



Biogeographical regions under track and cladistic scrutiny

A comment on C. Barry Cox (2001) The biogeographical regions reconsidered. *Journal of Biogeography*, 28, 511–523

GUEST
EDITORIAL

Cox (2001) has recently reviewed the biogeographical regions of the world. After analysing previous proposals and discussing some interesting problems, e.g. Wallace's line, Takhtajan's floristic system, and the delimitation of the Cape, Holarctic, Antarctic, and Tropical biogeographical kingdoms, he provided a system of phylogeographical kingdoms and another of mammal zoogeographical regions. Cox's (2001) most valuable contribution is his discussion of inconsistencies in previous schemes; however, I feel that a single biogeographical scheme for all organisms, to serve as a general reference system, would be a desirable goal. Furthermore, the development of panbiogeography (Croizat, 1958, 1964) and cladistic biogeography (Croizat *et al.*, 1974; Nelson & Platnick, 1981) has challenged traditional phyto- and zoogeographical systems, by showing that some of the units recognized in them do not represent natural units (Humphries, 1981; Patterson, 1981; Schuh & Stonedahl, 1986; Craw & Page, 1988; Crisci *et al.*, 1991; Amorim & Tozoni, 1994; Morrone, 1996; Lopretto & Morrone, 1998; Craw *et al.*, 1999; Humphries & Parenti, 1999; Katinas *et al.*, 1999). My objective is to review briefly these analyses and to present a general system of biogeographical kingdoms and regions, which intends to incorporate their conclusions.

Schuh & Stonedahl (1986) analysed the historical biogeography of the Indo-Pacific, through a cladistic biogeographical analysis of several insect taxa. Their general area cladogram shows two major components: Laurasic and Gondwanic. Within the latter, there is a trichotomy involving the Indo-Pacific (tropical Africa plus the Oriental region), tropical America, and the southern temperate areas (South Africa, temperate South America, and Australia). These results evidence the composite nature of South America and the closer relationship of the Oriental region and tropical Africa. Schuh & Stonedahl (1986) placed tropical America in an equivocal position, although they discussed its close relationship with tropical Africa.

Craw & Page (1988) and Craw *et al.* (1999) proposed a radical solution to the problem of biogeographical regions, based on the generalized tracks outlined by Croizat (1958). These authors argued convincingly that Croizat's generalized tracks had no relationship at all to the classic phyto- and zoogeographical regions, because they joined areas now widely separated by ocean and sea basins, evidencing that some regions were composite biogeographically rather than natural areas. These authors concluded that the natural regions were not present-day land areas but the world's major ocean basins (Craw & Page, 1988, fig. 12; Craw *et al.*, 1999, fig. 6-13).

Crisci *et al.* (1991) undertook a cladistic biogeographical analysis, based on several plant, fungal, and animal taxa, in order to elucidate the historical relationships of the southern temperate portion of South America. They concluded that South America was a composite area, with southern South America closely related to the southern temperate areas (Australia, Tasmania, New Zealand, New Guinea, and New Caledonia), and tropical South America closely related to Africa and North America.

Amorim & Tozoni (1994) carried out a global cladistic biogeographical analysis, based on area cladograms of several taxa. They presented a general area cladogram, which supported a basic separation between a Laurasic and a Gondwanic component, with a distinction within the latter of a circumtropical and a circumantarctic component, which evidenced the composite nature of both South America and Africa. Notwithstanding, the Oriental region resulted to have integrated circumtropical Gondwana, being closely related to tropical Africa.

Other cladistic (Humphries, 1981; Patterson, 1981) and panbiogeographical studies (Morrone, 1996; Lopretto & Morrone, 1998; Craw *et al.*, 1999; Katinas *et al.*, 1999) also supported the hypothesis that South America is a composite area, with its southern portion closely related to the southern temperate areas and the northern portion closely related to the Old World tropics. Other authors who also addressed the dual nature of South America are Kuschel (1969), Artigas & Papavero (1990), José de Paggi (1990), Crisci *et al.* (1993), and Almirón *et al.* (1997), among others.

Based on these studies, I propose the following biogeographical system (Fig. 1).

- (1) **Holarctic kingdom:** It comprises Europe, Asia north of the Himalayan mountains, northern Africa, North America (excluding southern Florida), and Greenland. From a palaeogeographical viewpoint, it corresponds to the palaeocontinent of Laurasia.

