps never place the regions together, they contend that the vicariant explanation is consistent with the regions merely being part of the same multi-continental land mass. That is, they argue that South America, Australia and New Zealand were "connected through Antarctica." But it should be noted that South America and Africa are also currently part of the same land mass, "connected through" Eurasia and North America. When the Bering or Thulean Bridge is above sea level, terrestrial taxa could, at least, theoretically move between South America and Africa without ever crossing a marine barrier. Indeed, this explanation was proffered by those favoring continental fixism for the South African and South American biotic ties.

The hypothesis of cross-Antarctica migration suffers a similar problem as well as many others. Antarctica, for example, is not a small continent –and the distance from the northern tip of the Antarctic peninsula to Victoria Land, the Antarctic region that was attached to Southern Australia, is ~ 5200 km, which is a little more than the width of North America from say, New York to San Francisco. This leads to two significant problems:

1. The trans-Pacific disjuncts are latitudinally stratified and include purely Neotropical taxa that link with taxa from Northeast Australia, New Guinea, New Caledonia and Fiji.

2. The trans-Pacific disjuncts are longitudinally stratified, predominantly linking *western* South America with *eastern* Australia, a pattern not immediately explainable by trans-Antarctic migration.

While trans-Antarctic migration would help solve the problem of eliminating major marine gaps, the range expansion and contraction required would still be imposing. As shown in McCarthy (2003), many of the South American sister taxa of Tasmanian taxa live in south central Chile, restricted between 35 N and 42 N. The distance between 35 N and the southern tip of Tierra del Fuego is more than 2000 km and the entire

width of Antarctica, as noted, is 5200 km, requiring more than 7200 km of range expansion for taxa with very narrow distributions. And this represents the smallest range expansion required by Australian-South American disjunctions.

For comparison, consider the biogeographical data from a corresponding Northern Hemisphere analysis (e.g., Sanmartín et al. 2001). Unlike the Southern Hemisphere disjunctions, none of the Northern Hemisphere patterns is problematic or surprising. Instead, regions that are closest together (like Western and Eastern North America or Western Eurasia and Eastern Eurasia) share the most closely related taxa, and regions that are further apart share the fewest (like Western North America and Western Eurasia). Note also that Eastern North America and Eastern Eurasia, are considered “disjunct” and share relatively few sister taxa despite the fact that (1) the Bering Land Bridge has been available for crossing far more recently than Antarctica; and (2) these regions are connected by less continental material than South Central Chile and Tasmania on conventional paleomaps. The same argument may be made for Western North America and Europe and their connection via the Thulean bridge.

Given the multi-continent range expansion required by the trans-Antarctic explanation, a problem arises for taxa that have a particularly narrow range and/or exclude Australia or New Zealand. New Zealand’s lizard-like tuatara, for example, is the only extant sphenodon, and its most recent fossil relatives occur, not in Australia, but in the Late Cretaceous of Patagonia (Apesteguía and Novas 2003). Another problem arises for groups that boast multiple trans-pacific disjunctions—as with the freshwater fish *Galaxias*, the midge *Botryocladus*, or the southern beeches *Nothofagus*. This is problematic because the assumption of vicariant-induced speciation assumes uninterrupted gene-flow across three continents—South America, Antarctica, Australia—until the rifting of Australia from Antarctica. Yet, multiple trans-Pacific sister taxa from the same genus requires allopatric speciation confined narrowly to one of the regions first. In other words, taxa originally divided by some unknown local barrier in, say, Chile must then all find no barriers to either dispersal or gene flow throughout Chile, all of Antarctica and into Australia. But are there any other pairs of regions so widely separated that exclusively share so many sister taxa—or exclusively share multiple sister taxa within the same group? In comparison, according to the Sanmartín and Ronquist dataset, none of the groups shared by Eastern North America and Eastern Asia, regions as disjunct as Chile and Tasmania on paleomaps, contains more than one sister relationship.

