

Some guiding principles of biogeography

Robert F. Thorne

Abstract

Thorne, Robert F. (Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711, United States of America) 1996. Some guiding principles of biogeography. Telopea 6(4): 845–850. Some years ago, as a response to the proponents of the currently popular vicariance biogeography and in defence of classical biogeography, I drew up a set of guiding principles of biogeography. Until now this set has remained unpublished. These statements of the obvious are guidelines that good biogeographers have been using through the centuries. They are here reorganized and elucidated by some pertinent examples, and submitted in honor of Dr. Lawrie Johnson who has exemplified many of them in his botanical publications (as Johnson & Briggs 1984, Hill & Johnson 1995).

Introduction

Some years ago in a Southern California Botanists symposium on biogeography at Fullerton, California, I was asked to defend classical biogeography against the then current onslaught of the 'vicariantists.' A few years earlier a group of museum zoologists, mostly ichthyologists, having discovered the prolix works of the botanist Croizat and the cladistic writings of the German zoologist Willi Hennig, had decided that all the biogeographers that had gone before were 'Darwinian dispersalists' (Rosen in Nelson & Rosen 1981) and essentially obsolete (Nelson in Nelson & Rosen 1981), and that now Biogeography based on the suggestions of Hennig and Croizat could become a True Science. This development was not a new phenomenon. Every ten years or so new procedural bandwagons, crowded with young zealots, appear on the biological scene to put the discipline on a Solid Scientific Basis. Their new techniques, often quite useful, new buzzwords, and new pantheon of biological gods, reign supreme at the U. S. National Science Foundation and in many university departments until the next bandwagon comes along to displace them.

To present classical biogeography fairly and to show that vicariance biogeography was not entirely new, I presented in the symposium as many of the guiding principles of biogeography as I could assemble. I made no claim for the originality nor the completeness of these principles, which are, of course, only statements of the obvious. They are guidelines that good biogeographers have been using through the centuries in their efforts to understand the distribution of plants and animals through time and space on our planet. I have since then reorganized these principles and assembled more pertinent examples to elucidate them. Any suggestions for their improvement or the addition of further principles will be gratefully received.

Guiding principles

1. Biogeographic inferences and conclusions should be based upon the study of the known past and present geographic distribution of all biotic groups, both plant and animal.

This would seem to be the most important dictum of all (Thorne 1963). Unfortunately, a couple of the vicariance biogeography books (Nelson & Platnick, 1981; and some

authors in Nelson & Rosen, 1981) are seriously lacking in references to modern plant geographic literature other than works by Croizat. Possibly this omission is due to ignorance of botanical literature, but more likely it is due to disregard of 'dispersalist' writings. As a botanist, I have found zoogeographic literature satisfying reading and highly informative; the vicariantists might find recent phytogeographic literature equally enlightening. For them, at least, it would seem good strategy to know what their rivals were up to.

2. Only carefully revised groups should be used in ascertaining biogeographic patterns, tracks, or regions. And only reliable distributional data should be used in the construction of distribution maps.

Faulty taxonomy can result in equally faulty biogeography. The case of *Miconia africana* Jacques-Felix is especially pertinent here. This species was the only reputed African representative of the very large tropical American melastome genus *Miconia* Ruiz & Pavón. Wurdack (1970) found that the type and only collection was actually a Brazilian *Leandra* Raddi of the same family. Presumably a misplacement of labels was involved. Instead of the African melastomes showing linkage with tropical America, Wurdack has assured me (pers. comm.) that they are actually strongly related to those of tropical Asia.

Giulietti and Meikle (1982) examined a problematic transatlantic disjunction in *Paepalanthus* Kunth of the Eriocaulaceae. The reported West African *P. pulvinatus* N. E. Br. proved to be synonymous with *P. hispidissimus* Herzog of northeastern Brazil and to be doubtfully present at all in Africa. Again a misplacement of labels seems indicated.