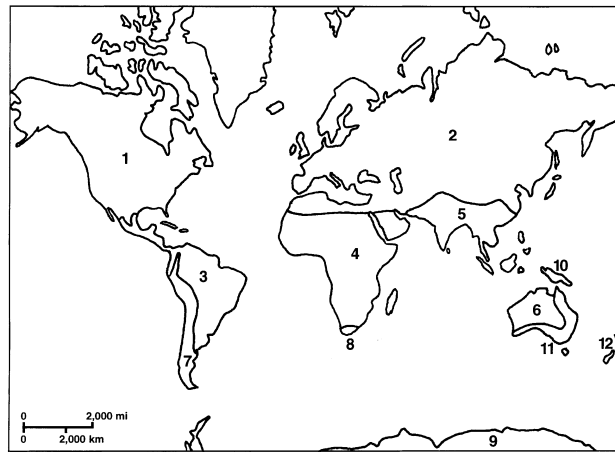


Figure 1 Biogeographical kingdoms and regions of the world. 1–2, Holarctic kingdom (= Laurasia): 1, Nearctic region; 2, Palearctic region; 3–6, Holotropical kingdom (= eastern Gondwana): 3, Neotropical region; 4, Afrotropical region; 5, Oriental region; 6, Australotropical region. 7–12: Austral kingdom (= western Gondwana): 7, Andean region; 8, Cape or Afrotropical region; 9, Antarctic region; 10, Neoguinean region; 11, Australotemperate region; 12, Neozelandic region.

- 1.1. Nearctic region: it corresponds to the New World, e.g. Canada, most of the USA, and northern Mexico.
- 1.2. Palearctic region: it corresponds to the Old World, e.g. Eurasia and Africa north of the Sahara.
- (2) **Holotropical kingdom:** basically the tropical areas of the world, between 30° south and 30° north latitudes. The Holotropical region has been previously recognized by Rapoport (1968) and would correspond to the eastern portion of the Gondwanaland palaeocontinent (Crisci *et al.*, 1993). In contrast with Rapoport's (1968) proposal, I include the north-western portion of Australia in the Holotropical region.
 - 2.1. Neotropical region: tropical South America, Central America, south-central Mexico, the West Indies, and southern Florida (Morrone, 2001).
 - 2.2. Afrotropical region: central Africa, the Arabian peninsula, Madagascar, and the West Indian Ocean islands.
 - 2.3. Oriental region: India, Himalaya, Burma, Malaysia, Indonesia, the Philippines, and the Pacific islands. In spite of the obvious tropical biotic elements of this region, it has been placed in earlier palaeogeographical reconstructions as part of Laurasia. Archbold *et al.* (1982) and Audley-Charles, (1984), however, have postulated that this area was part of Gondwanaland, which was also supported by the cladistic biogeographical analysis of Amorim & Tozoni (1994).
 - 2.4. Australotropical region: north-western Australia.
- (3) **Austral kingdom:** it comprises of the southern temperate areas in South America, South Africa, Australasia, and Antarctica. This region has been recognized previously by Kuschel (1969) and Rapoport (1968) and would correspond to the western portion of the palaeocontinent of Gondwanaland (Crisci *et al.* 1993). In contrast with Rapoport (1968), only south-eastern or temperate Australia is assigned to this kingdom.
 - 3.1. Andean region: southern South America below 30° south latitude, extending through the Andean highlands north of this latitude, to the Puna and North Andean Paramo (Morrone, 2001).
 - 3.2. Antarctic region: Antarctica.
 - 3.3. Cape or Afrotropical region: South Africa. Poynton (2000) considered that latitudinal and altitudinal changes in the composition of the African Amphibian fauna clearly indicated that it was inappropriate to classify the Afrotropical fauna as Afrotropical. He considered that the proper relationships of this region were with other temperate areas.
 - 3.4. Neoguinean region: New Guinea plus New Caledonia.
 - 3.5. Australotemperate region: south-eastern Australia.
 - 3.6. Neozelandic region: New Zealand.

JUAN J. MORRONE

Museo de Zoología,
 Departamento de Biología Evolutiva,
 Facultad de Ciencias, UNAM,
 Apdo. postal 70-399,
 04510 Mexico D.F.,
 Mexico
 E-mail: jjm@hp.fciencias.unam.mx

