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

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 Gondawana 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

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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 Pangaeangondwanan 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, crocodilians, 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 Botyrocadius (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 subimmita, 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 Paralumyctes using morphological and molecular data. They noted that Paralumyctes 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 ‘resembling’ 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...”
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 Madagascar 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 bioties 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 “cordant 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-

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**Fig. 6.** Distance from South America to Australia in Gondwana and its comparison with the current width of Eurasia.
nental 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 Botycocladius, 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 allopartic 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 Keroplutidae 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 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-est of the Amazonian Basin likely provided “a long-lasting, powerful barrier to dispersal,” and note that “[d]ispersal of South American animals was signifi-cantly 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 5a 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-Pacific 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. 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 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(epiooteuthis) lessoniana [Indonesia] and S(epiooteuthis) sepioidea (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 noth- 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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Integrando biogeografía histórica y ecológica: El caso de los mamíferos terrestres de México

POR TANIA ESCALANTE

En biogeografía primero se identifican los patrones y luego se establecen hipótesis sobre los procesos o agentes causales que los originaron (Vargas 1992). Según Myers & Giller (1988), existen básicamente cuatro tipos de procesos generadores de patrones biogeográficos: (a) abióticos a gran escala: por ejemplo, movimientos de las placas tectónicas y cambios en el nivel del mar, en el clima y la circulación oceánica; (b) abióticos locales: perturbaciones como incendios, inundaciones, huracanes y erupciones volcánicas; (c) bióticos: procesos de adaptación, extinción y especiación; y (d) ecológicos: interacciones bióticas como depredación, competencia y dispersión.

De manera general, podríamos decir que los procesos que originan los patrones biogeográficos —como los patrones de riqueza de especies, el endemismo y la disyunción— pueden ser de dos tipos: históricos y ecológicos. De hecho, Augustin P. De Candolle (1820) fue el primero en hacer la distinción de lo que hoy conocemos como biogeografía histórica y ecológica (ver Espinosa y Llorente 1993, Myers y Giller 1998, Crisci et al. 2006), al diferenciar las “estaciones” (la naturaleza particular de las localidades en las cuales las especies acostumbran crecer, relacionadas con los parámetros físicos que explican por qué las plantas [y los animales] viven en un determinado lugar), de las “habitaciones” (indicaciones generales geográficas y geológicas de las regiones en las cuales las especies crecen naturalmente, explican por qué aparecen especies diferentes en una misma área, aun cuando tienen diferentes requerimientos ecológicos) (ver Papavero et al. 2004). A partir de entonces, la mayoría de los biogeógrafos se ha dedicado a estudiar solo una de estas subdisciplinas de la biogeografía.

Crisci et al. (2006) publicaron un artículo titulado “Bridging historical and ecological approaches in biogeography”, donde hacen referencia a que sería preferible una integración de ambas subdisciplinas de la biogeografía, y que esto puede lograrse a través del análisis espacial. En esta publicación, Crisci y sus colegas proponen algunas ideas interesantes sobre cómo conseguir esta integración a través de cuatro temas: el arreglo espacial, la inferencia de procesos espaciotemporales, la predicción espacial y la retrodicción espacial. Además, discuten la incorporación de los efectos de las actividades humanas en los análisis de los patrones de distribución de las especies. Desde 2004, en los laboratorios de Sistemas de Información Geográfica y de Análisis Espaciales del Instituto de Biología de la UNAM, en colaboración con el Museo de Zoología de la Facultad de Ciencias de la UNAM, nos hemos enfocado a seguir un protocolo semejante, el cual expondré en esta contribución, de acuerdo con el esquema del artículo de Crisci et al. (2006).

Los mamíferos terrestres de México


Integrando historia y ecología

A continuación describo los cuatro temas del análisis espacial mencionados por Crisci et al. (2006), los cuales proporcionan un marco de referencia útil para discutir la integración de las corrientes ecológica e histórica, en
este caso, con los mamíferos terrestres de México.

**Arreglo espacial.** Se refiere a la descripción de las distribuciones de las especies a través del espacio geográfico (Crisci et al. 2006). Desde los puntos de vista histórico y ecológico, independientemente se puede llegar a distintas regionalizaciones de la superficie terrestre, identificando por un lado provincias bióticas y por otro ecorregiones. Sin embargo, es posible incluir la aproximación funcional a la identificación de áreas de endemismo mediante la conjunción de dos metodologías: el modelado de nichos ecológicos (MNE), proyectados como la distribución potencial de las especies (Soberón y Peterson 2005), por ejemplo, mediante un algoritmo genético como GARP (Stockwell & Peters 1999) y el Análisis de Parsimonia de Endemismos (PAE; Rosen 1988, Morrone 1994). Por un lado, los modelos de nicho ecológico representan las relaciones de las especies con su ambiente, basadas en hipótesis sobre cómo los factores ambientales controlan la distribución de las especies (Guisan y Zimmermann 2000); por otro lado, el PAE es un método que clasifica áreas con base en una analogía en la sistemática filogenética, de acuerdo con sus taxones comparados, mediante la solución más simple (criterio de parsimonia) (Crisci et al. 2000). El resultado de la combinación de MNE y PAE es la identificación de áreas de endemismo y de patrones de endemismo anidados, fundamentales para elaborar regionalizaciones biogeográficas jerárquicas naturales, que incorporan el componente ecológico. Además, la integración de los modelos de distribución tiene la ventaja de hacer más precisa la delimitación de las áreas de endemismo, ya que los datos puntuales de distribución de las especies pueden ser “mejorados” a través del uso del modelo de nichos. En México, identificamos siete áreas de endemismo empleando estas metodologías integradas, dos de ellas con patrones de endemismo anidados (Escalante et al. 2007b).

**Inferencia de procesos espacio-temporales.** El estudio de los procesos espacio-temporales describe cómo el movimiento o las interacciones espaciales modifican los arreglos espaciales (Crisci et al. 2006). Estos procesos incluyen eventos históricos (vicarianza, dispersión y extinción) y limitaciones ecológicas (factores bióticos, abióticos, evolutivos y geológicos). A través de estudios panbiogeográficos (Escalante et al. 2004; García-Marmolejo et al. en prensa), hemos realizado algunas inferencias acerca de cuáles procesos históricos podrían haber operado sobre los mamíferos terrestres de México y su diversificación en la Zona de Transición Mexicana. También, mediante el uso de las técnicas de modelado de nichos ecológicos habría la posibilidad de inferir procesos evolutivos y ecológicos o contrastar los propuestos desde el punto de vista histórico (v. gr. Peterson et al. 1999; Wiens y Donoghue 2004). Mediante la integración de los métodos de MNE y PAE, expuestos anteriormente, se logró obtener una regionalización biogeográfica de México, con dos regiones, una zona de transición, dos subregiones, cinco dominios y 15 provincias bióticas (Escalante et al. 2007c), a partir de la cual pueden establecerse hipótesis de homología espacial para comprobar con otras metodologías.

