



# Biogeography and evolution of the Galapagos: integration of the biological and geological evidence

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Biogeographic tracks are mapped for Galapagos endemics representing 25 plant and animal taxa and including organisms with good and poor means of dispersal. These patterns confirm standard biogeographic tracks linking Galapagos with Central America, western North and South America, the Caribbean, Asia and Australasia. Discovery of the Galapagos Gore in the 1970s corroborates the biogeographic prediction for a major tectonic centre associated with the Galapagos. The biogeographic model developed by Croizat in 1958 of Galapagos colonization involving an ancestral biota inhabiting eastern Pacific geosynclinal forelands is congruent with plate tectonic models supporting a Pacific island arc origin for western American terranes. American relatives of Galapagos endemics may have originated within an eastern Pacific paleogeography rather than representing centres of origin for dispersal to the Galapagos. Galapagos colonization by an eastern Pacific biota between late Cretaceous and mid-Tertiary has significant implications for understanding the tempo and mode for both the origins of island biota and general models of evolutionary differentiation. Popular assertions that overwater dispersal represents the only viable origin for the entire Galapagos biota is no longer biogeographically or geologically tenable.

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ADDITIONAL KEY WORDS: panbiogeography – dispersal – geology – tectonics – molecular clock.

## INTRODUCTION

The Galapagos ranks “among the most spectacular scientific discoveries of the twentieth century” (Bowman, Berson & Leviton, 1983) and perhaps nowhere else in evolutionary theory is the problem of geographic distribution brought into sharper focus than with this “living laboratory”. The 900 km of ocean separating the Galapagos from the nearest mainland represents a formidable biogeographic challenge. It was the ‘American’ character of the Galapagos species isolated deep within the Pacific that contributed to Darwin’s evolutionary perspective (Grinnell, 1974). In general, Darwin explained the origin of such isolation by the ability of organisms to disperse over barriers from their centres of origin (Croizat, 1964). For the Galapagos, however, Darwin (1871: 363) was also willing to consider some kind of “formerly continuous land” to bridge the evolutionary and geographic disconnection. Over

succeeding decades the two choices offered by Darwin were divided among proponents of oceanic and continental theories for origin of the Galapagos biota (Vinton, 1951). The exclusively volcanic character of the Galapagos and the largely inaccessible submarine geology of the eastern Pacific rendered landbridge theories largely speculative compared to dispersal mechanisms accessible to direct observation.

Carlquist (1965: 356) interpreted both the paucity of endemic Galapagos plant genera and their close relationships with American mainland groups as evidence for recent origin. He regarded the Galapagos flora as purely that of an oceanic island. Plant families with ‘good’ long-distance dispersal ability were most abundant while groups with ‘poor’ dispersal ability were absent. Dispersal over a former landbridge was also ruled out because the phylogenetic affinities of Galapagos species occurred in ‘exact’ proportion to the geographic distance of their mainland relatives. Thornton (1971) also characterized the Galapagos biota as ‘unbalanced’ or disharmonic with its preponderance of ‘good’ dispersers dominated by reptiles and birds, followed by a paucity of mammals and the absence of

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amphibians and freshwater fish. Porter (1983: 33) claimed the long controversy over whether the islands are oceanic or formerly connected to continents by land bridges might have been avoided altogether if more attention had been given to the disharmonic flora described by Hooker (1851a,b).

In an early attempt to examine the biodiversity and biogeography of the Galapagos flora Hooker (1851b: 254) recognized many Galapagos species to be conspecific with mainland or Pacific island species and it was evident to him that their presence in the Galapagos was a function of dispersal mechanisms involving wind, water and, to a much lesser extent, the agency of birds. Endemic species were, however, another matter. Recognizing contrasting biogeographic connections with the Caribbean (including Panama) and mainland America, Hooker (1851b: 250) rejected ecology as the explanation for Galapagos endemics. In treating the problem as a "mystery" that he was willing to portray but not explain, Hooker (1851b: 259) expressed a cautious approach to dispersal that if fully exploited by Darwin may have altered the history of biogeography and evolution (Croizat, 1961 I: 1298).

Geological evidence is often cited as 'proof' of an oceanic origin since the Galapagos Islands are entirely volcanic and the seafloor comprises oceanic plates. The only uncertainties were dating the volcanic activity and sequence of emergence (Thornton, 1971). A plate tectonic solution proposed by Holden & Deitz (1972) identified formation of the Pacific, Cocos and Nazca plate triple junction at the Galapagos 40 Mya followed by migration of the junction to its current position west of the Galapagos. This plate tectonic model allowed for the possibility of the Galapagos biota being inherited from a whole series of ancestral Galapagos Islands. By the 1980s geological opinion shifted entirely in favour of 'oceanic' origin. Cox (1983) asserted there was no evidence of any terrestrial link between the Galapagos and American mainland, and Simpkin (1984) characterized Galapagos geology entirely within the current tectonic configuration.

With geological consensus favouring 'oceanic' origin, over-water colonization became the only viable model for Galapagos evolution (Connor & Simberloff, 1978; Bowman *et al.*, 1983; Keast 1991; Cox & Moore, 2000; Finston, Peck & Perry, 1997; Yeakley & Weishampel, 2000). All Galapagos colonists must have crossed an oceanic barrier from their source areas in the Americas (Gertsch & Peck, 1992: 1197; Jackson, 1993) and "recent evidence from plate tectonics" precluded geologically mediated dispersal (Cook, Howden & Peck, 1995: 189). The ocean barrier also 'explained' as much what was present as what was absent (Peck, 1994: 55). Origin of the Galapagos biota was now the exclusive domain of long-distance over-water dispersal: "There is now no serious evidence to suggest that the islands

ever had direct land-bridge connections with the Central or South American mainland. They are true oceanic islands and all terrestrial colonists had to cross an oceanic barrier to reach them. The biota is entirely constructed by dispersal; there is no vicariant component" (Peck, 1996: 92). Colonization biogeography was reduced by Jackson (1993: 41) to a matter of faith: "We cannot prove that such events [of over-water dispersal to the Galapagos] took place in the past because there are no records, but we can infer conclusions that make what we believe consistent with what we see."

The Galapagos were viewed by Cox (1983: 11) as ideal natural laboratories in which to measure the rate of evolutionary divergence, provided the ages of the islands are known and the islands were never intermittently connected to the mainland by a landbridge or island chain. Galapagos colonization models were initially constrained by the 4–5 Myr age of the current islands and this led Steadman & Ray (1982) to rule out Galapagos–Caribbean connections as "illogical" because formation of the Panamanian isthmus was then considered to be synchronous with the earliest emergence of the Galapagos islands. Discovery of identified underwater seamounts along the Carnegie and Cocos ridges identified as former Galapagos islands corroborated the prediction of Holden & Deitz (1972) and extended the temporal window for colonization to at least 15–20 Myr and possibly the entire 80–90 Myr existence of the hotspot (Carson, 1992; Christie *et al.*, 1992). This geological reconstruction allowed for overwater dispersal as the initial origin of colonists, with a series of subsequent dispersal events onto newly emergent volcanoes while the original islands were transported east and eventually submerged. This conveyor-belt mechanism conforms to a general model proposed by Axelrod (1972) for many Pacific island biotas, and was used to 'explain' Galapagos organisms with molecular divergence estimates that exceeded the age of the modern islands (e.g. Wyles & Sarich, 1983; Peck, 1996; Rassmann, 1997).

Colonization models conform to a traditional biogeographic methodology reconstructing the evolutionary past based on geological theory (cf. Cox & Moore, 2000; Brown & Lomolino, 1998). These geologically dependent explanations restrict evolutionary studies to currently accepted knowledge rather than generating new historical insights (Craw & Weston, 1984; Craw, Grehan & Heads, 1999; Grehan, 2001). A biogeographic solution to this methodological problem proposed by Croizat (1952, 1958) focused on the geographic relationship between distribution and tectonics rather than hypothetical geological history (Craw, 1989). Croizat's (1958) approach capitalized on the possibility – intimated by Darwin's recognition of the 'American' character of the Galapagos biota and

Hooker's biogeographic observations – that direct analysis of geographic patterns will provide historical information. In this radical departure from biogeographic tradition, Croizat (1958) concluded there was no biogeographic correspondence between geographic distribution and dispersal ability for the Galapagos biota. The intersection of otherwise mutually exclusive distributions at the Galapagos suggested to Croizat a biogeographic pattern characteristic of a 'continental' or 'mainland' biota. It was as if the modern 'oceanic' setting of the Galapagos did not exist and Croizat (1952, 1958) allied himself in support of former land connections in the eastern Pacific with two notable differences from earlier theorists: his conception of land connections involved a dynamic model of geosynclinal arcs rather than static landbridges and he predicted the presence of a major, then unknown, tectonic formation at the Galapagos (Croizat, 1958 I: 801). In acknowledgement of the standard tracks (Rosen, 1976) suggested the Galapagos hotspot originally appeared adjacent to South America and moved westward to its current position. In a study of American tineid moths, Davis (1994) agreed with Croizat (1958) on Cocos Island being positioned within a standard, tectonically correlated, track between the Galapagos and Caribbean. In contrast, Mayr (1982), Porter (1983) and Keast (1991) rejected Croizat's proposed biogeographic history, claiming the geological evidence did not allow for a 'direct' connection between the Galapagos and American mainland.