The map of *Distylium* Siebold & Zucc. of the Hamamelidaceae presented by Balgooy (1966) shows a startling disjunction of the genus between southeastern Asia and Central America. However, when Endress (1969) examined the Mexican - Central American material, he found it to be a distinct genus *Molinadendron* Endress, not at all closely related to *Distylium*. Balgooy can hardly be blamed for accepting Standley's earlier placement of this species in *Distylium*. Similarly, I understand that the described Central American species of the buxaceous *Sarcococca* Lindley does not belong to that Asiatic genus.

3. Studies in the museum, herbarium, laboratory, and library, though surely necessary and highly informative, cannot adequately substitute for field studies.

Bottled or dried specimens, skins or skeletons, can hardly inform us of the natural history of the organism to the extent that living specimens in nature can. Field work continuously reveals phyletically and geographically important missing links. It is not just a coincidence that the greatest biogeographers of all time, Darwin, Diels, Engler, Guppy, Hooker, Hulten, Humboldt, Linnaeus, Mayr, Merrill, Ridley, Setchell, Simpson, and Wallace, among others, were or are great travellers and naturalists. A visit to a park or zoo is no substitute for a biological expedition. It was not until I saw *Canicomyrca* Guillaumin in New Caledonia that I could believe that the genus really belonged to the Myricaceae. Seeing apocarpous species of *Glossopetalon* A. Gray in the Mojave Desert ranges helped convince me that the genus belonged in Crossosomataceae rather than Celastraceae where traditionally placed (Thorne & Scogin 1978).

4. The proper understanding of present biogeography must, so far as possible, be based upon thorough knowledge of the known fossil record, past climates, and plate tectonics. Current distribution of a taxon is not necessarily indicative of its past distribution.

In fact, the current range may be quite misleading. Many archaic species today occupy a small fraction of their former ranges. Without an adequate fossil record the understanding of the present range might be very difficult, if possible at all. The

known present and past ranges of such gymnospermous genera as *Araucaria* Juss., *Cephalotaxus* Siebold & Zucc., *Cryptomeria* D. Don, *Cunninghamia* R. Br., *Ginkgo* L., *Glyptostrobus* Endl., *Metasequoia* Miki, *Sequoia* Endl., and *Sequoiadendron* Buchholz (Florin 1963) and dicotyledonous genera like *Cercidiphyllum* Siebold & Zucc., *Eucommia* Oliver, *Euptelea* Siebold & Zucc., *Gunnera* L., *Nelumbo* Adans., *Nypa* Steck., *Pterocarya* Kunth, *Symplocos* Jacq., *Tetracentron* Oliver, and *Trapa* L. (Krutzh 1989, Thorne 1972, 1989) are splendid botanical examples. Obvious zoological examples are furnished by the present indigenous distribution of the camels and horses, shown by paleozoologists to have evolved in North America before becoming extinct there in Pleistocene time.

5. In the study of patterns of biotic distribution there must be thorough understanding of the spread potential (vagility or dispersal) of diverse biotic groups. Extrapolation from knowledge of a single group can be most misleading.

An ichthyologist working with only primary-division fresh-water fishes might indeed think that long-distance dispersal is equally impossible for all organisms if he does not acquaint himself with the biology of other plant and animal groups. I suspect the antagonism displayed by vicariantists toward long-distance dispersal and toward oceanic islands stems from their preoccupation with nonvagile animal or plant groups. The relatively recent dispersal of the African cattle egret to and within the New World has been somewhat disconcerting for the more extreme vicariantists.

6. Because of continental displacement and changing climates, oceanic currents and changing sea-level, or because of their great vagility, biotic groups have ranged widely and often very rapidly over the earth's surface, a few species, some genera, and many higher categories becoming subcosmopolitan in range.

Some groups, like pelagic or migrating birds, normally range widely and rapidly. Many aquatic plants are widely dispersed about the world to suitable wetland habitats by water or shore birds. I have mapped or listed elsewhere (Thorne 1972) *Ceratophyllum demersum* L., *Montia fontana* L., *Najas marina* L., *Phragmites australis* (Cav.) Trin., *Potamogeton pectinatus* L., and many other subcosmopolitan aquatics. Many weedy species have become subcosmopolitan due to transportation similarly by man, his livestock, fodder for his livestock, farm implements, or ballast. Other biotic groups disperse hardly at all over long periods and remain narrowly endemic, either due to low vagility or to nonavailability of suitable habitats.