REFERENCES

- Almirón, A., Azpelicueta, M., Casciotta, J. & López Cazorla, A. (1997) Ichthyogeographic boundary between the Brazilian and Austral subregions in South America, Argentina. *Biogeographica*, **73**, 23–30.
- Amorim, D.S. & Tozoni, S.H.S. (1994) Phylogenetic and biogeographic analysis of the Anisopodoidea (Diptera, Bibionomorpha), with an area cladogram for intercontinental relationships. *Revista Brasileira de Entomologia*, **38**, 517–543.
- Archbold, N.W., Pigram, C.J., Ratman, N. & Hakim, S. (1982) Indonesian Permian brachiopod fauna and Gondwana-South East Asia relationships. *Nature*, **296**, 556–558.
- Artigas, J.N. & Papavero, N. (1990) Studies of Mydidae (Diptera). V. Phylogenetic and biogeographic notes, key to the American genera and illustrations of spermathecae. *Gayana Zoología*, **54**, 87–116.
- Audley-Charles, M.G. (1984) Reconstruction of eastern Gondwanaland. *Nature*, **306**, 48–50.
- Cox, C.B. (2001) The biogeographic regions reconsidered. *Journal of Biogeography*, **28**, 511–523.
- Craw, R.C., Grehan, J.R. & Heads, M.J. (1999) *Panbiogeography: tracking the history of life*. Oxford Biogeography Series 11. Oxford University Press, New York.
- Craw, R.C. & Page R.D.M. (1988) Panbiogeography: Method and metaphor in the new biogeography. In: M.-W. Ho, and S.W. Fox, eds. *Evolutionary processes and metaphors*. John Wiley and Sons Ltd, Chichester, pp. 163–189.
- Crisci, J.V., Cigliano, M.M., Morrone, J.J. & Roig-Juñent, S. (1991) Historical biogeography of southern South America. *Systematic Zoology*, **40**, 152–171.
- Crisci, J.V., de la Fuente, M.S., Lanteri, A.A., Morrone, J.J., Ortiz Jaureguizar, E., Pascual, R. & Prado, J.L. (1993) Patagonia, Gondwana Occidental (GW) y Oriental (GE), un modelo de biogeografía histórica. *Ameghiniana*, **30**, 104.
- Croizat, L. (1958) *Panbiogeography*, Vols. 1, 2a, and 2b. Published by the author, Caracas.
- Croizat, L. (1964) *Space, time, form: the biology synthesis*. Published by the author, Caracas.
- Croizat, L., Nelson, G. & Rosen, D.E. (1974) Centres of origin and related concepts. *Systematic Zoology*, **23**, 265–287.
- Humphries, C.J. (1981) Biogeographical methods and the southern beeches (Fagaceae: *Nothofagus*), pp. 177–207. In: *Advances in cladistics, 1, Proceedings of the first meeting of the Willi Hennig society* (V.A. Funk and D.R. Brooks, eds). New York Botanical Garden, Bronx, New York.
- Humphries, C.J. & Parenti, L.R. (1999) *Cladistic biogeography: interpreting patterns of plant and animal distributions*. Oxford Biogeography series no. 12. Oxford University Press, Oxford.
- José de Paggi, S. (1990) Ecological and biogeographical remarks on the rotifer fauna of Argentina. *Revue D'hydrobiologie Tropicale*, **23**, 297–311.
- Katins, L., Morrone, J.J. & Crisci, J.V. (1999) Track analysis reveals the composite nature of the Andean biota. *Australian Systematic Botany*, **47**, 111–130.
- Kuschel, G. (1969) Biogeography and ecology of South America Coleoptera, pp. 709–722. In: *Biogeography and ecology in South America, 2* (E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe and H. Sioli, eds). Junk, The Hague.
- Lopretto, E.C. & Morrone, J.J. (1998) Anaspidacea, Bathynellacea (Syncarida), generalised tracks, and the biogeographical relationships of South America. *Zoologica Scripta*, **27**, 311–318.
- Morrone, J.J. (1996) Austral biogeography and relict weevil taxa (Coleoptera: Nemonychidae, Belidae, Brentidae, and Caridae). *Journal of Comparative Biology*, **1**, 123–127.
- Morrone, J.J. (2001) *Biogeografía de América Latina y El Caribe*. M & T-Manuales & Tesis SEA, Vol. 3, Sociedad Entomológica Aragonesa, Zaragoza, Spain.
- Nelson, G. & Platnick, N.I. (1981) *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.
- Patterson, C. (1981) Methods of paleobiogeography, pp. 446–489. In: *Vicariance biogeography: a critique* (G. Nelson and D.E. Rosen, eds). Columbia University Press, New York.

- Poynton, J.C. (2000) Evidence for an Afrotropical Amphibian fauna. *African Journal of Herpetology*, **49**, 33–41.
- Rapoport, E.H. (1968) Algunos problemas biogeográficos del Nuevo Mundo con especial referencia a la región Neotropical, pp. 54–110. In: *Biologie de l'Amérique Australe*, 4 (C. Delamare Deboutteville and E.H. Rapoport, eds). CNRS and CNICT, Paris.
- Schuh, R.T. & Stonedahl, G.M. (1986) Historical biogeography in the Indo-Pacific: a cladistic approach. *Cladistics*, **2**, 337–355.

BIOSKETCH

Juan J. Morrone is Professor of Biogeography, Systematics, and Comparative Biology, and Chairman of the Department of Evolutionary Biology at the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Mexico, D.F. His main interests are the systematics and biogeography of Neotropical weevils (Coleoptera: Curculionoidea). He has published more than 120 scientific articles and nine books. His last books are *Biogeografía de América Latina y el Caribe* (M & T- Manuales & Tesis SEA, vol. 3, Sociedad Entomológica Aragonesa, Zaragoza, Spain, 2001) and *Introducción a la biogeografía en Latinoamérica: Conceptos, teorías, métodos y aplicaciones* (J. Llorente & J. J. Morrone, eds., Las prensas de Ciencias, UNAM, Mexico, D.F., México, 2001).