The geographically isolated biota of the Galapagos presents, therefore, a critical test for biogeographic theory and methodology since a biogeographic method must be applicable to these islands as well as anywhere else if it is to meet general scientific standards (Mayr, 1982: 618). In this paper the distribution patterns identified by Croizat (1958) are substantiated by a range of examples derived from systematic studies of plant and animal groups with endemic representatives in the Galapagos archipelago. The historical implications of these tracks are discussed in relation to current geological and evolutionary models for the eastern Pacific and the Caribbean plate. Croizat's (1952, 1958) panbiogeographic approach to the Galapagos biota is shown to represent a methodologically successful and useful contribution to evolutionary theory and emphasizes the necessity for transforming traditional biogeographic modes that fail to integrate historical geology with evolutionary theory.

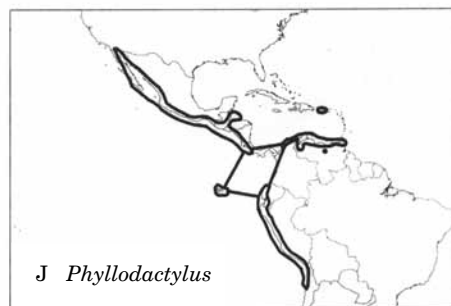
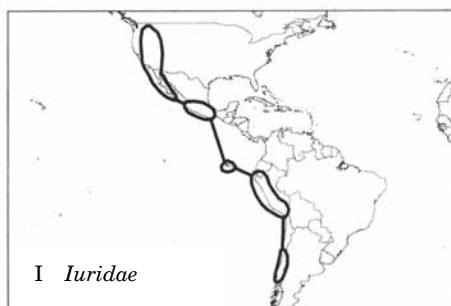
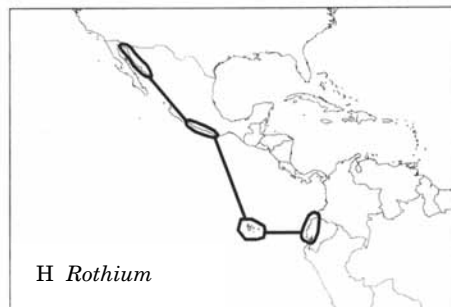
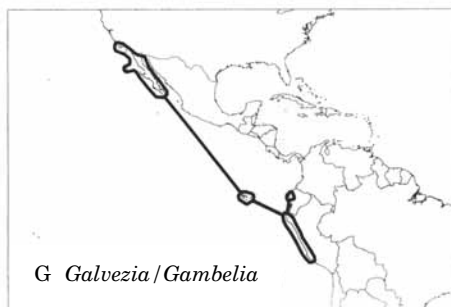
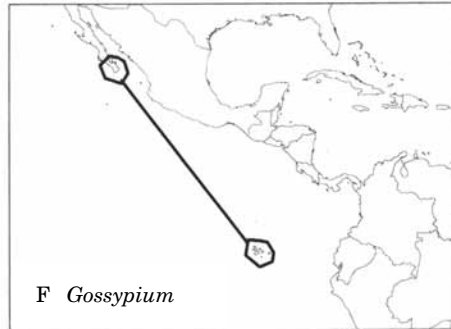
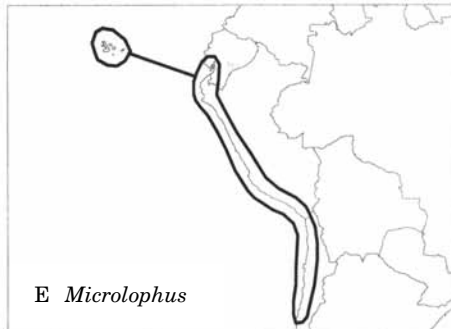
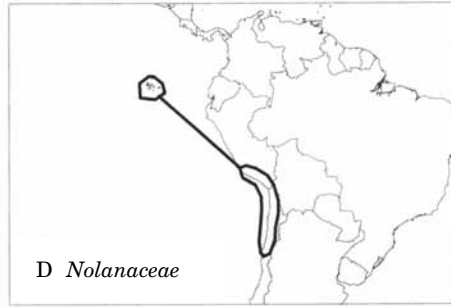
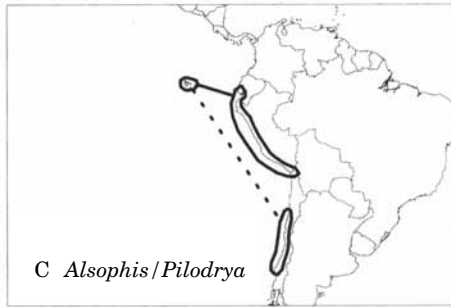
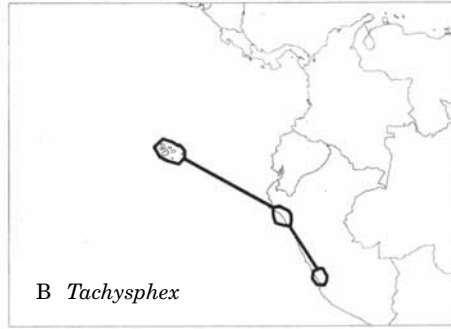
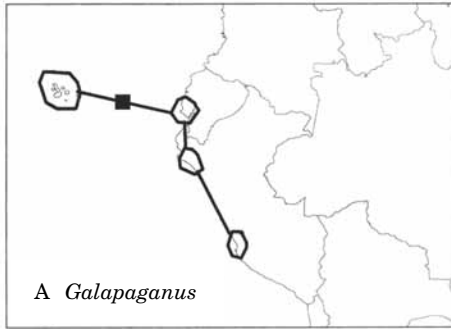
## METHODS

Disjunct distributions of Galapagos endemics and their relatives are mapped as line graphs (tracks) by linking localities to form minimal spanning trees (Page, 1987). In this paper 'locality' is delineated as a generalized

polygon enclosing a disjunct distribution range with respect to the Galapagos. In the absence of phylogenetic information this procedure links nearest neighbor localities to construct the shortest line length for the combined localities. The minimum distance criterion permits a precise comparison of spatial structure between the different tracks of individual taxa and reveals patterns of distribution that share a common spatial geometry (Craw *et al.*, 1999). Where phylogenetic information suggests particular taxa are most closely related, their localities are first connected together by a minimal spanning link before adding track links to more distantly related taxa (Craw, 1988; Craw & Page, 1988; Crisci & Morrone, 1992; Morrone & Crisci, 1995).

Different distribution patterns are grouped together into standard tracks if they share the same sequence of localities or comprise nested sets of localities (i.e. adding localities does not alter the track geometry). Geographic points of intersection between two or more tracks comprised a biogeographic boundary or node. Since nodes identify areas or localities comprising more than one spatial relationship, they identify areas with composite or multiple biogeographic origins, suggesting more than one historical geological or biological 'event' contributes to the evolutionary origin of the biota at a node (Craw, 1979, 1982; Craw & Weston, 1984; Heads, 1990).

Standard tracks imply a common origin and history for the component taxa (Craw & Page, 1988; Morrone & Crisci, 1995). An earth history hypothesis for a track is predicted by correlating the track with an overlapping or intersecting geological or geomorphic feature such as a tectonic basin, spreading ridge, suture zone, transform fault or other zones of geomorphologic disturbance such as former coastlines (Heads, 1999). The geographic concentration of taxa (main massing) for a particular group may be used to orient a track with respect to a proposed baseline such as an ocean basin. The spatial correlation technique of panbiogeography contrasts with dispersal and vicariance biogeographic methods where distributions are correlated with hypothesized historical events without a geographic criterion for linking the distribution to a particular geographic sector (Craw *et al.*, 1999). A correlated geological/geomorphic feature is referred to as the 'baseline' linking the origin of a distribution with the earth history of a particular geographic sector. The baseline provides a spatial criterion unique to particular biogeographic patterns, and therefore functions as a spatial synapomorphy for proposing historical models of earth history linked with the origin of component distributions that may be compared with historical models proposed from geology (Craw, 1983; Morrone & Crisci, 1995).



