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3 A Brief Look at Pacific Biogeography: The Trans-Oceanic Travels of *Microseris* (Angiosperms: Asteraceae)

John R. Grehan

ABSTRACT

The modern revolution in biogeography did not begin with plate tectonics. It began two decades earlier when Leon Croizat established geographic distributions as the empirical foundation of evolutionary biogeography. Comparative map analysis reveals patterns that are not accessible through other methods. The biogeography of *Microseris* (Angiosperms: Asteraceae) is used to illustrate the power of geographic analysis to provide unique insights into the biogeographic distributions and relationships of organisms. Explanations of dispersal as physical movement for *Microseris* are shown to be problematic by the congruent distributions and Pacific homology of this genus with groups of diverse means of dispersal such as daisies, dragonflies, millipedes, eyebrights, and seaweeds. The role of tectonics and the historical implications of *Microseris* biogeography for molecular clock theory are briefly discussed.

INTRODUCTION

Biogeography has not changed much from the time of Darwin (1859). After 150 years of evolutionary biogeography, most biogeographers still follow Darwin's theory of geographic distribution requiring dispersal from geographically restricted centers of origin. Never mind whether the dispersal takes place before (process of vicariance) or after (process of ecological dispersal) the formation of barriers, the underlying principle of Darwinian biogeography is that organisms move about so their actual distributions are historically uninformative. To discern the geographic context of evolution, Darwinian biogeographers look to historical theories of ecology, systematics, molecular clocks, and geology — anything but distributions themselves — as the empirical data of biogeography.

The historical narratives of these non-biogeographic disciplines are transformed into actual reality as the platform upon which the biogeography plays itself out. And perhaps this is not surprising, as most of those who enter the field of biogeography are actually more interested in other aspects of evolution such as a particular group of organisms or a biological field such as ecology, systematics, or genetics. Interest in biogeography as such — the analysis of geographic relationships for life in general — is something that often does not enter into consideration. One only has to see how often distribution maps are left out of the picture, even for papers focusing on biogeographic theory and method.

MOLECULAR MYTHOLOGY

Over the last ten years or so, Darwinian biogeography has claimed a newfound sense of authority through the application of molecular clock theory as the final solution to that holy grail of Darwinian biogeography — the individual separation of dispersal and vicariance. Amidst a fanfare of rhetoric and propaganda these practitioners claim to have transformed biogeography (DeQueiroz, 2005; Didham, 2005; Waters, 2005), while in reality their approach is no more than a molecular application of Darwinian biogeography (Heads, 2005a). Molecular clocks are supposed to finally test the dispersal vs. vicariance problem of Darwinian biogeography according to whether the divergence estimates match or postdate a hypothesized geological event (Waters, 2005). The method is so simple that one can support its authority even without being a biogeographer (e.g., Didham, 2005), or criticize Croizat (1964) without reading the work — as did Waters & Roy (2004) based on a characterization of panbiogeography by Humphries (2000), an error acknowledged by J. Waters (pers. comm.).

Apart from the assumption that a geological theory has some kind of necessary empirical reality, the Darwinian practitioners usually overlook the fact that molecular clock scenarios based on minimum age of fossilization cannot generate maximum estimates of divergence. Even though molecular theorists admit as much, they somehow forget this maxim when final judgments are rendered upon group after group — with a common refrain being that the estimated divergence postdates theorized geological events and therefore falsify vicariance (Heads, 2005a).

GEOLOGY FIRST?

Biogeography does get complicated if one attempts to apply Darwinian theory to systematics and geography. The possibilities become almost as numerous as the number of branches of a cladogram. All of these approaches share in common the presumption that biogeographic reconstruction is confined to background knowledge derived from ecology, fossils, and stratigraphy all mixed together with various, and sometimes contradictory, notions of centers of origin and dispersal (Croizat, 1952). Islands such as the Galapagos are seen as self-evident proofs of long-distance dispersal followed by isolation and differentiation because they are obviously volcanic, oceanic in origin, and without any historical connections with continental mainland areas. Mayr (1982) made this argument when dismissing Croizat's (1958) support for ancient Galapagos plant and animal life being inherited as a whole from the American continent as "… so totally refuted by the geological and biological evidence that no further comment is necessary". Clearly the message here is that background knowledge is beyond challenge.