7. The closest living relatives of a phyletically unplaced taxon are more likely than not to be found in the same or adjacent areas rather than on distant continents.

This principle of phytogeographic plausibility has enabled me to place a number of anomalous angiosperm taxa and recognize such apparently natural groupings as the Bruniales of southern Africa and Madagascar; Stilbaceae of the Cape Region of South Africa, Balanopales in the Rosanae; *Drosophyllum* Link and *Triphyophyllum* Airy Shaw in the Nepenthineae; and *Simmondsia chinensis* (Link) C. Schneider in the Euphorbiales (Thorne 1975, 1977, 1983, 1985, 1989, 1992).

8. Major disjunctions on or between continents, when part of a repeated pattern, are usually due to normal short-distance dispersal with subsequent major disruption in range caused by catastrophic events, geologic or climatic.

Such catastrophic events are now called vicariance events, some vicariantists thinking they have discovered an entirely new approach to biogeography. Biogeographers have been using such explanations for centuries. It is true, however, that the revolution in geomorphological thinking, namely plate tectonics, has added a significant dimension to our vicariance explanations (Thorne 1973, 1978).

9. Similar major disjunctions involving oceanic islands and many transoceanic ranges, on the other hand, generally involve long-range, overseas dispersal including transport by aboriginal or modern man.

The fragmentary, disharmonic nature of the biota and the high proportion of endemism on oceanic islands are indicative of this waif origin of highly vagile organisms from many directions, often over long periods of time (Balgooy 1971, Barlow & Schodde 1993, Fosberg 1948, Thorne 1963, Zimmerman 1948). Many transoceanic range disjunctions, as those involving Africa and South America (Thorne 1972, 1973, 1978) seem to require long-distance dispersal as the most reasonable explanation. Similarly, the rather common western North American-temperate South American transtropical disjunction is best explained by long-distance dispersal, probably by shore- or water-birds (Raven 1963, Thorne 1970, 1978, 1986).

10. Coincidence in biogeographic patterns, tracks, or range disjunctions, though often suggestive, does not guarantee that two or more taxa have similar dispersal histories.

Often taxa with similar ranges or disjunction patterns have achieved those ranges from different source areas, at different times, by different vectors, and by different routes. Thus each taxon should be studied on its own merits. The primary goal of vicariantists to identify similar patterns is commendable, but to attempt to explain all similar patterns by the same vicariant event is overly simplistic. The bipolar disjunct distributions of *Empetrum* L., *Hippuris* L., *Littorella* P. Bergius, and other genera probably indicate long-distance dispersal from northern North America in Pleistocene or later time. However, *Euphrasia* L. is, at least, an exception to this probable route and explanation. According to Du Rietz (1960) and Barker (1986), the South American species of the genus are more closely related to the western and southern Pacific species than they are to the boreal North American species (Thorne 1972). A similar Gondwanic distribution pattern to that of *Euphrasia* is discussed by Wilson (1986) for various alpine species of Cyperaceae and Juncaceae.

11. Interpretation of range disjunctions must involve careful reference to a time frame, probable time of origin of the group under study as well as the time when the suspected catastrophic event, continental displacement, mountain building, inundation by epicontinental seaway, glaciation, desertification, etc. might have occurred.

It is naive to argue that separation of continents explains a major continental disjunction when the group concerned had apparently not evolved until after the continental disjunction. This has been done regularly for tropical African – tropical American disjuncts, even for *Rhipsalis baccifera* (J.S.Miller) Stearn, so obviously specialized for bird dispersal in its succulent, white berries with viscous pulp (Thorne 1973).

12. Degree of differentiation between vicariant groups of two disjunct areas reflects the amount of evolution that has occurred since the origin of the sister groups from a common ancestor and very roughly the time that has been available for that evolution.