## RESULTS

Three principal track patterns connect Galapagos with the Eastern Pacific, Caribbean, and Pacific basin respectively. Distributions connecting Galapagos with North and South America that bypass Central America comprise an East Pacific track with the tectonic baseline represented by the East Pacific rise and Galapagos spreading centre. Distributions shared between Galapagos and the Caribbean comprise a Galapagos–Caribbean track with a tectonic baseline at the Caribbean/Cocos/Nazca plate boundary. Distributions involving the Galapagos, America, and eastern Asia/Australasia represent a Pacific basin track.

## EAST PACIFIC TRACKS

The following examples illustrate the range of individual distributions comprising the East Pacific pattern. These distributions share Galapagos and exclude all or most of Central America while connecting to either or both North and South America. These tracks exemplify a common spatial pattern for organisms with passive (e.g. flightless weevils) and active (e.g. wasps) dispersal mechanisms. The American relatives of some groups comprise vicariant distributions over a geographic range that is similar to other taxa also comprising more than one vicariant taxon.

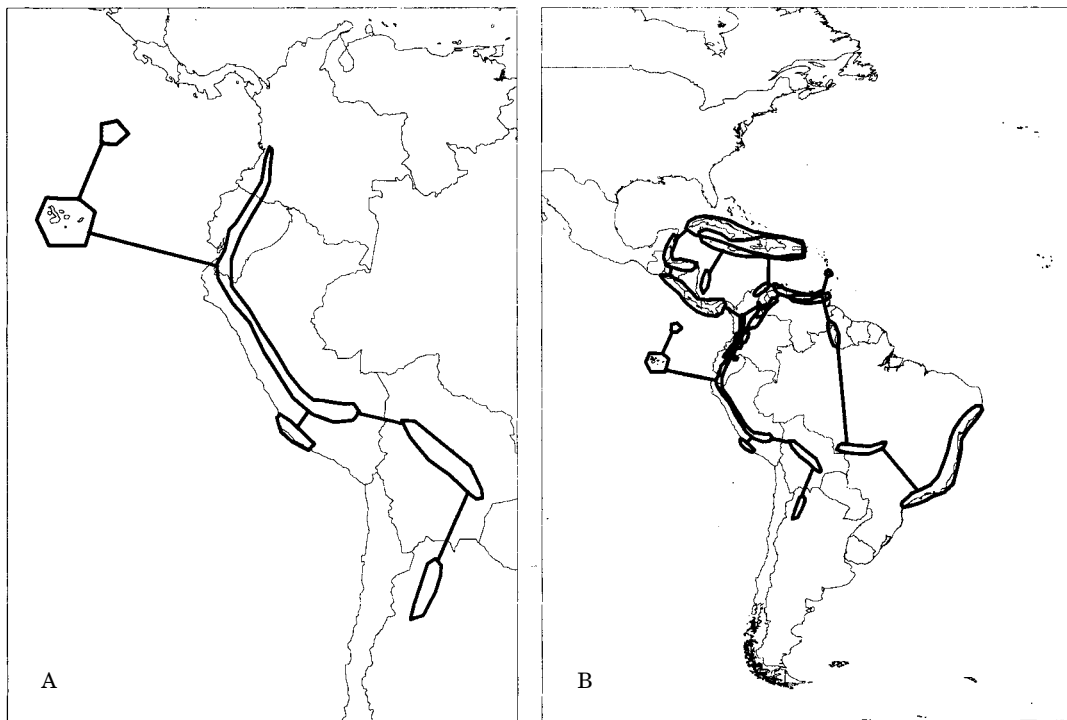
The most localized track connects the Galapagos with Peru and Ecuador. The flightless *Galapaganus* weevils (Lanteri, 1992) (Fig. 1A) comprise five Galapagos species and three species in Ecuador and Peru. The track for the wasp sister species *Tachysphex galapagensis* and *T. peruanus* (Fig. 1B) links Galapagos with Peru (Pulawski, 1986) and the Galapagos snake *Alsophis biserialis* is linked with its sister species *A. elegans* in Peru and southern Ecuador (Fig. 1C). Further south the sister species relationship connects the Galapagos snake *Pilodrya hoodensis* with its Chilean relative *P. chamissonis* (Thomas, 1997) (Fig. 1C). The single species of Galapagos Nolanaceae (Porter, 1983; Heywood, 1993) is linked to the remaining 82 species of the family distributed through Peru and Chile (Fig. 1D). The lizard genus *Microlophus* comprises at least three Galapagos species and 14 mainland species with

a combined range between Ecuador and northern Chile (Frost, 1992) (Fig. 1E).

A northern track is represented by the cotton sister species *Gossypium klotzschianum* and *G. davidsoni* linking the Galapagos with Baja California (Wendel, Schnabel & Seelanan, 1995) (Fig. 1F). A similar link occurs for the sister genus relationship of the foxglove genus *Gambelia* in California and Mexico and *Galvezia* in Galapagos (Sutton, 1988; Elisens, 1992) (Fig. 1G). The track for *Galvezia* comprises Galapagos, Ecuador and Peru (Fig. 1G). The staphylinid beetle genus *Rothium* connects Galapagos with both Mexico and Ecuador (Ahn & Ashe, 1996) (Fig. 1H). A more extensive American range occurs in the scorpion family Iuridae with an endemic genus on Galapagos and related genera distributed between western North America and Chile (Lourenço, 1998) (Fig. 1I).

An extension of the East Pacific track into the Caribbean occurs with the *Phyllodactylus* lizards of Galapagos and their relatives in Columbia, Venezuela and Puerto Rico (Fig. 1J). This track bypasses Panamanian central America as do the other East Pacific tracks with an additional extension into the southern and western Caribbean (Dixon, 1973; Wright, 1983). This Caribbean connection via North and South America is also found in the distribution of the plant genus *Lycium* where the Galapagos ‘fills’ a geographic gap west of Central America complementing the Caribbean distribution to the east (Bernardello, 1986). This interrelationship between East Pacific and Caribbean distributions may also apply to the Galapagos finches. Designation of *Tiaris obscura* as the nearest mainland relative (Sato *et al.*, 2001) results in a Galapagos–South America track (Fig. 2A). Baptista & Trail (1988) suggest both *Tiaris* and the Caribbean *Melanospiza* comprise the Galapagos finch sister group thus extending the East Pacific track to include the Caribbean basin (Fig. 2B). This biogeographic connection is also implied by genetic clustering (Sato *et al.*, 2001) of Galapagos/Cocos Island finches with the genera *Tiaris* (Caribbean, Central and South America), *Melanospiza* (Caribbean), *Loxigilla* (Antilles/Bahamas), and *Volatinia* (Caribbean, Central and South America), and by Webster & Webster’s (1999: 1071) proposal of *Tiaris*, *Volatinia*,

**Figure 1.** East Pacific tracks. (A) *Galapaganus* weevils (Lanteri, 1992); (B) Wasp sister species *Tachysphex galapagensis* (Galapagos) and *T. peruanus* (Peru) (Pulawski, 1986); (C) Snake sister species *Alsophis biserialis* (Galapagos) and *A. elegans* (Peru) a solid line; Snake sister species *Pilodrya hoodensis* (Galapagos) and *P. chamissonis* (Chile) as dashed line (Thomas, 1997); (D) Nolanaceae shrubs (Porter 1983; Heywood, 1993); (E) Tropicurini lizards (Frost, 1992); (F) Cotton sister species *Gossypium klotzschianum* (Galapagos) and *G. davidsonii* (Baja California) (Wendel & Albert, 1992); (G) Foxglove genera *Galvezia* (Galapagos/Peru/Ecuador) and *Gambelia* (California/Baja California) (Sutton, 1988; Elisens, 1992); (H) *Rothium* beetles (Ahn & Ashe, 1996); (I) Iuridae scorpions (Lourenço, 1998); (J) *Phyllodactylus* lizards (Dixon, 1972; Wright, 1983); (K) *Lycium* shrubs (Van Steenis & Van Balgooy, 1966; Bernardello, 1986).