But even as Mayr wrote those words, geologists had already discovered that the Galapagos was an integral part of a major tectonic structure (the Galapagos Gore) extending between the East Pacific Rise and the Americas. This discovery corroborated Croizat's (1958) earlier prediction, made before seafloor mapping, that the Galapagos were associated with a major undiscovered tectonic center. This prediction was necessary because the biogeographic patterns involving the Galapagos conformed to a 'continental' pattern as if the Galapagos were embedded within a continent rather than the ocean. A number of geologists were also contemplating complex tectonic models that predicted Mesozoic and Cenozoic island arcs or micro continents in the eastern Pacific that overlapped the Galapagos and are now embedded within continental America. Some geological models even included connections with Asia across what is now the Pacific basin (Grehan, 2001a). These geological discoveries show that, just because a biogeographic hypothesis conflicts with current background knowledge, it does not mean to say the biogeography is necessarily wrong (in contrast to the belief of Mayr 1982).

A PRIMER IN BIOGEOGRAPHY

Above all, it is the lack of biogeographic knowledge that haunts biogeography. Ask the basic question, as did Croizat (1952) over half a century ago, whether certain place names such as Kerguelen, Madagascar, Mascarenes, Rapa, etc., bring forth a geographic image in the mind. Croizat (1952) saw the ability to answer such a seemingly simplistic question as the necessary starting point for following a discussion on dispersal. It was this fundamental shift that revolutionized biogeography, not the later acceptance of plate tectonics as belatedly claimed by Darwinian biogeographers. The revolution took place when, for the first time, **biogeographic maps** became the foundation of biogeographic analysis. Biogeographic maps are not biogeographic distributions; they are maps of the spatial structure and homology of distributions (Croizat, 1952; Craw et al., 1999; Grehan, 2001b). Distributions only document spatial location. Regrettably, many practitioners of biogeography seem to be little better prepared in biogeography now than in Croizat's time. Biogeographers often seem profoundly ignorant of the principal patterns of biogeography — the tracks and nodes of life that are the empirical traces of evolution in space/time — when they continue to dismiss individual distributions as puzzling or mysterious (Craw et al., 1999).

It is knowledge of distributions that may be the most powerful tool for any evolutionary biologist: "If species evolve from preexisting species, then the geographic distribution of species should tell us something about the actual course that phylogeny has taken" (Hull, 1988). Attention to actual distribution assumes that the geographic structure of distributions — the distributional limits, the spatial geometry, the boundaries and range, taxa present, taxa absent, etc., are all potentially informative about the evolutionary structure of life (Craw et al., 1999). If dispersal forever repeats (Croizat, 1964), then so too does biogeography. In the following section the consequences and the possibilities are considered for an obscure group of daisies that are supposed to be the result of the fortunes of ecology, but whose distributions may speak for a very different evolutionary history.

LOGIC OF DISPERSAL

Dispersal in evolutionary biogeography is all about the evolution of distributions or dispersal in the broad sense that comprises two empirical elements: relative locations and geographically differentiated biological forms ranging from individual genetic and morphological differences to those that are delineated by formal taxonomic ranks. Dispersal must, therefore, account for both spatial and biological differences. Darwinian biogeography attempted to encompass dispersal within the ecological meaning of the term to refer to physical movement through the active or passive migration of organisms. In this Darwinian context, dispersal is a concept borrowed from the science of ecology and refers to the movement of organisms.

Croizat (1964) recognized a biogeographic concept of dispersal that encompassed both the spatial and the biological differentiation of form, and he therefore proposed a purely biogeographic definition of dispersal as translation in space + form-making. Dispersal in this context is a biogeographic concept referring to the evolution of both spatial structure and biological differentiation of form (Grehan, 2001b). Evolution can, by itself, bring about the presence of a taxon at a particular location without physical movement. This is a radical departure from earlier convention, and perhaps Croizat could be criticized for not developing an entirely novel terminology. But in this logic of dispersal one can look at biogeographic evolution in terms of either mobility (ecological dispersal) or differentiation (biogeographic dispersal) or as a combination of the two. The following sections examine the different contexts of dispersal from Darwinian and panbiogeographic perspectives.