**Predicción espacial.** Se refiere a hacer pronósticos sobre arreglos espaciales futuros (Crisci et al. 2006). Desde el punto de vista histórico, esto es casi imposible, pues es difícil predecir cuando ocurrirá un proceso de vicarianza (aunque algunos datos que brindan las ciencias geológicas podrían ser de utilidad, por ejemplo, la separación de la Península de Baja California del resto del continente con un movimiento hacia el noroeste; Aguayo y Trápaga 1996), cuando una dispersión a larga distancia será exitosa o la ocurrencia de extinciones masivas. Por el lado de la biogeografía ecológica, ha cobrado un gran auge la investigación acerca de predicciones sobre cambios en la conformación de las distribuciones individuales de las especies a través de los modelos de nicho ecológico y el uso de modelos de cambio climático y cartografía de cambio de uso de suelo (Sánchez-Cordeiro et al. 2004, 2005a, b).

**Retrodicción espacial.** Se enfoca en establecer, con base en la evidencia presente, cuáles arreglos espacioles existieron en el pasado (Crisci et al. 2006). Este es uno de los principales objetivos de la biogeografía histórica, donde, a través del uso de los datos de distribución actuales y la información filogenética, pueden reconstruirse eventos del pasado, usando métodos de la biogeografía cladística. Puesto que aún no todos los mamíferos de México se encuentran representados en las filogenias existentes, se realizó un análisis cladístico ampliando las fuentes de datos a otros grupos taxonómicos (plantas, insectos, anfibios, reptiles, mamíferos y aves). Como resultado, se lograron inferir procesos espaciales anteriores al Gran Intercambio Biótico Americano (Escalante et al. 2007a). Aunque Crisci et al. (2006) proponen que no es posible realizar retrodicción espacial desde el punto de vista ecológico, existen algunos trabajos que claramente podrían entrar en este tema del análisis espacial (Rice et al. 2003, Peterson et al. 2004, Martínez-Meyer y Peterson 2006).

**Integrando las actividades humanas**

Los procesos históricos y ecológicos se encuentran moldeando continuamente los patrones de distribución geográfica de la biota, a veces tan simultáneamente...
mente, que es imposible separarlos. Los cambios en los patrones espaciales de la biota influyen en las actividades humanas, pero también (y más dramáticamente) las actividades humanas influyen en los patrones biogeográficos (Crisci et al. 2006). Integrando los métodos de MNE y PAE, obtuvimos una regionalización biogeográfica alternativa de los mamíferos de México, donde elaboramos modelos de nicho ecológico proyectados como la distribución geográfica de las especies, en un escenario de cambio en el uso de suelo basado principalmente en la deforestación. Encontramos que los cambios en las distribuciones individuales de las especies debido a la deforestación, reflejaron cambios importantes en la regionalización biogeográfica (Escalante et al. 2007c). Resulta sorprendente que los cambios en las regionalizaciones biogeográficas, esperados en amplias escalas temporales, están ocurriendo en sólo doscientos años de cambio en el uso del suelo en México.

Conclusiones y perspectivas

De Candolle (1820, en Papavero et al. 2004) mencionó que la confusión entre las estaciones y las habitaciones es una causa que atrasó el desarrollo de la biogeografía y que le impidió adquirir exactitud. Sin embargo, hoy en día sería necesaria la integración de las aproximaciones histórica y ecológica con la finalidad de tener una mejor comprensión de los patrones que exhibe la biota y de los procesos que los han generado. En la práctica, quizá los investigadores prefieran enfocarse en solo alguna de las dos, pero no deben perder de vista la visión complementaria, ya que siempre será preferible mantener una visión integradora. También será necesario realizar estudios en diferentes escalas de trabajo (v. gr. Morrone y Escalante 2002) en ambas aproximaciones y lograr integralos. Algunos autores incluso han comentado que la división ecología/historia es un obstáculo para el progreso de la biogeografía, y que sólo la integración de sus intereses permitirá entender los patrones de distribución de la biota mundial (Myers y Giller 1988, Morrone 1993).

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Dwight W. Taylor (1932-2006): A pioneering panbiogeographer

BY JOHN R. GREHAN

Panbiogeography first entered the biogeographic stage through Croizat's (1952) *Manual of phytogeography*, and then as a concerted methodological and conceptual framework in his 1958 *Panbiogeography*. While prominent biogeographic theorists such as George Gaylord Simpson and Ernst Mayr maintained the pretense that panbiogeography did not exist and it was rarely considered by other biogeographers in scientific journals and books, there were some sympathetic readers around the world, including editors who supported Croizat’s biogeographic monographs during the 1960’s (Heads 2005). It was to be another decade before panbiogeography became a central issue though attempts in the 1970’s to combine the method with cladistics (Nelson and Platnick 1981), and another decade more before it became promoted as a independent research program (Craw 1982).

But panbiogeography did not initially fall entirely upon deaf ears. Within a year of publication panbiogeography came to the attention of the North American mollusk specialist Dwight Taylor (Figure 1), who immediately embraced the new methods and concepts. Unlike the later attempts by Gary Nelson, Robin Craw, and others, Taylor did not attempt to take on the institutions of traditional dispersalism. Instead, he quietly applied the new principles to his studies and over the following decades expressed his support in several publications, beginning with a paper (Taylor 1960) where he recognized that recent and fossil freshwater clam distributions were similar to those of fishes and other freshwater snails. He concluded that relict mollusks and fishes could be related to a single pattern of distribution, with faunal links between different drainage basins, and acknowledged Léon Croizat who “contributed essential parts of the method of analyzing distribution”.