These trans-Antarctic relationships become even more bewildering when all of these problems occur within the same genus—as with the plant genus

Abrotanella. *Abrotanella forsteroides* from eastern Tasmania is the sister taxon to a Chilean *Abrotanella*—not to the Western Tasmania species. Thus, the most recent common ancestor to this disjunct group must either have migrated across Antarctica or must have been transported across the full width of the Pacific and Tasman Sea while either avoiding or disappearing from New Zealand, and all the rest of Australia including Western Tasmania. Within the same genus, we also find *A. muscosa*, which is endemic to Stewart Island, and *A. fertilis* from New Zealand, which are most closely related, not to each other, but to other Chilean species, again requiring extraordinary jaunts, whether through Antarctica or across the Pacific, between Chile and very specific Western Pacific locations, while avoiding all the habitable regions significantly closer, such as all intervening ocean islands or Australia to the west. But the most persistent doubts must follow from the effort to use Antarctica to explain tropical trans-Pacific links. Sanmartín and Ronquist define “southern South America” as “the southern temperate region (Argentina, Chile, Paraguay, Bolivia, and the Falklands and Antarctic islands), and north-central South America west of the Andes.” “Northern South America,” in contrast, refers to “north-central South America east of the Andes (Brazil, Colombia and Venezuela).” Thus, “southern South America” really describes essentially all of western South America and likely extends into the Northern Hemisphere perhaps as far north as “northern South America.” “Northern South America” may have been just as easily named “eastern South America.”

On the other side of the Pacific, Australia is treated as a single biogeographical unit, from the southern tip of Tasmania to the northern most points of Australia. Thus, some of the taxa that link “southern South America” with “Australia” in their analysis more specifically link taxa exclusively found in tropical South America and/or exclusively found in tropical Australasia. For example, part of their data included distributions of Keroplatidae of Matile (1990), but a number of these taxa have exclusively tropical trans-Pacific distributions and Matile considered them as evidence that tropical South America was once juxtaposed with north-east Australia, New Caledonia, and parts of Indonesia (See Matile 1990 or McCarthy 2003). Sanmartín and Ronquist also reference some of P. Cranston’s analyses of the Chironomidae. In 1999, Cranston noted that one trans-Pacific disjunct Chironomidae genus, *Nandeva*, found in Brazil and south central Chile, has not been discovered south of 16°S in Australia, “despite continent-wide exuvial sampling” (Cranston 1999, p. 298). Cranston (1999) also noted that another trans-Pacific genus, *Fissimentum*, occurs from Indonesia to Southern Australia but is restricted to the Neotropics in South America. Cracraft (1999 2001) records many tropical trans-Pacific disjunctions among birds, including the

most primitive relatives of chickens and pheasants – the megapodes from Australasia and the guans and curassows from tropical America. Cracraft also notes that the weakly flying sun bittern (*Eurypyga helias*), from tropical South and Central America, is the closest relative of the flightless kagu of New Caledonia and two extinct flightless species (*Apterornis*) from New Zealand. One of the more notorious trans-Pacific disjunctions involves the astonishing fact that iguanas, a predominantly Neotropical taxon, live on Fiji-Tonga, while no other iguanas occur anywhere in the West or Central Pacific. Recent phylogenetic analyses hypothesize that both *Brachylophus* (Fiji and Tonga) and *Dipsosaurus* (California) occupy basal positions among Iguanidae (Sites et al. 1996.)

From the equator in South America, west of the Andes to the southern tip of Tierra del Fuego is more than 6300 km. Across the full width of Antarctica, as has been noted, is more than 5200 km. And from Tasmania to Queensland (20 S) is more than 2500 km. This totals more than 14000 km of multi-continental range expansion and then significant range contraction to only the tropical regions in one or both areas. To give a comparison, the entire width of Eurasia from the Western coast of Portugal to the Eastern coast of Japan (at 40 N) is a little less than 10,600 km. Thus, while Northern Peru and Northeast Australia are “connected through Antarctica” on conventional paleomaps, these regions would have been separated by more continental material than are Portugal and Japan. Yet, Portugal and Japan, of course, do not share an unusual number of sister taxa found nowhere else in the world. And if they did, it might be considered one of the world’s greatest biogeographical mysteries.