DISPERSAL THROUGH MIGRATION

Comprising about 13 species of annual and perennial daisies, the genus *Microseris* is generally found in grasslands or other open habitats from wooded to desert and scrub communities (Chambers, 1955). Three species are found in western North America. One species occurs in southern South America, another in New Zealand and Australia, and a third in eastern and Western Australia. In a paper presenting DNA evidence for *Microseris* evolving in Australia and New Zealand after long-distance dispersal from western North America, Vijverberg *et al.* (1999) note that adaptive radiations on various islands are supposed to have evolved "from one or few individuals after long distance dispersal", and that molecular diversification among oceanic island relatives suggests the sampling effect of genetic drift following a founding event. Having established these suppositions, they acknowledge Carlquist's (1983) documentation of intercontinental disjunctions between the west coast of North America and southern South America. Vijverberg *et al.* (1999) suppose these disjunctions are, like floras of the oceanic islands, the result of bird dispersal rather than tectonic plate movement.

Here is the reasoning. First, suppose adaptive radiations on oceanic islands are the result of chance long-distance dispersal. Then, suppose a low level of molecular diversification is evidence of long-distance dispersal. And also suppose that long-distance disjunctions between western North and South America are the result of the same process. One has effectively already arrived at the conclusion of long-distance dispersal whereby the DNA result will, by definition, provide evidence of that dispersal. Vijverberg *et al.* (1999) illustrate this reasoning in characterizing the Australian and New Zealand *Microseris* species as a pattern of adaptive radiation following intercontinental dispersal of an annual and perennial North American hybrid that reached Australia and New Zealand by long distance dispersal. After constructing a chloroplast DNA phylogeny showing the Australian and New Zealand species to be a monophyletic clade, Vijverberg *et al.* (1999) present this phylogeny as evidence for the distribution originating from a single or a few closely spaced colonizing events. The single origin was anticipated because of the supposed hybrid origin in North America, and the uniformity of its allotetraploid karyotype was seen to be compatible with this process.

The study by Vijverberg *et al.* (1999) repeats similar contentions made by Bachman (1983), who also accepted the migrations of *Microseris* as a biogeographic fact. He reports on two "unrelated" long-distance dispersal events, one for Australia and New Zealand, and one for Chile. The latter was considered to be "less spectacular and easier to analyze". Having accepted long-distance dispersal, the developmental genetics of *Microseris* was interpreted both as the result of this process as well as "testing" the hypothesis itself. Here a theoretical conjecture is transformed into fact informing empirical studies of genetics that in turn are supposed to give insight into the process theorized in the first place. There is the very real danger of making a round trip back and forth from one theory to another.

Carlquist (1983) argued for intercontinental dispersal between western North and South America, because separation of tectonic plates could not explain the disjunction. He also saw the ability to hybridize species from the two continents and the occurrence of conspecifics as evidence that these migrations occurred recently. Migratory birds were the obvious link, and this mode of theorized migration was congruent with a seed and fruit morphology that would allow transport through ingestion or external attachment.

MICROSERIS (PANBIO)GEOGRAPHY

According to Chambers (1963), the single southern South American species is the result of bird dispersal carrying seeds from North America on a one-way trip that happened to occur in a variety of plant groups. This might be possible, but what about the other side of the Pacific? The species *M. lanceolata* is found only in Australia, and then only above 200 m in certain parts of Australia: southwestern Australia above 200 m at Esperance, and southeastern Australia from Spencer Gulf inland southeast to the east and west of Melbourne, and northeast to Bundarra and Armidale in New South Wales. The distribution vicariates with another New South Wales species (*M. scapigera*) centered on localities around Melbourne, central Tasmania, and New Zealand east of the Southern Alps in the South Island near Mt.

Cook to the Kaikouras, and in the North Island from the southeastern coast to inland Tongariro. Again, what is the biogeographic meaning of this pattern? What is the biogeographic meaning of these localities? How is it that the species come to be just where they are?