**Figure 2.** Biogeographic relationships of Galapagos finches: (A) Sister group relationship of Galapagos and Cocos Island finches with *Tiaris obscura* proposed by Sato *et al.* (2000); (B) Sister group relationship of Galapagos and Cocos Island finches with *Tiaris* and *Melanospiza* proposed by Baptista & Trail (1988) (Distribution data from Ridgely & Tudor, 1989).

*Melanospiza* (or an extinct genus) as possible candidates for Galapagos finches ancestry.

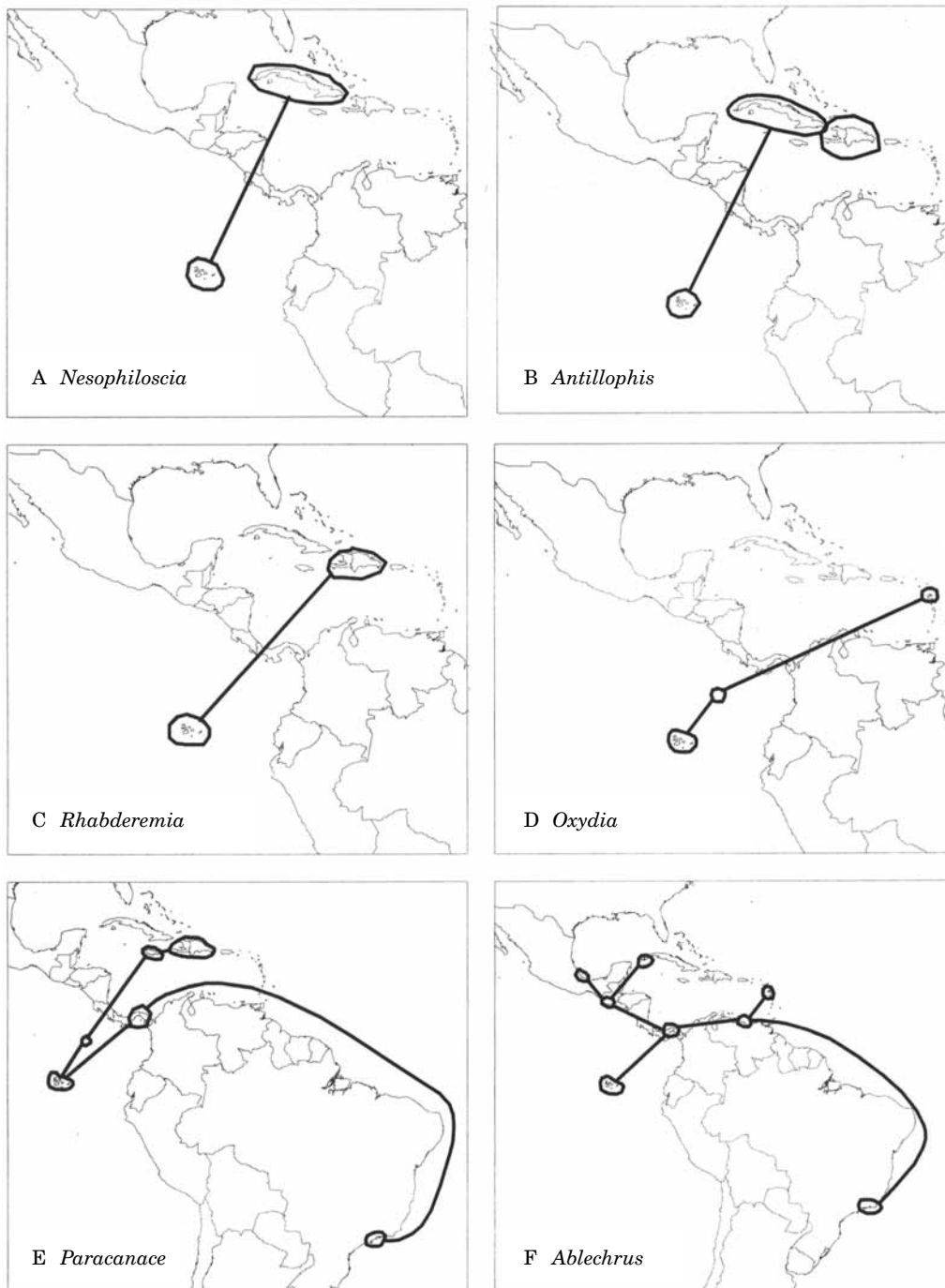
#### GALAPAGOS–CENTRAL AMERICA/CARIBBEAN TRACKS

The Caribbean and East Pacific biogeography of *Phyllodactylus* lizards, *Lycium*, and Galapagos finches provides examples of an intimate biogeographic link between the Caribbean and East Pacific as emphasized by Rosen (1976). This relationship is also evident in tracks connecting Galapagos and the Caribbean to the exclusion of western North and South America. These Galapagos–Caribbean tracks may also include Central America as noted by Hooker (1851b). Disjunctions across Central America are illustrated by the Galapagos terrestrial isopod genus *Nesophiloscia* and its possible closest relative *Troglophiloscia* in Cuba (Vandel, 1968) (Fig. 3A). A similar track is found for the snake genus *Antillophis*, with two endemic species in Galapagos and one each in Cuba and Hispaniola (Thomas, 1997) (Fig. 3B), and a sister species relationship between the marine sponges *Rhabdermia destituta* and *R. mona* connects the Galapagos with Puerto Rico (Van Soest & Hooper, 1993) (Fig. 3C).

Caribbean connections involving Central America appear to be more common. An endemic Galapagos species of *Oxydia* moths (Fig. 3D) may be closely related to species of *Oxydia* on Cocos Island that, in turn, appear to be closely related to a species in the island of Guadeloupe (Brown, Donahue & Miller, 1991; Landry & Rindge, 1995). A similar pattern occurs in an unnamed subgenus of the coastal shore-fly genus *Paracanace* with a track between Galapagos, Cocos Island and Jamaica/Cuba (Fig. 3E). Another subgenus of *Paracanace* forms a track between Galapagos, Panama and Brazil (Fig. 3E), but not Cocos Island (Mathis & Wirth, 1978). The track of the beetle genus *Ablechrus* (Fig. 3F) also connects Galapagos, Central America, the Caribbean and coastal Brazil (Wittmer, 1984).