Moreover, Sanmartín and Ronquist note, there has been remarkably little biotic exchange between Northern and Southern South America –and the small number of taxa that they do share appear to have been infiltrations from the South:

“...the biotas of northern South America and southern South America do not appear to be closely related. Southern South America appears more closely related to the austral landmasses (Australia, New Zealand) than to northern South America in the plant and all animal area cladograms. The frequency of trans-American dispersal between northern and southern South America is significantly lower than that between northern South America and the Holarctic in the animal and insect data sets... This result confirms previous biogeographic results suggesting that the South American biota is formed by a northern tropical component and a southern temperate component, each with different biogeographic affinities (Crisci et al. 1991; Amorim and Tozoni 1994; Lopretto and Morrone 1998)” (Sanmartín and Ronquist 2004, p. 239).

Sanmartín and Ronquist suggest the tropical for-

ests of the Amazonian Basin likely provided “a long-lasting, powerful barrier to dispersal,” and note that “[d]ispersal of South American animals was significantly more frequent from the southern to the northern region than in the other direction...” (Sanmartín and Ronquist 2004, p. 239). But if Neotropical taxa have found it difficult to move into Southern South America how reasonable is it to use Antarctica to explain tropical trans-Pacific disjunctions?

Still another problem, as noted, is that the trans-Pacific taxa are longitudinally stratified. If Antarctica served as the biotic corridor between South America and Australia, one would expect to find all of Southern South America, particularly south of 42 degrees S, linking with all of Southern Australia –and that neither the eastern or western coastal regions of either South America or Australia should be particularly favored. As the conventional paleomaps in Figure 5 a and b show, the eastern coast of South America is just as close to the Antarctic Peninsula as the western coast of South America. For example, the Antarctic Peninsula is much closer to regions in eastern Brazil than to, say, Bolivia or Peru. The same point stands for Western Australia. Taxa that have migrated across the full extent of Antarctica should also include links that exclude Eastern Australia and Western South America. But why are there few if any taxa exclusively shared by Western Australia with Eastern South America? Trans-Antarctic migration cannot effectively explain why the disjunct taxa appear to link very specific regions along Eastern Australia with specific regions along Western South America.

The geological facts

Given all the difficulties generated by attempts to explain disjuncts assuming conventional reconstructions, one would assume that the geological characteristics of the seafloor between Australasia and South America overwhelmingly support this view, and that the current distributional explanations, like the cross-ocean rafting of the Fijian iguanas, are hypotheses of last resort. Yet the South Pacific seafloor data confirm that essentially all of it is less than 83 my old –and the vast majority of it is less than 40 my old. This is consistent with the fact that Australia/New Zealand and South America share so many more closely related extant taxa than Africa and Madagascar or Africa and South America. Based on crustal age of the seafloor, we know, as Sanmartín and Ronquist note, that Madagascar rifted from East Africa 121 MYA and that Northern South America rifted from Western African regions about 100 MYA. This same reasoning based on crustal age data would imply South America and Australasia remained in proximity until a much later date. The biogeographical links predict the difference in ages of

seafloor between the various Gondwanan regions, with the strong trans-Pacific links supporting the juvenile age of the South Pacific.