In a later study of Pliocene-early Pleistocene freshwater mollusk distributions in North America, Taylor (1966) expressed a panbiogeographic understanding of distribution by correlating local endemism with areas of recent tectonic activity and comparing geographic differences between faunas. He noted that tectonic activity promoted the differentiation of mollusks by changing their environments and separating or joining particular habitats, and supported earlier predictions that faunal differences either side of the eastern edge of the Rocky Mountains probably go back to early Tertiary or Cretaceous times. These panbiogeographic perspectives were otherwise an anathema among the biogeographic and evolutionary community of the time which was preoccupied with finding imaginary centers or origin and looking to dispersal ability as the key to distribution. In the acknowledgements he noted that C.W. Hibbard and D. E. Savage, who were largely responsible for the scope and synthesis “do not necessarily endorse all statements I have made”.

Fig. 1. Portrait of Dwight D. Taylor (courtesy of D. W. Taylor).
Nearly two further decades were to pass before Dwight Taylor was to again publish on panbiogeography. Interestingly, this interregnum also marked both the formulation of vicariance or cladistic biogeography, which was linked by its authors to panbiogeography, and the panbiogeographic research program in New Zealand. In 1983, only a year after Craw’s (1982) declaration in support of panbiogeography as an independent research program, Taylor (1983) drew attention to the trans-Pacific track of *Batillaria* connecting members of the genus in East Asia to those of the western United States, the Caribbean, and the Galápagos (Figure 2). This was followed by a paper on the evolution of freshwater drainages and mollusks in western North America (Taylor 1985). He identified past drainages as the simplest explanation of distribution patterns and inferred species relationships and considered it a fundamental principle that individual animals spread with their habitats as part of a biota. He also distanced himself from vicariance biogeography and repeated his “great debt” to Léon Croizat, asserting that his critical emphasis on detailed data of distributions in contrast to theoretical preconceptions, was largely derived largely from the works of Croizat, who has reiterated the principle that ‘earth and life evolve together’.

Three years later, Taylor (1988) published a major review of freshwater mollusk ecological biogeography where he argued for a strong historical component in the present-day distributions of species and higher groups. He noted that the Atlantic and Indo-Pacific oceans have vastly different relations to the range of freshwater mollusks, with the Atlantic cutting across genera and sets of genera as if it came into being after the evolution of those groups. In contrast, he found that the Pacific Ocean was bordered with primitive and local families, as if the development of the Pacific basin was earlier and accompanied the origin of living pulmonate families. With regions retaining their distinctiveness today, he dismissed supposed migrations to South America and Australia. Taylor felt that even though Darwin believed in evolution, he was compelled to deal with geographic distribution in a Lyellian, non-evolutionary way, and that the efforts to deal with animal geography by numbers of immigrants, flying birds, floating rafts, and even moving tectonic plates (see comments below on plate tectonics) go back beyond Darwin to Lyell’s special creation. The review includes numerous distributional maps as well some track analyses such as the classic Tethyan track illustrated for living and fossil (Cretaceous) members of *Melanopsis* (Figure 3).

Biogeographic discussions by Taylor (1988) include the incompatibility between Darwin’s center of origin theory and the widespread phenomenon of geographic replacement of related organisms, noting that even Darwin himself observed this basic attribute of life. He also commented on the historical change in Darwin’s thinking about dispersal, and the prevalence and importance of vicariism. Although supporting Croizat’s principle that “earth and life evolve together”, Taylor distanced himself from plate tectonic theory, noting that the lack of gondwanic elements in Australia and the degree of relationship with Southeast Asia suggest a long history of proximity, in opposition to conventional ideas of continental drift or plate tectonics. In his acknowledgements, Taylor attributed the source of his insights to the work of Claude W. Hibbard em-

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**Fig. 2. Dispersal of Batillaria (modified from Taylor 1983).**
phasizing that the spread of species occurs through their habitat; and to Léon Croizat, for showing the way to understanding the significance of global distributions and endemism. Taylor (1988) concluded his acknowledgements with the observation that withering criticism by Winston Ponder of the Australian Museum made him decide to discard the paper, but editors Jane Gray and Arthur Boucot finally extracted a revised paper from “the reluctant author”. Taylor suggested that “The future will determine whether they merit censure or praise; but anyway they have my thanks.” This detailed work was followed by another hiatus of 16 years, when Taylor (2004) published his final comments in support of panbiogeography, in which he also acknowledged the New Zealand contributions (Craw et al. 1999). This was to be his last biogeographic paper as only two years later he passed away.

I first learned of Dwight Taylor’s historical position in panbiogeography from Robin Craw, who drew attention to Croizat’s (1964) reference to Taylor’s (1960) work. But it was not until 1996 that when in the US I was able to make contact with Dwight, with the assistance of Dr. Jane Gray at the University of Oregon. Gray was coincidentally (if one may believe in coincidences) also a close friend of another early sympathizer of panbiogeography, the New Zealand palynologist Dr. Lucy Cranwell Smith (perhaps the subject of another article in Biogeografía). Taylor never became embroiled in the controversies over biogeographic theory and method that dominated the discipline from the 1970’s through to the present. He also never published extensively, even though what he did write was both prescient and perceptive compared with most other practicing biogeographers. His 1988 acknowledgement hints at some hostility with which his support for panbiogeography was received by his contemporaries. Fortunately for posterity, Dwight Taylor was kind enough to describe for me his experiences both with his interest in panbiogeography, his understanding of Croizat, and just what it was like to be a panbiogeographer in 1960. These insights are historically significant as a unique window into the origin and reception to panbiogeography by a person who was able to recognize something in the method and synthesis that was opaque to so many of his time. For the record, I have excerpted most of his comments from a letter he wrote to me in October 20, 1996.

Excerpts from Dwight Taylor letter, October 20, 1996

“As a general statement of my viewpoint, I urge you to give up an interest in biogeography, and do something more rewarding. Join an international community, study viticulture, computer graphics, holistic medicine, or almost anything else! Biogeography is a field that involves conflicts all the time, and one is greeted with extraordinary emotion on subjects of no conceivable relationship to human welfare, health, or economics.

I’m long gone from the fields of academia, but I can give you a background on why I found (and still find) Croizat’s work insightful.

Already in college, in the 1950’s, I had an interest in historical biogeography. This was partly due to the example of Hubbs and Miller (1948: although I later came to rate that work as flawed from the standpoint of biogeography), partly to my early interest in collecting fossil and modern shells. Thus I had seen that in the Mojave Desert, close to my home in southern California, where

Fig. 3. Dispersal of Melanopsis. Fossil localities – solid circles (modified from Taylor 1988).
formerly lived a variety of mollusks that survived elsewhere but were no longer found in the region. This early interest in paleoecology was embodied in a college term paper, later published (Taylor, 1954).