#### PACIFIC TRACKS

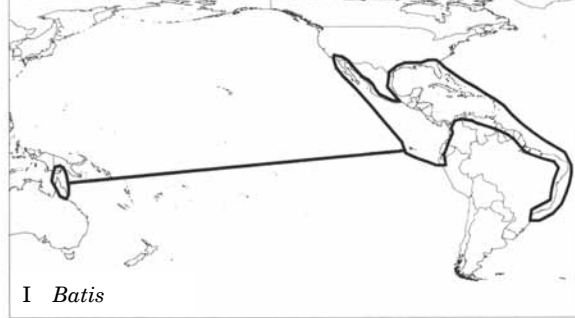
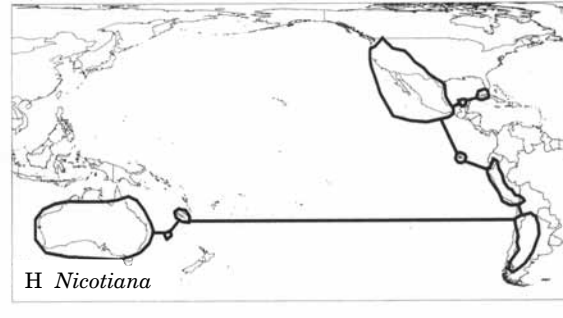
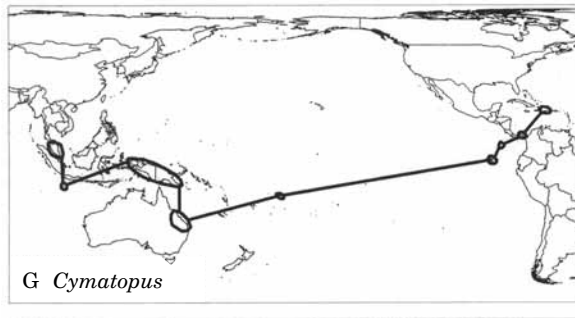
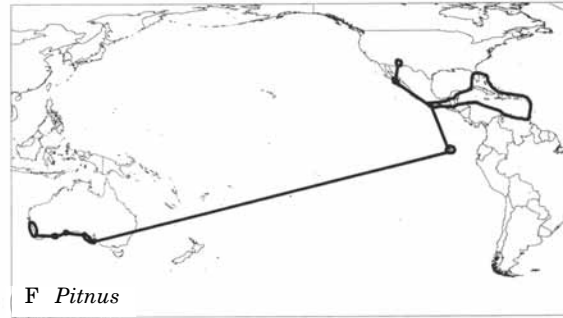
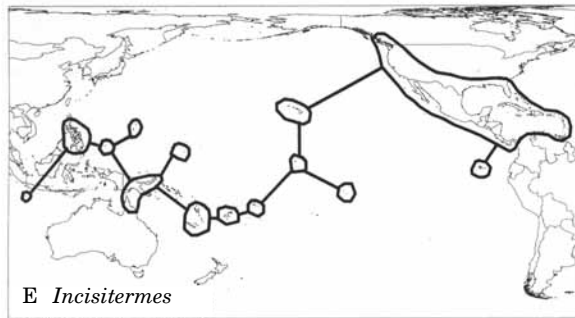
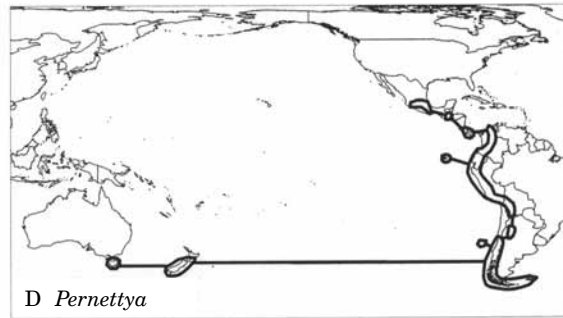
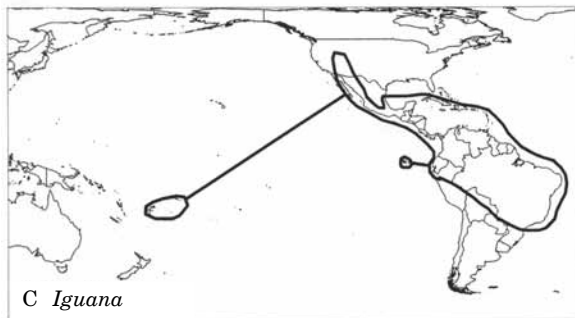
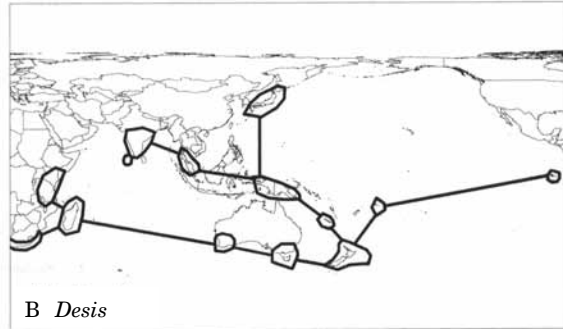
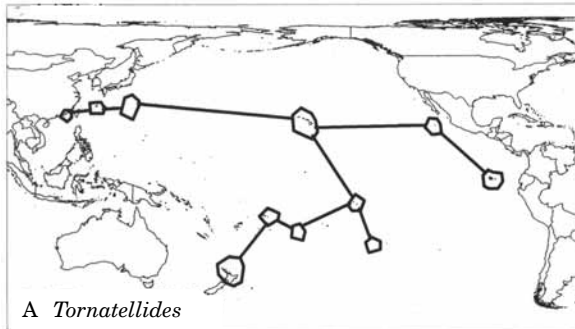
Pacific relationships for Galapagos organisms are particularly evident where the distributions do not include the American mainland. For example the Galapagos represents the easternmost locality for the landsnail genus *Tornatellides* confined to the Pacific basin (Fig. 4A) (Carlquist, 1965) and the coastal marine spider genus *Desis* (Fig. 4B) also widely distributed across



**Figure 3.** Galapagos–Central America–Caribbean tracks. (A) the related isopods *Nesophilosia* (Galapagos) and *Troglophilosia* (Cuba) (Vandel, 1968); (B) *Antillophis* snakes (Thomas, 1997); (C) sister species marine sponges *Rhabderemia destituta* (Galapagos) and *R. mona* (Puerto Rico) (Van Soest & Hooper, 1993); (D) *Oxydia* moths (Brown *et al.*, 1991; Landry & Rindge, 1995); (E) *Paracanace* fly lineages (Mathis & Wirth, 1978); (F) *Ablechrus* beetles (Wittmer, 1984). The minimum distance criterion for *Paracanace* and *Ablechrus* is modified for the Caribbean–southern Brazil component to suggest ancestral or undiscovered locality records along the coastline rather than inland.

the Indian and Pacific Ocean basins (Platnick, 2000). Galapagos organisms are generally most closely related to species on the American mainland and their

origin is traditionally viewed as a predominantly “American” problem (Peck, 1996). This local geographic focus obscures biogeographic relationships that extend





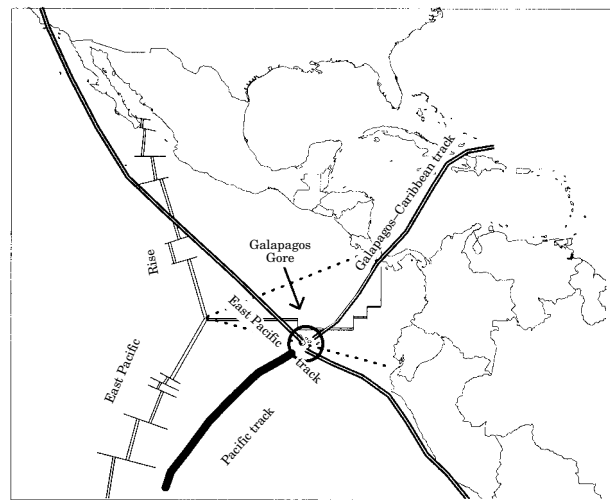
beyond the Galapagos and Americas to include the Pacific basin.

Galapagos organisms with American and Pacific relatives include the two Galapagos iguanid genera and their relatives comprising five genera ranging over much of Central and South America and a Pacific genus confined to Fiji and Samoa (Fig. 4C) that is one of the most basal lineage of this 'New World' group (de Queiroz, 1987; Sites *et al.*, 1996; Rassmann, 1997). Similarly, the endemic Galapagos plant *Pernettya howellii* belongs to a genus with a track connecting Central/Western America with localities in the South-west Pacific (Porter, 1983; Van Steenis & Van Balgooy, 1966) (Fig. 4D) and the termite genus *Incisitermes* includes an endemic Galapagos species as well as species in western North America and Central America, the Caribbean, South East Asia and various Pacific islands (Emerson, 1969; Gay, 1975; Constantino, 1998) (Fig. 4E). The Galapagos supports an endemic species of the beetle genus *Pitnus* with a track between the Caribbean, Central America, southern North America and Australia (Belles, 1992) (Fig. 4F).

A Pacific track involving a more restricted American distribution is represented by the fly genus *Cymatopus* in Hispaniola, Panama, Cocos Island, Galapagos, Samoa and parts of South East Asia/Australasia (Meuffels & Grootaert, 1984; Bickel & Sinclair, 1997) (Fig. 4G). The tobacco genus *Nicotiana* comprises a Pacific track with species in Australia, North and South America, the Greater Antilles, and several Pacific islands including Galapagos while absent from Central America (Fig. 4H). The coastal plant *Batis* also forms a Pacific track with two vicariant species, one in Galapagos and coastal North and South America and the other endemic to Australia and New Guinea (Van Steenis & Van Balgooy, 1966; Porter, 1983; Heywood (1993) (Fig. 4I).

#### CONCLUSIONS

Colonization models for Galapagos evolution emphasize a very generalized biogeographic pattern characterized by the delineation of source areas providing the waifs and strays transported by ocean and wind currents to the Galapagos archipelago. Panbiogeographic analysis presented here confirms a precise geographic separation of different distribution patterns regardless of differences in the dispersal ability



**Figure 5.** Spatial correlation of biogeographic and tectonic relationships of the Galapagos archipelago. Three main distributional relationships are mapped as minimal spanning line graphs (solid lines) connecting Galapagos endemics with their nearest relatives in North and South America (eastern Pacific track), Central America Galapagos–Central America/Caribbean track) and the Pacific basin (Pacific track merging with Galapagos–American tracks). These tracks imply the former presence of three different ancestral distribution ranges in the East Pacific that overlapped within the region now occupied by the Galapagos. The triple track connection parallels the triple tectonic junction between the Pacific, Nazca and Cocos plates and its connection with Central America via the Galapagos rift. The location of the Galapagos archipelago within the boundaries of the Galapagos Gore (dashed lines) and its associated tectonic structures corroborates Leon Croizat's prediction of the Galapagos being located at a major tectonic centre (modified from Croizat, 1958; Holden & Deitz, 1972).

of individual taxa. As the geographic intersection between these vicariant tracks, the Galapagos is biogeographically nodal with respect to the biogeographic history of the region (Fig. 5). Even taxa with trans-Pacific distributions may locally conform to distinct tracks with respect to the eastern Pacific (e.g. *Nicotiana*) and Caribbean (e.g. *Cymatopus*). These alternative track relationships are indicated in Fig. 5 as a general 'Pacific track' merging with American tracks with respect to the Galapagos.