Understood, of course, is the truism that evolutionary rates do vary greatly among different organisms and different organs of different taxa. Nonetheless, subspeciation and speciation surely take place much more rapidly than the evolution of genera, tribes, subfamilies, families, or even higher categories. The separation of South America from Africa, suggested from 100 to 90 million years ago, is not necessarily a valid explanation for those species and genera, and even perhaps most families, that are transatlantic in their ranges. It may well be the explanation for those caryophyllalean families that are endemic or largely so to Madagascar, Africa, and America. The protocaryophyllalean ancestors were probably isolated on the resulting

continental masses by the breakup of West Gondwana, then evolved into those families now totally or largely restricted to them, as the Didieriaceae in Madagascar, the Aizoaceae, especially the mesembryanthemoid taxa, in Africa, and Cactaceae and other families in the American continents and islands (Thorne 1978).

13. The lower the rank of a taxon under consideration, generally the more instructive may be its disjunct range.

Higher categories have had so much time to disperse about the earth's surface that often they tell us little about the causes of their disjunctions. Disjunct species or genera, depending upon their degree of vagility and the prevalence of their pattern of disjunction, can tell us much about how and possibly when the disjunction took place. Among other things lower categories can be analyzed biosystematically, biochemically, or through molecular studies.

14. Parsimony, which is a fashionable term for Occam's razor, though highly logical, is not necessarily how evolution has taken place nor how patterns of distribution and disjunction have developed in space and time.

It is surely parsimonious to explain all transatlantic disjunctions by the breakup of West Gondwana but it is not realistic to ignore the time frame of events, the categorical ranks of the taxa under study, nor the spread potential of said taxa. Mother Nature unfortunately does not always operate on a parsimonious basis.

15. Though often fascinating to the practitioner, the techniques and procedures used in developing biogeographical conclusions should not become more important than the results achieved.

We must avoid losing sight of the biogeographical forest because of concentration on procedural trees. A corollary here is that buzzwords, though impressive additions to our trendy vocabulary and often very helpful in obtaining substantial grants for our research, cannot substitute for careful accumulation and synthesis of biogeographical information, inductive reasoning, and application of prudent good judgment in our efforts.

Conclusion

The principles just discussed should show that the division of biogeographers into 'dispersalists' and 'vicariantists' is not only artificial and arbitrary, but counterproductive for our science. We should appreciate the efforts of our peers and dispense with fanciful hypotheses and polemics. Vicariance biogeography has new ideas and new techniques to offer that can be useful to all of us. At the same time, there is no need to empty our biogeographic tool-chest just to accept one more new, shiny, useful tool. The chest is a big one with plenty of room for many more useful tools, including cladistics and molecular taxonomy.

References

- Balgooy, M.M.J.van. (1971) Plant-geography of the Pacific. *Blumea* Suppl. 6: 1-222.
- Barker, W. R. (1986) Biogeography and evolution in Euphrasia (Scrophulariaceae), particularly relating to Australasia. Pp. 489-510 in B.A. Barlow (ed.), *Flora and Fauna of Alpine Australasia: ages and origins* (CSIRO Australia: Leiden).
- Barlow, B. A. & Schodde, R. (1993) Bird dispersal of loranthaceous mistletoes to remote Pacific islands: symbiosis in default. *Beaufortia* 43: 124-129.