My freshman year in college (1949-1950) was at the University of Michigan, where I met C.W. Hubbard, a life-long influence on me. He was a brilliant naturalist, and although principally active in the stuffy of late Cenozoic mammals, was interested in and conversant with the study of other animal and plants (modern and fossil) and geology. I learned more from him informally than in most classes. My 1950 summer as a member of his field party was a stimulating and educational experience. Somehow I survived the work.

My graduate work (MA, PhD) was at Berkeley. Anxious to get out of school and being work, I did not take full advantage of the opportunities available. By studying and writing furiously, I finished my MA work in one year, and all PhD course work in the second year (I still regret not having spent more time learning in other fields, nor exploring San Francisco). So I catapulted out of Berkeley in June 1955, to take up employment with the US Geological Survey with the understanding that I would write my PhD thesis while employed.

I had no desire to go to Washington, DC, but that was an unavoidable evil. I had the enormous task of dealing with identifications of fossils sent currently, dealing with a great backlog of material to be identified and collections badly in need of organization, and learning stratigraphy and faunas new to me. But it was all fun in the early years.

In those days I was interested in building my own library, and received catalogues from the English firm of Wheldon & Wesley. I saw the title “Panbiogeography” and ordered the work with no basis beyond my interest in biogeography. This would have been in 1958 or 1959; at any rate, it was the first listing in their catalogues. What a terrific time I was in for! Never before or since have I stayed up late, night after night, in a mental turmoil of learning and unlearning. If you have ever been through the unlearning process, you will understand what I mean. If not, and if you are lucky, you will find out. Unlearning is vastly more difficult that learning.

To explain why this was a revolutionary time in my thought I need to give you some of my background at Berkeley. Although I was a student in invertebrate paleontology, my interests were in non-marine fossils – thus non-marine stratigraphy, non-marine paleoecology. I had far more in common with the students of paleobotany and fossil mammals than with those of marine invertebrates. (Jane Gray, by the way, was a student at Berkeley at the same time). The library in the department of Paleontology was called the Matthew Library, after W. D. Matthew (you will recall the name from the “Panbiogeography”), who was prominent, early, and fundamental in the Department. The interpretive basis of much of the mammalian paleontology was that of Matthew. And now I was encountering a massive work, explicitly hostile to the ideas of Matthew, Simpson, Mayr, and Darlington – but in which I could find explanations of mollusk distribution familiar to me, where the grand masters in the east had revealed nothing. How could this be? Obviously, it had to be a method (what was obvious to me has eluded a lot of people since).

Croizat suggested (Panbiogeography, xxix) that anyone interested should test his approach. Fair enough! So I began a paper on a subject I knew, but outside the scope of his own researches. This was published in due course (Taylor 1960); of course more information has become available, but none of that undercuts the method or conclusions of that work. Although I would not now write the paper in the same way, it still stands up well to my current reading. For later versions of the known distributions of groups treated in that early paper, see Taylor and Smith (1981; you can verify that the basic pattern is reinforced).

My interest in biogeography of the Pacific Northwest was reinforced by the practical need to understand biostatigraphy of the region. How could one explain the similarity or dissimilarity of supposedly contemporaneous faunas? My synthesis of Blancan faunas (Taylor 1966) was based on the need to resolve maters of inference of biogeographic patterns as overlays correlated with age and geological changes. Today, the time span I was dealing with is the whole Pliocene (and some Miocene), and not merely part of the Pliocene as I believed then. But still the paper has stood the test of time well. As to its influence, you can consult Smith (1975), who thought well of it.

Other reactions to my papers (from mammalian paleontologists at the American Museum) have, of course, been negative, with responses from frigidity to burning hostility. I do not want to dwell on a painful subject.

After publication of that short paper of 1960, I sent my copy of the whole volume in which it was published, to Croizat, as a way of expressing thanks, in addition to acknowledgement of his work therein.

The consequences of this sending were real, if not momentous. In “Space, Time, Form” (p. vii, fn) you will see that he confirmed I understood his work correctly. You can see also that he read and commented on some other papers published in that same volume. But the true reward for me was a prompt invitation to visit him in Caracas.

There was a magical quality to that trip, involving a change of state of consciousness along with the change in environments. I remember clearly leaving the airport on Long Island, New York, where patches of snow still clung to the ground. Puerto Rico (my first
sight of that island) seemed so small far below. And then Caracas (as I thought, but it wasn’t). The airport is some distance from the city, on the coast, where I was met by Léon and Catalina. Seeing the Mercedes, I thought, well, this fist may be intellectually hard, but at least not physically tough. They proved warm and informal, and we got along famously from the start. Only a few hours from New York, I was relaxing in a tropical garden, sounds of traffic dim and distant, caged birds singing, the scent of unknown flowers in the air, a tall cool glass in my hand. Catalina had a good business in landscape architecture/nursery sales, and the grounds of their home were a demonstration of what was for sale or could be obtained for clients. It was a golden interlude. I had no need to argue — I understood his method. He saw that. I had a lot to learn of geography, of other groups, but all matters of detail. I did ask if his method was basically the comparative analysis of distribution. “Yes.” He was a Latin, given to prolixity in an idiosyncratic style; I am an Anglo-Saxon. Yet we were in tune with one another.

The subject was from the exaggerated title, it was quite worthwhile. As to writing a paper for your proposed volume: First, thank you for the invitation. But I could not contribute anything useful. I am not conversant with recent literature in the field, and have always been concerned with (pan)biogeographic application and not theory. You belong to the new generation, I to that past.

I sent a few pages from an article by Norman Macbeth that may be of interest. I find the reference to Croizat demeaning, if not insulting; but of course he was only repeating what he had heard, without attempting to get other points of view. From that article, no one would ever take Croizat seriously.

One of the strong points of Croizat’s work is that he refused to mix geological data or interpretations with biogeography. Thus biogeography could provide an independent source of information, and its conclusions could be compared with those from geology. The New Zealand interest-group seems not to have understood this or its importance. I can see no merit whatever in geological area cladograms. As to Rosen’s papers being “seminal” in combining Croizat’s track analysis with Hennig’s phylogenetic systematics, well, there are good seeds and bad seeds. For Croizat’s discussion of Hennig’s approach, see “Biogeografía de las Américas”. And in your 1991 paper on p. 351 you refer to Croizat’s (1961) plate tectonic model for the formation of the Americas, but on re-reading Croizat’s work I cannot find that he said anything of the sort. So you can see that we are far apart.