**Figure 4.** Pacific basin tracks. (A) *Tornatellides* landsnails (Carlquist, 1965); (B) *Desis* spiders (Platnick, 2000). (C) "American" iguana lizards (de Queiroz, 1987; Sites *et al.*, 1996; Rassmann, 1997); (D) *Pernettya* heath plants (Porter, 1983; Van Steenis & Van Balgooy, 1966); (E) *Incisitermes* termites (Emerson, 1969; Gay, 1975; Constantino, 1998); (F) *Pitnus* beetles (Belles, 1992) (G) *Cymatopus* flies (Meuffels & Grootaert, 1984; Bickel & Sinclair, 1997); (H) *Nicotiana* tobacco (Van Steenis & Van Balgooy, 1966; Porter, 1983; Heywood, 1993); (I) *Batis* saltwort plants (Van Steenis & Van Balgooy, 1966; Porter, 1983; Heywood, 1993).

## DISCUSSION

## GEOLOGY AND TECTONICS

Discovery of the 'Galapagos Gore', a geological and topographical region with its apex at the triple junction of the Pacific, Cocos and Pacific plates (Holden & Deitz, 1972), corroborated Croizat's (1958) prediction for an important tectonic structure being associated with the Galapagos (Fig. 5). The east Pacific rise and Galapagos rift system, extending between the triple junction and the Panama fracture zone, confirm a tectonic connection between Galapagos, Central America and western North and South America paralleling the biogeographic relationships between these areas (Craw *et al.*, 1999). Given the nodal position of the Galapagos, Croizat (1952, 1958, 1976) predicted a former Pacific 'shoreline' that included Galapagos and also extended out into the Pacific south to Chile and north-west to Hawaii. Croizat (1958) referred to this former land-limit as a mobile coastline extending along the rims of geosynclinal forelands and insular island clusters.

According to Cox (1983) nowhere has plate tectonics served to illuminate the geological history of a complex part of the globe more successfully than in the Galapagos. And yet historical models for eastern Pacific geology are in a greater state of flux and uncertainty than one may perceive solely from the Galapagos literature. Much of geological debate for the eastern Pacific is centred on the origin and evolution of the Caribbean plate. A widely circulated model suggests the Caribbean plate formed from oceanic flood basalt produced at the Galapagos hotspot about 90 Myr (Duncan & Hargraves, 1984; Pindell & Barrett, 1991; Mauffret & Leroy, 1997). Supporting evidence includes paleomagnetic and geophysical data, radiolarian fossil assemblages, and the presence of Jurassic fragments (including a remnant seamount and island arc) of Pacific origin (Montgomery *et al.* 1994; Sinton *et al.*, 1998; Sallarès & Dañoibeitia, 2001). An alternative geological model predicts formation of the Caribbean plate at an unknown mantle plume between North and South America without involvement of the Galapagos hotspot (Meschede & Frisch, 1998). This *in situ* origin finds less general acceptance among geologists because of conflicting plate tectonic reconstructions and paleontological data (Révillon *et al.*, 2000: 656). Donnelly (1989) proposed the Caribbean originated about 119 Myr west of North and South America where it remained in a largely static position while the North and South American plates moved westwards around it. Formation of the plate was attributed to oceanic flood basalt from mantle melting rather than from a hotspot source at the Galapagos. A Galapagos source for the Caribbean was also rejected by Acton, Galbrun & King *et al.* (2000) since it would require the Farallon plate to move eastwards at 130 km/Myr – far in excess

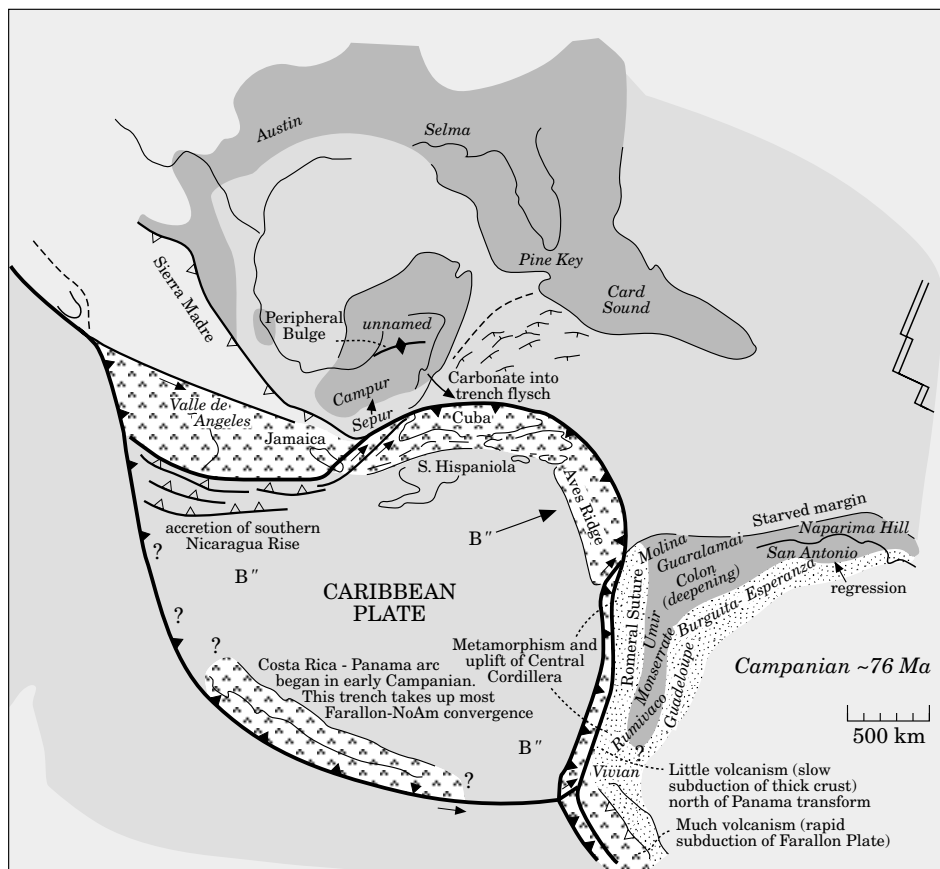
of what they considered to be the 'estimated rates of motion'.

The Caribbean plateau comprises magmas dated at 90 and 76 Myr. If they were produced from the same source such as the Galapagos hotspot they should be geographically separated due to movement of the Farallon plate during the intervening period. Révillon *et al.* (2000) suggest the Galapagos represents a magma source for only one of the events. The Caribbean plate may have formed south of the Galapagos hotspot at 90 Myr and the magma of 76 Myr was generated as the plate moved north over the hotspot. Alternatively the 90 Myr magma was generated at the hotspot while the 76 Myr magma was produced later from another source such as lithospheric thinning (Révillon *et al.*, 2000).

While the Caribbean plateau itself is considered to be oceanic in origin, geological evidence of subaerial environments and buried seamounts also suggest the plateau supported emergent volcanoes (Donnelly, 1989: 316). Further terrestrial environments are represented by two major island arc systems (Fig. 6), an inner or eastern Greater Antillean arc positioned between Mexico and Ecuador at 90 Mya, and an outer or western Costa Rica–Panama island arc along the eastern boundary of the Caribbean plate between Mexico and Ecuador 76 Mya (Duncan & Hargraves, 1984; Mattson, 1984; Durnham, 1985; Pindell, 1993; Pindell & Barrett, 1991; Kellogg & Vega, 1995; Laj *et al.*, 1989; Mann, 1995; Mourier *et al.*, 1988; Stockhert *et al.*, 1995).