The distribution of *Microseris* within North America may not seem all that significant for biogeography in general. After all, there are many other plants and animals with similar distributions. But that is just the point. Why does the genus have a North American range limited to the western region? If biogeography is the combined act of individual and unrelated histories, such questions may not have general significance. After all, in looking to the migratory abilities of animals and plants anything is possible, and distributional limits are simply the result of chance. This would leave *Microseris* within an evolutionary universe of its own, and its biogeographic history is that of itself. No other organisms need matter unless they are providing the means of dispersal such as birds carrying *Microseris* seeds. And yet, to the biogeographer these localities may be as telling about *Microseris* as they are about the evolution of distributions in general because they are not biogeographic features of *Microseris* alone. Chambers (1955) hinted at this possibility when he predicted that a better knowledge of the origin of *M. scapigera* may have very interesting consequences for studies of plant distribution and relationships in the southern hemisphere.

What is interesting to the (pan)biogeographer is the geographic pattern. *Microseris* has a classic biogeographic range with respect to all its main locations. Its main massing (geographic concentration of diversity) is unambiguously around the Pacific basin (Figure 3.1). All species are located adjacent to, or closer to the Pacific basin than any other ocean basin. This is a spatial homology. It cannot be derived from any method that does not incorporate spatial characters. It cannot be derived from an area cladogram constructed from biological relationships. With a spatial homology one may recognize not only the shared biogeographic homology of *Microseris* with other Pacific distributions, but also individual localities. The pattern of biogeographic dispersal (as translation in space + form-making) involving Western North America, southern South America (in this case west of the Andes) and Australia/New Zealand is biogeographically standard (Craw et al., 1999). The pattern is found in organisms with such diverse means of dispersal as petalurid dragonflies, heterochordeumatoid millipedes, eyebrights (*Euphrasia*), and blennospermatinae daisies (Figure 3.2). All of these distributions are more widespread than that of *Microseris,* but they share the localized ranges of Western North America, southern South America, and Australia. In detail, the distributions of Heterochordeumatoidea, *Euphrasia*, and *Abrotanella* share with *Microseris* the southern Australian range of Western Australia and the connection between Tasmania and New South Wales. *Blennosperma* and *Microseris* each occur in both Western North America and southern South America, but *Blennosperma* also vicariates with *Crocidium* and *Abrotanella* in North and South America, respectively (Heads, 1999). For all that one might theorize about *Microseris* being ferried by birds, the Pacific biogeography of *Microseris* is biogeographically as one with millipedes, dragonflies, eyebrights, and blennospermatid daisies.

Perhaps the coincidence of distributions is purely chance. As one contributor recently commented on TAXACOM, even blind pigs can occasionally find acorns. Well, perhaps. Whether 'coincidence' or not, a biogeography of *Microseris* must

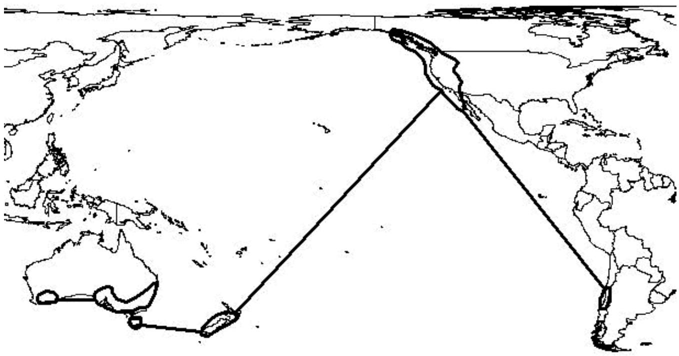
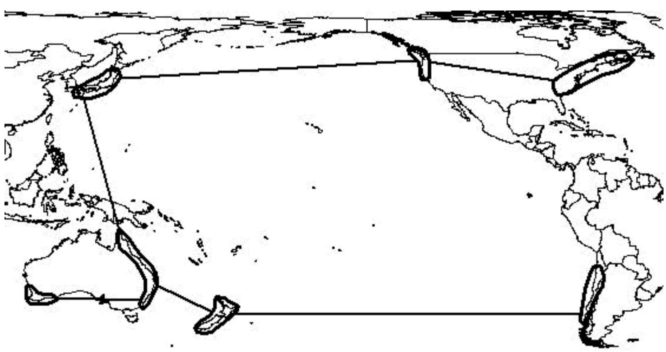
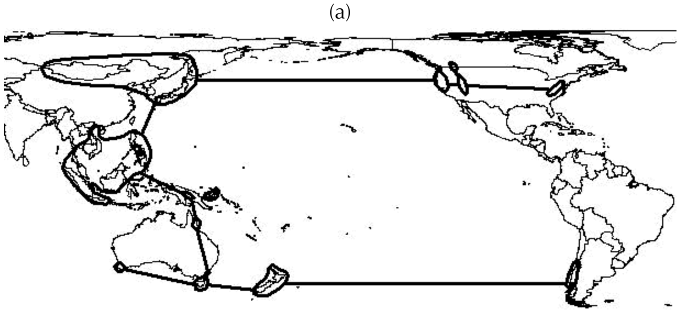