My own viewpoint is that the geological model most consistent with Croizat’s biogeography is that of Carey (1988). Only a minority of geologists support his ideas, but nevertheless Carey’s work is consistent with all that I know about mollusk distribution, past and present. On p. 289-301 of Carey’s book you can find an outline showing the care with which he reconstructed several regions. Of course, he would deny that those were final, because new information is accumulated all the time.”

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Although biogeography, the study of plant and animal distributions in space through time, originated as a modern scientific discipline with Linnaeus and Buffon in the 17th century (Llorente et al. 2001), only in the last three decades has it begun to emerge as a stand-alone field of biological inquiry—while still hampered by a confusing plethora of approaches and methods which suggests a discipline amidst a scientific revolution (Crisci 2001). It should not be surprising, therefore, that only after about 70 years after the appearance of the “New Systematics” classic—the book edited by Huxley (1940), which turned out to be the first volume in a very important series of special publications—has the Systematics Association published a book dedicated to the subject of biogeography. However, it may have been worth waiting for, as this Biogeography in a Changing World is a precious little gem. This book brings together the papers from a symposium held in August 2005, in Cardiff, UK, with the title ‘What is Biogeography’, to provide a broad-based perspective on the nature of biogeography and the way it is practiced. The wide range of authors came from all across Europe and America (but unfortunately none from Latin America, where an active school of historical biogeography has flourished over the last decade). After a short (but provocative) opening by Neal Adams, and an historical introduction by Malte Ebach, in the first chapter David Williams presents a fascinating account of the fierce dispute between two relatively little known 19th century men of science: Ernst Haeckel and Louis Agassiz. This is the most extensive chapter in the book, extending over 59 pages and including a very comprehensive list of bibliographic references.

Chapter Two, by Lynne Parenti, provides a thoughtful discussion of cladistic biogeography and its application to unraveling the relationships between Earth history and distribution patterns using phylogenies. This is by far the clearest account of the subject I have ever read, with well-chosen and brilliantly discussed examples from the marine realm, which nicely complement and extend the many presented in Heads (2005) important review on marine vicariance biogeography.

In Chapter Three, John Grehan cogently presents yet another crystal-clear example of the powerful pan-biogeographical method and synthesis of Croizat (1958, 1964), in a study of the distribution of “an obscure group of daisies”, which, however, has important implications for the understanding of the evolutionary history of the entire Pacific Basin biota.

Bernhard Hausdorf and Christian Hennig provide, in Chapter Four, a summary of their “biotic elements analysis”, a quantitative method for clustering distribution areas which they have implemented as an add-on package in the powerful free, open-source R statistical system (Ihaka and Gentleman 1996). While I am not convinced that their method (or any other such method) can be able to distinguish between vicariance and dispersal as easily as they claim, nevertheless I found their criticism of the delimitation of areas of endemism very well reasoned. Moreover, biotic element analysis might offer a promising alternative (or substitute altogether), with a sound statistical basis, to parsimony analysis of endemity (PAE) in the analysis of presence-absence distribution matrices.

In Chapter Five, Tod Stuessy offers an interesting hypothesis for the “ontogeny” of island biotas, based on a synthesis of recent studies (many of them based on molecular data) of insular floras. I found tempting to compare his model with the classical “taxon cycle” model for the evolution of island biotas proposed by Wilson (1961) (who, by the way, is not mentioned in...
the list of references of this chapter), which describes similar sequential phases of expansion and contraction of the ranges of insular species, usually associated with shifts in ecological distribution (see Ricklefs and Bermingham 2002 for a recent review).

Chapter Six, by Isabel Sanmartín, is a presentation of “event-based biogeography” and its methodological cornerstones, “dispersal-vicariance analysis” (DIVA) and “parsimony based tree-fitting”. The author bravely attempts to demonstrate the advantages of this approach, which she claims to “have led to an extraordinary revolution in biogeographic studies”. I cannot share her optimism towards these methodological developments, as “event-based” biogeography adds to the two major problems of cladistic biogeography –namely, the delimitation of areas of endemism and the availability of well-supported phylogenies– the further need to correctly estimate the “costs” to be attributed to the processes of dispersal and vicariance in a given analysis. This puts “event-based” biogeography in danger of becoming nothing more than just another computer-based game –the results of which are such fantastic constructs as “concerted dispersal”, which brings to mind Croizat’s (1988) words: out of nothing, nothing comes.

As a contrast, in Chapter Seven Brett Riddle and David Hafner present a fairly good review of phylogeography, with a serious and well-founded effort to integrate the conceptual and methodological developments of area-based historical biogeography with the results of phylogeographic research. Although the real possibility of such integration is, in my opinion, questionable, the authors nevertheless provide a clear and mature discussion of phylogeography and its potential to offer useful insights on the evolutionary history of entire biotas over geographic space, in the context of “comparative phylogeography”. In so doing, they successfully avoid the easy “explanations” so common in the contemporary literature of molecular biogeography which not only reach the most non-sense conclusions, but at times even approach the miraculous (in sharp contrast to the excellent earlier works by Avise 1992; Avise et al. 1987; Bermingham and Avise 1986).

The last chapter, by Dennis McCarthy, summarizes and adds further evidence to his views on the impossibility to account for, on the basis of long-distance dispersal, the trans-Pacific disjunctions observed in so many taxa, both terrestrial and marine, living and extinct, with varied ecologies and means of dispersal. This leads to the inescapable conclusion that the Pacific Basin was closed in the Late Mesozoic and the recurrent patterns observed in the distribution of the biota around that ocean resulted from a single vicariant event, i.e., the opening and expansion of the Pacific in connection with an Expanding Earth (see also McCarthy 2003, 2005). While this idea may look strange (at least, to the more conservative minds), so looked equally strange the ideas of Du Troit and Wegener on continental drift when first presented to a hostile scientific community before the geological facts of sea-floor spreading turned these ideas into the overall consensus of today.

It is clear that the editors of this volume made every effort to make the book as complete as possible, and they must be congratulated for that. It may be expected that just as the first special volume of the Systematics Association published in the first half of the last century was the basis for a new evolutionary synthesis, the papers in this book will provide the much needed insights which should turn biogeography into the true synthetic and integrative biodiversity science of the 21st century. It surely deserves to be so.