Spatial correlation of Galapagos tracks with eastern Pacific tectonics represents the best available evidence of direct contact between the Galapagos hotspot and proposed former Pacific–Caribbean island arcs. Where an island arc moved over the hotspot it would be possible for island arc biota to disperse onto the volcanic landscape while their relatives were transported eastwards until the arcs accreted with the American mainland (Fig. 7). This model suggests the American relatives originated to the west of their current position rather than themselves representing eastern sources of the Galapagos biota as represented in traditional colonization models. Sequential dispersal onto newer volcanoes by direct geographic contact or geographic proximity adjacent volcanic islands would be necessary for the island arc biota to persist at the Galapagos into the present. It is also possible that some mainland relatives are the product of former Galapagos Islands that remained subaerial before they accreted with America with their biota (Hauff *et al.*, 1997).

Croizat (1981: 511) referred to the Galapagos as a "fragment of geological America" reduced to a series of volcanic islands in the early Tertiary with animal and plant life corresponding to the 'American' biota of that time. The geosynclinal mechanism proposed by Croizat (1958) is compatible with the plate tectonic depiction



**Figure 6.** Island arc model for an eastern Pacific origin of the Caribbean plate (adapted from Pindell, 1993, fig. 6H) at 76 Myr with the Panama–Costa Rica arc along the western boundary at an undetermined longitude, and the Antillean arc along the eastern boundary.

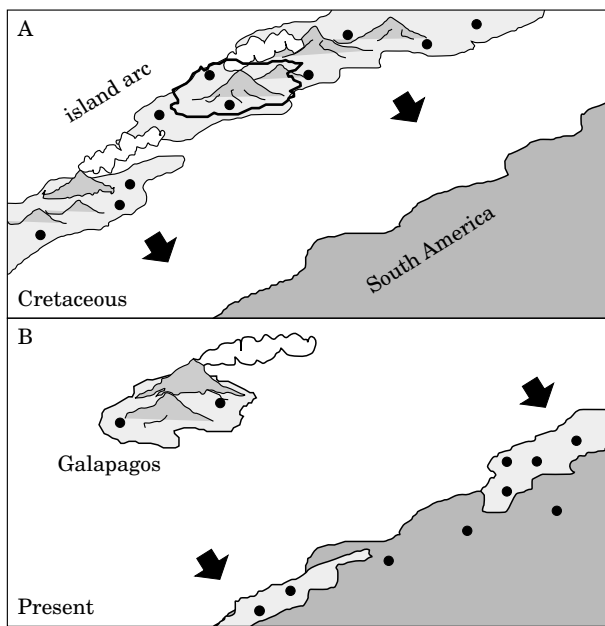
of submarine trenches associated with volcanic island arcs (cf. Mitchell & Reading, 1969) and it is also compatible with Caribbean plate tectonic models that allow for indirect contact between the Galapagos hot-spot and American mainland mediated by island arcs transport. Even though volcanic activity is responsible for the geological formation and persistence of the Galapagos, organisms inherited from an island arc or other mobile Pacific landscape represent an older 'geological' layer re-deposited onto a younger geological stratigraphy (cf. Heads, 1990).

#### PACIFIC HISTORY

Transpacific distributions involving the Galapagos are examples of a globally distinct biogeographic pattern centred on the Pacific basin with member taxa absent or poorly represented in regions bordering the Atlantic and Indian Ocean basins (Croizat, 1952, 1958, 1961; Rosen, 1976; Craw, 1988, 1989; Grehan, 1991; Morrone 1996; Contreras-Mendoza, Luna Vega & Morrone, 1999; Craw *et al.*, 1999; Katinas, Morrone & Crisci, 1999; De Marmels, 2000). These Pacific connections

were sufficiently prominent for Charles Darwin to propose an early theory of continental drift uniting Asia, Africa, Australia and America (Grinnell, 1974; Craw, 1984). The Galapagos–East Pacific track conforms to many Pacific patterns with distributional disjunctions across Central America (Heads, 1999). Tectonic correlations with terrane boundaries of Pacific or Tethyan origin are demonstrated for the plant genus *Abrotanella* (Heads, 1999), the Triassic bivalve genus *Monotis* (Heads, 1990) and the Triassic dinosaur clade *Saruropterygia* (Rieppel, 1999). A large concentration of Pacific affinities is also known for the Cordillera terranes of Pacific origin in north-western North America (Croizat, 1958; Craw & Page, 1988).

Lomize & Zakharov (1999) suggest a series of island arc formations were present in the East Pacific from Jurassic through Cretaceous time until finally absorbed by the westward movement of the American continents. Allochthonous terranes of Pacific origin are known in western North America from Alaska to Chile (Craw, 1988; Craw & Page, 1988; Bahlburg & Hervé, 1997). Geological components of Central America are hypothesized to have originated along the east Pacific



**Figure 7.** Generalized biogeographic interpretation for island arc elements in the Galapagos biota: (A) An eastward moving island arc system crosses the Galapagos hotspot (bold outline within arc) allowing animals and plants (solid circles) to colonize the volcanic landscapes. (B) Island arc organisms are stranded at the Galapagos hotspot while their relatives are transported east and colonize the mainland as the arc is accreted to North and South America as well as comprising parts of Central America.

rise (Di Marco, 1994) and the Cretaceous Piñón terrane of western Ecuador exhibits geochemical similarities with the Nauru, Ontong Java and Caribbean oceanic plateaus (although this alone does not prove historical juxtaposition). Historical extrapolation of movement by the Farallon plate led Reynaud *et al.* (1999) and Lapierre *et al.* (2000) to predict the Piñón terrane originated about 3000 km further south and west of its current position.

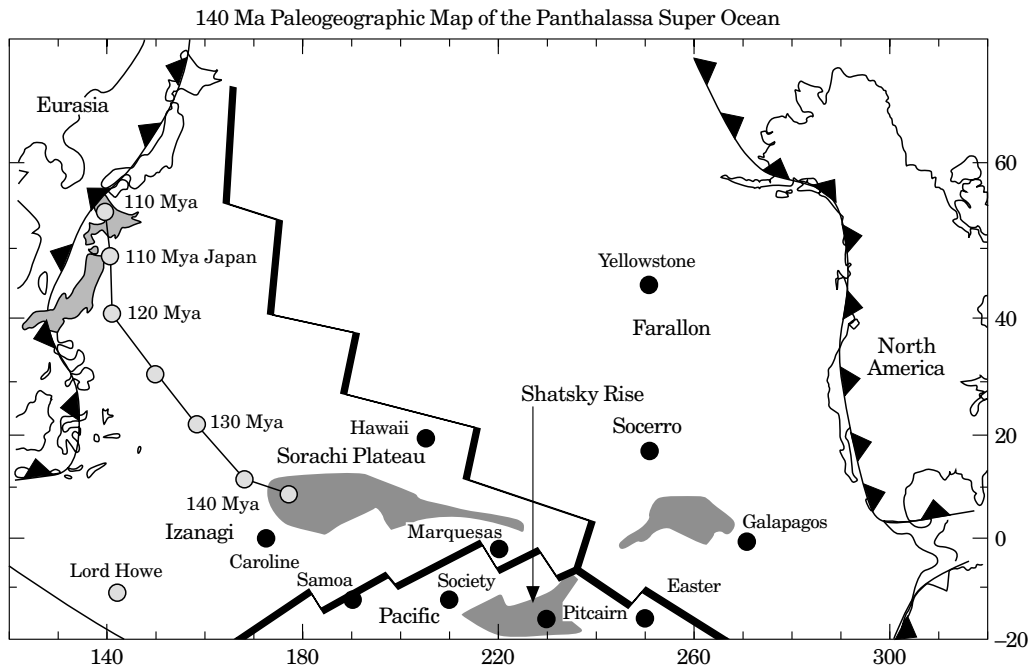
Geological models to which most evolutionary biogeographers attach historical narratives treat the Pacific basin as a permanent ocean. Croizat (1961) predicted a composite geological origin of the Americas involving fusion of Atlantic (Gondwana/Laurasia) and Pacific basin sources. This was the first explicit continental drift/plate tectonic prediction involving a composite tectonic Pacific and Atlantic basin structure for the Americas (Craw & Weston, 1984; Grehan, 2001). The presence of exotic terranes in western America and Eurasia in the vicinity of the Tethyan geosyncline also fuelled geological speculation of a common historical origin. Nur & Ben-Avraham (1977) proposed fragmentation of a 'Pacifica' landmass in the modern

South-west Pacific with displacement of micro-continental fragments across the Pacific and Tethyan basins. Kimura, Sakakibara & Okamura (1994) propose an equatorial proximity of the Sorachi Plateau of Japan with the Shatsky Rise along with the Wrangellia superterrane west of the Galapagos hotspot position at 140 Myr (Fig. 8), and a similar proximity of Pacific mantle domains is also proposed by Smith & Lewis (1999). Wrangellia is characterized by Kimura *et al.* (1994) as a terrane of superplume-related flood basalts on a continental-type basement representing a "continent or island arc". Nur & Ben-Avraham (1989: 17) suggest their 'Pacifica' model may explain the Triassic continental deposits and the "strong evidence" for continental rifting in an unknown location near the equator. Moores (1998) proposed the former existence of extensive Mesozoic island arcs on the periphery of a 'Philippine-like' plate in the Pacific (Fig. 9) and he also suggested the Caribbean basement represents a fragment still bounded by Pacific island arc remnants.