FIGURE 3.1 Pacific dispersal (translation in space) of *Microseris,* showing main massing of distribution around the Pacific basin with local massing in Western North America (about 13 species), South West Pacific (about two species), and southern South West South America (one species which is also recorded near Lima, Peru. This location is not included on the map at this time, pending further corroboration of its evolutionary status — see Lohwasser *et al.* (2004). Tracks drawn across the Pacific reflect published opinion about affinities between species at each location.



(a)



(b)

FIGURE 3.2 Pacific dispersal (translation in space) of: (a) petalurid dragonflies (Eskov and Golovatch 1986; Watson et al., 1991; Carle, 1995; Davies 1998), (b) heterochordeumatoid millipedes (Shear, 1999), (c) eyebrights (*Euphrasia*) (Barker, 1982), and (d) Blenospermatinae daisies (Heads, 1999).

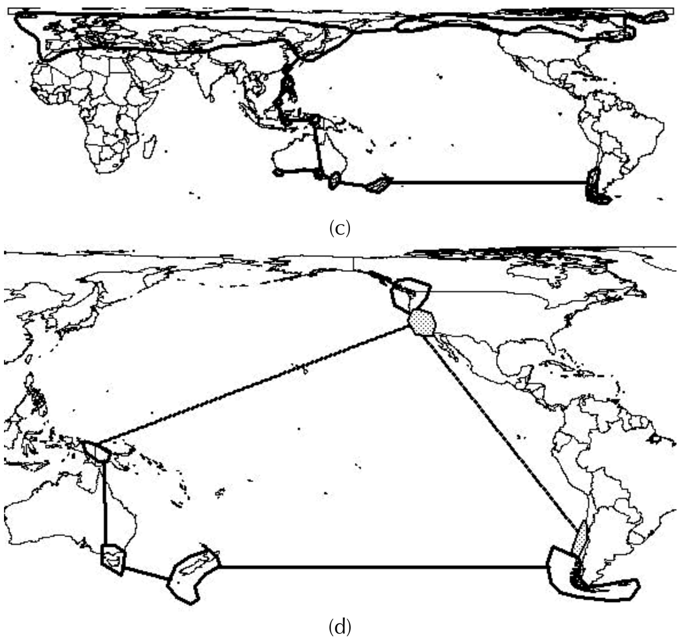


FIGURE 3.2 (Continued)

also be satisfactory for millipedes, dragonflies, eyebrights, and everything else. One might ask, in this respect, whether it is just meaningless coincidence that the North and South American connection is also found in marine organisms such as the seaweed *Macrosytus,* which is also found in southern New Zealand and Tasmania as well as other islands in the south Atlantic and Indian Ocean (Chin et al., 1991). An appeal to bird dispersal for *Microseris* is not very satisfactory in these respects. It might 'explain' the disjunctions if one could imagine eyebrights, millipedes, dragonflies, and seaweeds taking the same trip, but not the geological correlations.

And what about the geology? Plate tectonics were ruled out for *Microseris* by Carlquist (1983) and Vijverberg *et al.* (1999), but plate tectonics and *Microseris* do share some geographic features. The region of Western North America was predicted by Croizat (1958) to comprise a tectonically distinct area with strong Pacific relationships. This prediction was later corroborated by geologists who recognized that the region comprises tectonic terranes of Pacific origin (Craw et al., 1999). In addition, southern South America, New Zealand, and southeastern Australia all comprise terranes with Pacific affinities (Craw et al., 1999; Heads, 1999). The northern limits of *Microseris* in Australia happen to coincide with one of the continent's pre-eminent biogeographic landmarks — the MacPherson-Macleay Overlap (Ladiges, 1998). This biogeographic node locates the intersection of biogeographic tracks which run throughout the region, and across the Pacific (Croizat 1964), and it is also characterized by accreted terranes from the Tasman orogen (Heads, 2001).