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Ricklefs RE, Bermingham E. 2002. The concept of the taxon cycle

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What is the current state of historical biogeography today? This is not an easy question to answer as it contains several different questions. Our objective herein is to address this subject by analyzing the last two published volumes of the *Journal of Biogeography* (2005, 2006). The *Journal of Biogeography* is currently one of the most prestigious journals in biogeography, having progressively become more and more visible by the scientific community since its first issue in 1974. Presently, it has an Impact Factor (IF) of 2.878 and has been ranked as 3/30 (Geography, Physical) and 27/114 (Ecology) according to ISI (2006). The mission statement, published on the Journal’s homepage (2007) claims that: “the mission of the journal is to contribute to the growth and societal relevance of the discipline of biogeography through its role in the dissemination of biogeographical research. To that end, the editorial policy is that the journal seeks to be representative of the discipline of biogeography, to be global in scope, and to be inclusive of major traditions and viewpoints within the discipline”. Given this, we decided that by analyzing articles published in the *Journal of Biogeography* would be a good starting point to unravel the question of the state of biogeography today.

**Questions**

Our study begins by asking a series of questions that cover different aspects of historical biogeography.

How many works of historical biogeography have been published in the last two volumes of the *Journal of Biogeography*? Eighty-four papers dealing with historical biogeography have been published in the two volumes we are considering. Remarkably, exactly 42 papers on historical biogeography appeared in each one of them (volume 32 -2005- and 33 -2006-).

What proportion of the papers published in this journal do they represent? During the last two years, 371 papers were published in the *Journal of Biogeography*. This number includes “Guest Editorials”, “Original Papers” as well as commentaries and replies. During this period, papers on historical biogeography represent just 23% of published papers.

How many authors published these papers? The 84 historical biogeographical papers considered here were authored by 234 authors, with a mean of 2.8 authors per paper. When considering individually each volume, volume 32 involved 133 authors in its 42 historical biogeographical papers with a mean of 3.2 authors per paper, and for volume 33, authors were 101 with a mean of 2.4 per paper. As Figure 1 shows, 74% of the papers were authored by one to three authors. The maximum number of contributing authors to a single paper was six, and such a number was achieved in only 5% of the considered papers.

![Fig. 1. Number of papers published on Journal of Biogeography vols. 32 and 33 according to the number of authors.](image-url)
What kinds of papers were published? Empirical papers represented the 73% of the 84 historical biogeographic papers analyzed. Papers dealing with theoretical questions account for the 19% of them. The remaining 8% are replies or comments.

A geography of historical biogeography

Possibly the most interesting question is where do the authors who published in the Journal of Biogeography live? Considering only the place of residence of the three first authors of each paper at a continental level (that is 194 of the 234 authors included in this analysis), we observed (Figure 2) that circa 80% of published authors live in Europe, North America or in Latin America, including the Caribbean (LAC). Table 1 shows the residence of first, second, and third authors at continental level. When authorship was analyzed by countries (Figure 3), always considering just the three first authors, we noted that 30 countries were represented according to authorship. United States of America has the highest number of contributing authors (48), followed by Australia (18), Mexico (14), Canada (11), and Argentina, Norway and United Kingdom (each one with 9 authors).

What biogeographical areas were analyzed in historical biogeographic papers? As shown in table 2, most historical biogeographic papers considered herein dealt with more than one biogeographic region: Worldwide (3), Nearctic plus Neotropical and/or Andean (4), Ethiopian plus Australasian and/or Oriental (3), Neotropical plus Andean or Ethiopian (3), Gondwanan (3), Australasian + Oriental (2), and Nearctic plus Paleartic (1). Regarding those papers that dealt with a unique area, the Paleartic region ranks first; followed by the Australasian and Nearctic regions in second place. Latin America and the Caribbean have been considered in 13 papers (more than that devoted to the Paleartic) but they were considered here as two separate biogeographic units (Neotropical and Andean regions) following Morrone (2001). It is interesting to note that the Nearctic region is not the best represented considering that most authors come from USA (see above).

Taxa inquiries

What taxonomic groups were preferred? Only for 68 of the 84 papers, it was possible to analyze which taxonomic group or groups were considered. At the highest level, 48 papers of the 68 here considered dealt with animal taxa (66%), 18 papers dealt with plant taxa (27%), and 5 dealt with both plant and animal.
taxa (7%). When we consider those papers which involved animal taxa and analyze them at a lower taxonomic rank (when possible), we find that most studies are devoted to Chordata (almost 50% of the considered papers), followed by Arthropoda (Table 3). This fact reflects an important bias regarding biodiversity since Chordata represents less than 5% of the animal diversity. More papers were devoted to supraspecific taxa, although many works were focused at infraspecific level.

What habitats were considered? As shown in Figure 4 most papers were devoted to terrestrial habitats, only 34% corresponded to aquatic habitats and just 10 papers analyzed historical biogeographic questions related to marine taxa.

Theoretical and methodological framework

What approaches of historical biogeography were applied? Figure 5 most strikingly summarizes the answer to this question. In accordance to the classification of biogeographical methods outlined in Crisci et al. (2003), phylogeography ranks first as the most used method. Cladistic biogeography, parsimony analysis of endemicity, and molecular biogeography shared the second place with 10 papers each. By “molecular biogeography” we refer to those papers that explore historical biogeographic questions by mapping distributional information of taxa on a molecular based phylogeny, but which do not apply a particular methodology. It is interesting to note that there are as many as five papers which did not apply a particular ap-

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**Table 3. Animal taxa analyzed.**

<table>
<thead>
<tr>
<th>Animal taxa</th>
<th>Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chordata</td>
<td>19</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>13</td>
</tr>
<tr>
<td>Mollusca</td>
<td>4</td>
</tr>
<tr>
<td>Annelida</td>
<td>1</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>1</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>1</td>
</tr>
<tr>
<td>Nematoda</td>
<td>1</td>
</tr>
<tr>
<td>Platyhelminthes</td>
<td>1</td>
</tr>
</tbody>
</table>
These articles used methodological tools from different approaches resulting in what we term herein as a “combined approach” (see table 4). It is important to note that even though phylogeography is most applied approach, there is no correlation between the use of phylogeography and the proportion of infraspecific treatment of taxa. Such a correlation would be expected since phylogeography was originally developed to analyze infraspecific biogeographic patterns (Avise 2000). Furthermore, we noted that many papers applied phylogeographic principles to supraspecific taxa (species or genera).