Conventional paleomaps that indicate a significant separation of these trans-Pacific regions during the Mesozoic assume the existence of enormous ocean-wide tracts of hypothetical seafloor crust that have since been subducted. But all evidence for precisely how much of this seafloor actually existed has been forever lost at trenches. As noted earlier, Briggs (2003) and Metcalfe (1998) have now juxtaposed regions that were previously thought to have been separated by the Tethys. The reason their views are geologically viable is because the ancient Tethys has now been completely subducted. Regardless of what used to be conventionally drawn on paleomaps, no one really knows how large the marine gap was between any of the circum-Tethys regions. Briggs (2003) and Metcalfe (1998) have both narrowed or closed these gaps due, either in whole or in part, to problematic trans-Tethys disjunctions.

The same reasoning applies in the Pacific. Not only has all pre-Pacific seafloor been subducted, the disjunct regions actually share many more closely related taxa than do any other disjunct regions now known to have been juxtaposed –such as Africa-South America, India-Madagascar, or the amphi-Tethys regions brought together by Briggs (2003) and Metcalfe (1998). Like Wegener, du Toit, Briggs, and Metcalfe, those biogeographers who argue for the juxtaposition of the trans-Pacific regions are merely contesting well known drawings –not actual geological facts.

The regions on opposite sides of the Pacific –particularly Australia and South America, fit together neatly. Reuniting the matching outlines closes the biotic disjunctions and brings together many trans-Pacific sister taxa. The trans-Pacific regions also share geological links. For example, geological correlations between north-east Australia and Mexico involving Grenville-type Proterozoic basement material have led some geologists to juxtapose these trans-Pacific regions at that time. The resulting configuration is now known as “AUSMEX.” We also find Proterozoic Grenvillian material in Southern Peru (Martignole et al. 2005), showing a correlation between these regions and eastern Australia. Also, not only did the Caribbean and Ontong Java Plateaus, just northeast of New Guinea, form at the same time, with eruption peaks at 120 ma and again at 90 ma, they also are remarkably similar in chemical and isotopic composition (Arndt and Weis 2002).

Reconstructions that juxtapose Australia and New Zealand with South America predict that we should find matching trans-Pacific outlines, geological correlations, and a great number of disjunct sister taxa. In contrast, those working from conventional paleomaps often express some measure of surprise at the trans-

Pacific relationships. For example, Anderson (2000, p. 202) noted that his molecular DNA analyses of loliginid squid, which lack teleplanic larvae, “suggest *S(epioteuthis) lessoniana* [Indonesia] and *S(epioteuthis) sepiodea* (Caribbean) –a species found on the other side of the planet from *S. lessoniana*– are sister species.” About the occurrence of iguanas on Fiji-Tonga, Pregill and Steadman (2004, p. 18) wrote that “long-distance dispersal from the Americas, incredible as that seems, is the only viable hypothesis that explains their presence in the southwest Pacific...” In a discussion of the multiple trans-Pacific disjunctions among *Abrotanella*, Swenson and Bremer (1997, p. 505) wrote that “possible long distance dispersal events of *Abrotanella* are hard to envision, however.” Phrases like “incredible as that seems,” “hard to envision,” and “on the other side of the planet” help underscore that extraordinariness of these distributions and seem to imply that the researchers understand that their own biogeographical hypotheses may seem improbable. These improbabilities continue to multiply with every disjunction – and as noted the regions share hundreds of identical or closely related taxa.

Those who place the Southern Pacific continental regions in proximity in the Mesozoic are doing nothing more than letting the biogeographical facts speak for themselves. They are letting the data determine their conclusions –regardless of challenges to convention. The situation is reminiscent of a legendary story in physics involving Paul Dirac and the development of the Dirac Equation, an equation that requires the existence of a particle very much like the electron but that is opposite in sign. This consequence of the Dirac equation was famously confirmed in 1932 by the discovery of the positron, but Dirac, himself, had never formally predicted its existence. When later asked why he did not underscore this unconventional but natural consequence of his equation and boldly and formally predict the existence of the positron, Dirac responded flatly, “pure cowardice.”

At some point, biogeographers are going to have to stop acting like Dirac and admit frankly and aloud what their analyses so conspicuously demand.

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