The local and global spatial correlations between the distribution of *Microseris* and tectonic structure suggest the possibility of a shared geological and biological history as a key to its geographic evolution both around the Pacific and between North and South America. The role of tectonic plate movements cannot, therefore, be ruled out as suggested by Carlquist (1983). In an evolutionary sense the biogeography of the present represents the ecology of the past (Craw et al., 1999). The predictive success (blind pigs aside) for correlating distributions with tectonic history in panbiogeography does show that biogeographic theory was ahead of the background geological knowledge for that time (Craw and Weston, 1984; Craw and Page, 1988). The method works.

DISPERSAL THROUGH FORM-MAKING

An evolutionary model of dispersal that would account for *Microseris* as well the other Pacific distributions is vicariant form-making. *Microseris* species occur where they do because the immediate ancestor of all *Microseris* occurred in all these localities together. *Microseris* is distributed around the Pacific because the main massing of its common ancestor was distributed over the Pacific (this does not mean that the entire range of this ancestor, or that of related genera was necessarily Pacific), and each species originated in its current region without individually dispersing between them. In Australia and New Zealand *Microseris* still retains the ancestral vicariism even though one species has become disjunct following the separation of New Zealand and Australia by the Tasman Sea at the close of the Mesozoic. This pattern of vicarious descent within the ancestral main massing is a general biogeographic process repeated in other broadly distributed groups such as the *Nothofagus* alliance (Heads, 2006).

The Pacific disjunction of *Microseris* reflects loss of former geographic continuity that may be due to any number of geological mechanisms such as mobile continents, micro-continents, or island arcs foundering, or land-bridges through an expanding Earth. Whatever the geological model, it is the tectonic correlation that is historically predictive. It is quite possible that the ancestor of *Microseris* was more widely distributed and occurred in other areas around the Pacific basin. The panbiogeographic model predicts that the ancestor of *Microseris* was less likely to have occurred in central Gondwana regions of Africa, India, and eastern America, while more likely to have occurred in eastern Asia. The correlation suggests the evolutionary origin of *Microseris* may be as old as the Pacific basin — the Jurassic — or that it represents a later period of mobilism correlated with subsequent tectonic history in the Pacific region in the Mesozoic. Molecular clock estimates are currently unresolved for *Microseris* (Wallace & Jansen 1999), but post-Mesozoic divergence estimates would not falsify the tectonic prediction unless an earlier molecular divergence is predicted — assuming that the molecular clock is constant (cf. Heads, 2005a).

PAST, PRESENT, FUTURE

Biogeographers need not reduce themselves to being the inferior subordinates of geologists, molecular theorists, or historical ecologists when it comes to generating new knowledge. Progress in science always comes from uncertainty at the edge (Craw & Heads, 1988). At the center of scientific popularity one may find life to be quiet and predictable, and also rather dull. I first looked at the biogeographic edge of biology as a graduate student when I became aware from Robin Craw and Michael Heads that there were unanswered questions in evolution, and simply ignoring these questions (which was the standard approach of the time) was not a realistic scientific solution. I found it was not necessary to follow the accepted views on evolution simply because they were stated by prominent and influential evolutionists. I could follow a path in which biogeographic maps represented the real scientific authority.

But there is a considerable price for contesting established ideas (Colacino & Grehan, 2003). Croizat paid that price in losing his position at the Arnold Arboretum for the simple crime of publishing a critique on botanical theory that was supported by I. W. Bailey (Craw, 1984). Biogeographic exploration has since been stultified in New Zealand (Heads, 2005b). With publication in journals such as *Candollea, Cladistics,* the botanical and biological journals of the Linnean Society, *Journal of Biogeography,* and *Telopea,* the situation has improved outside New Zealand since the early 1980s when *Systematic Zoology* was the only international English language journal that would consider discussing panbiogeography. Emergence of the Latin American 'school' of panbiogeography has also generated many publications (see, e.g., Morrone & Llorente, 2003; Llorente & Morrone, 2005). However, there are new challenges ahead, as some molecular biologists and editors believe that molecular clocks have now falsified both the panbiogeographic method and the panbiogeographic synthesis.

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