**Which historical biogeographic techniques were applied?** Once the papers were classified according to the historical biogeographic approach in which they are framed, a new question arises, namely “which techniques are applied to analyze data?” Table 4 best summarizes the answer to this question. We recorded 12 different techniques plus 4 different technique combinations. In most papers, these techniques are applied to analyze data, although a several articles, the aim of the paper was the technique itself. (For example, Morrone [2005] offers a discussion over a particular approach and Wojcicki and Brooks [2005] introduce a new method and algorithm.)
Which biogeographical processes were considered? Fifty percent of the papers considered dispersal and vicariance as complementary processes, which model the distribution of taxa. While 24% considered or dis-

cuss only dispersal events and 18% deal only with vicariance. Remaining 8% did not make inferences about any particular processes.

How many papers used timing through molecular clocks? Most of the papers considered here which use phylogenetic information were based on molecular phylogenies. Nonetheless, timing through molecular clocks seems not to be of common use among historical biogeographers (Figure 6) even when timing has been postulated as a priority item on historical biogeography (Crisci et al. 2003; Donoghue and Moore 2003; Hunn and Upchurch 2001). The accuracy of molecular clocks have been discussed elsewhere, for example see Heads (2005) and Pulquério & Nichols (2006) and literature cited therein.

Conclusions

Here we attempted to summarize the current state of Historical Biogeography. We posed a set of questions trying to address a fairly large topic although there are many more questions which still are unanswered. However, some generalities could be extracted of this analysis:

1. Latin American and Caribbean authors have made an important contribution to the Journal of Biogeography, equaling those made by their European and North American colleagues, using the limited re-

ources available to them (see Ebach et al. 2007). As an example, expenditure on Science and Technology (ST) as a percentage of GDP (Gross Domestic Product) was less than 0.5% for Mexico and Argentina (the two LAC countries with more authors regarding this study,
see Figure 3) and 0.91% of GDP for Brazil (RICYT 2007). On the other hand, North American resident authors work in countries which exhibited for 2004 an expenditure on ST was 2.66% of GDP for USA and 1.96% of GDP for Canada (RICYT 2007).

2. Molecular biogeography and phylogeography articles were unique in that they contain a biogeographical discussion as well as a phylogenetic analysis, rather than using existing systematic data published elsewhere. Most articles that applied a particular biogeographic technique to a particular taxon (taxon biogeography approach) rather than searching for common biotic patterns (area biogeography approach), a topic that was strongly developed in past decades.

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The computer programs NDM/ VNDM (Goloboff 2005) implement a grid-based method developed by Szumik et al. (2002) and subsequently improved by Szumik and Goloboff (2004), providing a formalized way to identify areas of endemism.

The notion of areas of endemism is an old one, and can be traced back to the 1800’s. Naturalists observed that some groups (species or higher taxa) seemed confined to certain regions of the globe, and called them endemic. Hence, those regions which have many endemic taxa were called areas of endemism.

From the modern point of view, if a given factor (e.g. barriers or ecological factors) affects numerous groups of organisms at the same time, it is expected that they will respond in a similar way – so that the distribution of those organisms be similar. While discovering the causal factors behind those similar distributions may be of great scientific interest, the first step towards discovering the patterns they produced. The patterns themselves can be studied, regardless of whether those causal factors have been identified – or even hypothesized.

The identification of areas of endemism, however, has traditionally been done intuitively, which is not incorrect in principle, except that in practice the patterns are not so clear, so that proposals from different workers are often in conflict. Additionally, the criterion given worker uses is not always explicit. This makes it difficult to compare the relative merits of the proposal by different authors.

Some years ago (starting with Morrone’s [1994] proposal) people began using algorithms from phylogenetic analysis to identify areas of endemism. In phylogenetic analysis, we have a series of observations on the animals (or plants), and the purpose is to find the tree that best explains the observations in terms of common ancestry. This means that the only way to choose a phylogeny is to determine how well each tree explains observations, and choose the best trees. Although the criterion (common ancestry explanation) is well established, the problem is that there are many trees (e.g. for 1000 species, there are $10^{10236}$ possible trees). It is widely known that the computer programs for phylogenetic analysis cannot truly examine all possible trees (except for trivially small data sets). Searches require looking at hundreds of millions of trees, so this is time consuming. Phylogenetic computer programs operate by trial-and-error or heuristic methods: take the best tree(s) found, change some branch, re-evaluate the new tree, and if better, keep it. Lots of work has been done in this area and now it is possible to evaluate each rearrangement without using much time. For example, on fast computers, PAUP* (Swofford) can look for trees with 1000-3000 taxa at about 200,000 rearrangements/second. TNT (Goloboff, Farris, and Nixon), which uses significant improvements to the existing algorithms for tree-evaluation, can look for trees at about 150,000,000 rearrangements/second (i.e. 50 to 200 times faster than PAUP*).

At this point, the reader may wonder about the connection between the problems of phylogeny and areas of endemism. There are two aspects in which evaluation of areas of endemism may have similarities with evaluation of phylogenies:

- the criterion for evaluation of a given tree is well established; the problem lies in finding the tree(s) which best fulfill that criterion.
- modern computer programs find the best tree(s) by using trial-and-error methods, starting from promising trees, and improving them by gradual modifications.

But there are potentially serious problems with using phylogeny programs to evaluate areas of endemism:

- phylogeny programs deal only with trees (i.e. non-overlapping, hierarchical subsets).
- the criterion of tree evaluation considers common ancestry, which is not applicable to endemism (areas of endemism do not descend from each other). In fact, areas of endemism could be discovered in a manner analogous to phylogeny by evaluating possible areas, determining a rational criterion to measure how well the data support a region as an area of endemism and then choose, from among possible ar-
eas, those that are best supported by the observations.

A criterion

Following that reasoning, Szumik and Goloboff (2004) have taken into account the traditional notion of endemism and tried to formalize it. A taxon is endemic to an area when it is found there and nowhere else. Whether a given taxon can be considered as “endemic” to an area depends on how the limits of the area are defined. This provides a natural measure: with more taxa that can be considered as endemic, the area (=set of cells) is better supported as an area of endemism. For this purpose, a formula was devised to determine how strongly endemic a given taxon can be considered, for a given area. This simple formula takes into account, for a given species \( s \), the proportion of cells inside the area where it is found, and the number of observations outside the area. Two types of records are considered, actual presences (=observations) and assumed presences (uncertain).

\[
V_s = \frac{p + (i \times f_i) + (a \times f_a)}{\text{size} + \frac{o}{fo} + \frac{d}{fd} + \frac{n}{fn}}
\]

Where (for more detail of the formula see Szumik and Goloboff 2004):

- \( p \): number of cells of the area where the species is actually present.
- \( i \): number of cells of the area where the species is inferred (i.e. when it satisfies the evenness rule).
- \( a \): number of cells of the area where the species is assumed.
- \( \text{size} \): size of the area (number of cells which is evaluated)
- \( o \): number of observed records - cells where the species is actually present - outside the area
- \( d \): number of assumed records - in adjacent cells - outside the area
- \( n \): number of assumed records - in non-adjacent cells - outside the area

The factors \( F_i \), \( F_a \), \( F_o \), \( F_d \) and \( F_n \) are used to make the terms more or less influential; the factor may be changed by the user.