- Du Rietz, G.E. (1960) Remarks on the botany of the southern cold temperate zone. Pp. 500–507 in C.F.A. Pantin (ed.), A discussion on the biology of the southern cold temperate zone. *Proc. Roy. Soc. (London), Ser. B, Biol. Sci.*, 152: 429–682.
- Endress, P.K. (1969) *Molinadendron*, eine neue Hamamelidaceen-Gattung aus Zentralamerika. *Bot. Jb.* 89: 353–358.
- Florin, R. (1963) The distribution of conifer and taxad genera in time and space. *Acta Hort. Berg.* 20: 121–312.
- Giulietti, A.M., & Meikle, R.D. (1982) A problematic transatlantic disjunction in *Paepalanthus* (Eriocaulaceae). *Kew Bull.* 37: 291–293.
- Hill, K.D. & Johnson, L.A.S. (1995) Systematic studies in the eucalypts. 7. A revision of the bloodwoods, genus *Corymbia* (Myrtaceae). *Telopea* 6: 185–504.
- Johnson, L.A.S. & Briggs, B. G. (1984) Myrtales and Myrtaceae — a phylogenetic analysis. *Ann. Missouri Bot. Gard.* 71: 700–756.
- Krutzsch, W. (1989) Paleogeography and historical phytogeography (paleochorology) in the Neophyticum. *Pl. Syst. Evol.* 162: 5–61.
- Nelson, G. & Platnick, N. (1981) *Systematics and Biogeography: Cladistics and Vicariance* (Columbia University Press: New York).
- Nelson, G. & Rosen, D. E. (eds.) (1981) *Vicariance biogeography: a critique* (Columbia University Press: New York).
- Raven, P.H. (1963) Amphitropical relationships in the floras of North and South America. *Quart. Rev. Biol.* 38: 151–177.
- Thorne, R.F. (1963) Biotic distribution patterns in the tropical Pacific. Pp. 311–354 in J.L. Gressitt (ed.), *Pacific Basin Biogeography* (Bishop Museum: Honolulu).
- Thorne, R.F. (1970) *Pilularia americana* on the Santa Rosa Plateau, Riverside County, California. *Aliso* 7 (2): 149–155.
- Thorne, R.F. (1972) Major disjunctions in the geographic ranges of seed plants. *Quart. Rev. Biol.* 47: 365–411.
- Thorne, R.F. (1973) Floristic relationships between tropical Africa and tropical America. Pp. 27–47 in B.J. Meggers, E.S. Ayensu & W.D. Duckworth (eds.), *Tropical forest ecosystems in Africa and South America: A comparative review* (Smithsonian Inst. Press: Washington).
- Thorne, R.F. (1975) Angiosperm phylogeny and geography. *Ann. Missouri Bot. Gard.* 62: 362–367.
- Thorne, R.F. (1977) Some realignments in the Angiospermae. *Pl. Syst. Evol. Suppl.* 1: 299–319.
- Thorne, R.F. (1978) Plate tectonics and angiosperm distribution. *Notes Roy. Bot. Gard. Edinburgh* 36: 297–315.
- Thorne, R.F. (1983) Proposed new realignments in the angiosperms. *Nord. J. Bot.* 3: 85–117.
- Thorne, R.F. (1985) Phylogenetic relationships of the monotypic family Simmondsiaceae. *Jojoba Happen.* 13 (2): 8.
- Thorne, R.F. (1986) A historical sketch of the vegetation of the Mojave and Colorado deserts of the American Southwest. *Ann. Missouri Bot. Gard.* 73: 642–651.
- Thorne, R.F. (1989) Phylogeny and phytogeography. *Rhodora* 91: 10–24.
- Thorne, R. F. (1992) Classification and geography of the flowering plants. *Bot. Rev.* 58 (3): 225–348.
- Thorne, R.F. & Scogin, R. (1978) *Forsellesia* Greene (*Glossopetalon* A.Gray), a third genus in the Crossosomataceae, Rosineae, Rosales. *Aliso* 9 (2): 171–178.
- Wilson, K.L. (1986) Alpine species of Cyperaceae and Juncaceae. Pp. 471–488 in B.A. Barlow (ed.) *Flora and Fauna of Alpine Australasia: Ages and Origins* (CSIRO Australia: Leiden).
- Wurdach, J.J. (1970) Certamen Melastomataceis. XV. *Phytologia* 20: 369–389.
- Zimmerman, E.C. (1948) *Insects of Hawaii*. Vol. 1, *Introduction* (Univ. Hawaii Press: Honolulu).

Manuscript received 30 November 1995

Manuscript accepted 8 March 1996