Note that the formula considers the spatial component of the problem, obviously a fundamental aspect when evaluating areas of endemism.

An example

Given the grid of Figure 1, the endemcity value of the yellow set of cells depends on how well the “blue”, “green” and “red” taxa are adjusted. The blue taxon will have the maximum value given that it is present in each cell of the yellow set and is absent in the rest of the grid. The green taxon will have a lower value given that it is absent in one cell of the yellow set. Finally, the red taxon will have an even lower value; it is present, both in each cell of the yellow set and outside the set, in an adjacent cell.

A problem

One of the problems to find all the areas (=sets of cells) which have many species as endemic is that there are many possible sets of cells. The number of set combinations for 2 cells of the grid of Figure 2 is:

\[
\binom{(8 \times 10)!}{2! (8 \times 10 - 2)!}
\]

Where 8 \((r)\) is the number of rows and 10 \((c)\) is the number of columns in a given grid. The number of set combinations for 3 cells is:

\[
\binom{(r \times c)!}{3! (r \times c - 3)!}
\]

And the number considering all cell combinations is:
In the example of Figure 2 this is $34,284,628,541,061,130,000$ possible sets.

**How?**

That is what NDM (search engine) and VNDM (a graphic shell) implement. As many methods and programs, NDM converts observed records (points) into a matrix (grid) of presences/absences. It is here where the bioinformatics comes into play: we need a computer to generate all the possible sets of cells—or as many as possible. The similarity between programs for endemism and phylogeny now becomes clearer. NDM is based on the same principle as phylogeny programs: it searches for sets of cells by gradual modifications of existing sets. The initial sets are created by considering the observed distributions. The derivative areas (obtained from “swapping” cells) that have a score which is as good as the original one are stored in memory for subsequent swapping (and comparisons). Since each new area differs from the original one in only one cell, it is possible to recalculate the score of each new area with less effort than the work required if the score was to be recalculated de novo. For example, the original area can expand at most one square (Figure 3), so that the number of records outside a given “frame” does not need to be counted again. NDM takes advantage of this, but even so, the number of rearrangements it examines per unit time is much lower than phylogeny programs.

Although some improvements could be made to the basic method of evaluation, the running times for the program are strongly determined by another problem. In phylogeny, as it may be recalled, it is possible to obtain a single tree with the best score. Also, it is possible to find multiple trees with equal score, which means that the data are ambiguous regarding tree
choice. But then all trees of a score lower than the best one can safely be discarded. When examining areas of endemism, that need not be the case. Two partially overlapping sets (Figure 4) of different score can be both perfectly supported as areas of endemism, if they have their scores given by different sets of species. This means that, unlike phylogeny, a search cannot retain only the areas with highest score; areas with lower score may have to be retained as well, if they are distinct in this sense. This, in turn, introduces a series of new problems. One of those is that the program must save large numbers of candidate areas during searches. These areas are compared—after the search is completed—so that conflicting areas are retained only if they have their endemism scores given by different sets of species; saving so many areas slows down searches. After the search is completed, NDM retains partially overlapping areas if the unique species are above a certain percentage. Even so, the number of areas (sets) found by NDM may be large (hundreds) because small differences when including/excluding just one cell often do not affect the endemism scores.

How can areas be “consensed”?

A widely used method in phylogenetics, when ambiguous data produce many trees as alternatives, is using consensus trees—i.e. trees that summarize the information common to many trees. The areas to include in a consensus should somehow represent the same in terms of cell composition which is tricky and hard to define. However, what determines sameness in different areas is the species that appear as endemic. Thus, a consensus area can be created by considering all the areas that have, approximately, the same species giving score, and this takes care, indirectly, of the cell-composition problem (because the criterion to determine whether a species gives score to an area is a spatial one). Thus, a larger set can be formed if two areas have their scores given by two sets of species, with X percent of the species in common. VNDM calculates these consensus areas; areas of varying scores can be included in the set, keeping track of the maximum score of the areas in which a cell is included. A diagram showing different colors for cells that are less strongly endemic is also desirable (see the example below), for cases where the limits of an area of endemism are not sharp (Goloboff and Szumik in prep.).

Some characteristics of the programs

Editing the data. VNDM reads the geographic coordinates of the taxa and transforms the data into a binary matrix for NDM (Figure 5).

Defining grids. VNDM allows the user to generate several grids with different sizes for the same data. VNDM includes many commands that allow re-editing the data before the analysis (for more detailed explanation see the manual of the programs at www.zmuc.dk/public/phylogeny/endemism) (Figure 6).

Analyzing the data. The characteristics of the searches are defined with VNDM but the actual analysis is made by NDM. For that reason, both programs must be in the same folder (Figures 7-8).

Exploring the resulting areas. When the analysis is finished it is possible to see on the screen the basic information of the sets found by NDM (Figure 9).

Exploring the endemic species of a given area. VNDM also enables to evaluate how strongly endemic the species is for a particular set of cells (Figure 10).

Calculating consensus areas. (Figure 11).

Conclusions

• areas of endemism can be hypothesized by using a specific criterion, instead of ad hoc application of programs designed for other purposes.
• in practice, the results obtained with that criterion seem to have a general correspondence with traditionally recognized ecological regions.

Fig. 5. Format of data input files for VNDM.
Figs. 6-11. 6, Determining size and position of grid for automatic conversion of point data into matrix; 7, factors for importance of absences within area and presences outside area; 8, settings for the search of areas of endemism; 9, using VNMDM to view one of the areas found; 10, viewing each of the species that contribute score to the area; 11, viewing a consensus area.
• computer programs for endemism must deal with some problems common to phylogenetic analysis, as well as with some new problems as well.

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References


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