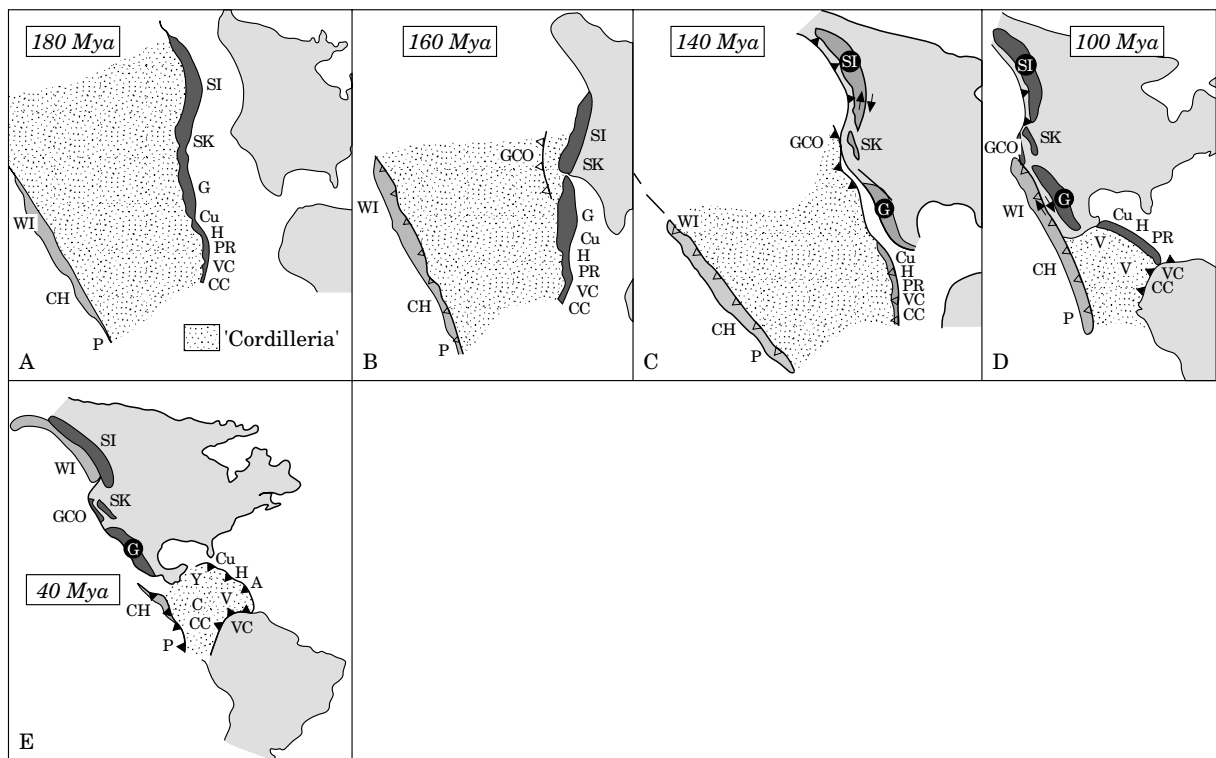
Historical geological models for the Pacific represent theoretical and methodological developments in historical geology that attempt to address circum-Pacific terranes as a general, rather than local, geological problem. The panbiogeographic approach similarly links the origin of Galapagos endemics to the origin of Galapagos relatives rather than treating each in isolation. The presence of *Pitnus* in Galapagos, for example, is not simply a Galapagos matter, but a more general problem of why *Pitnus* also happens to be in the Caribbean and Australia. This global context is exemplified by the distribution of iurid scorpions where the western American and Galapagos range is disjunct with respect to the eastern Mediterranean and Caucasus region. This disjunction may be due to the opening of the Atlantic basin with subsequent extinction in eastern North and South America. However, the localization of the family to western North and South America conforms to a common pattern for Pacific groups, suggesting the Galapagos Iuridae originated as elements of a Pacific group possibly connected with the Mediterranean-Caucasus outlier via the Tethys geosyncline (Fig. 10).

#### EVOLUTIONARY AGE

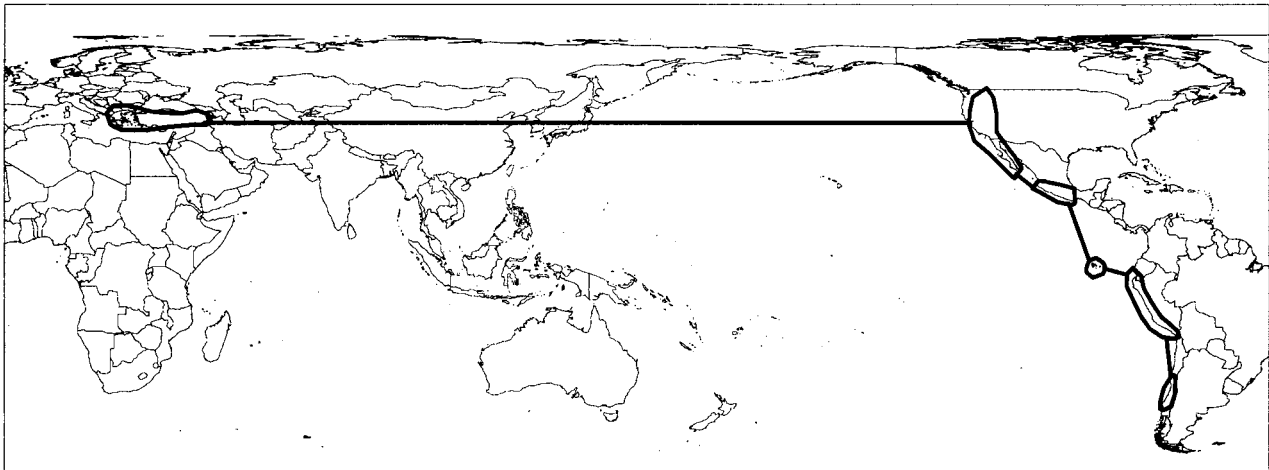
One of the prominent inferences for Galapagos organisms concerns the age of colonization. In the absence of fossils (particularly from the Galapagos) molecular clock techniques are widely used to determine the temporal window of colonization and divergence. Molecular clocks for Galapagos organisms rely on fossil or geological information for other taxa to provide the calibration criteria necessary for estimating an absolute time scale for divergence. Molecular estimates for Galapagos taxa appear to be



**Figure 8.** Paleogeographic reconstruction at about 140 Mya proposing the proximate location of the Shatsky Rise, Sorchi Plateau and possibly the Wrangellia terrane (from Kimura *et al.* (1994)).



**Figure 9.** Island arc model for the Pacific origin of American terranes at the western and eastern boundary of a former Philippine-like eastern Pacific plate ('Cordilleria') that progressively merged with North, South, and Central America between Mesozoic and Tertiary time (from Moores, 1998).



**Figure 10.** Hypothesis of Pacific baseline for the Iuridae to suggest the geological history of the Pacific is responsible for the origin of the scorpions on the Galapagos, western North and South America and the Mediterranean/Caucasus region.

plagued with problematic calibrations that are poorly documented and often emphasize previous use in the literature as justification for the model.

According to Wendel & Percival (1990: 110), limited allelic novelty, lack of unique alleles and similarity of interspecific genetic identities between the Galapagos *Gossypium klotzschianum* and the intraspecific identities of *G. davidsonii* in Baja California is evidence for a "relatively recent" founding event and associated severe genetic bottleneck. They claim (Wendel & Percival, 1990: 112) "we know the maximum age of divergence" because the oldest part of the Galapagos Islands is 3–4 Myr, and this "geological evidence" is correlated with "independent estimates" from genetic data. Substitution rates proposed for isozyme data and sequence divergence rates assumed for cpDNA resulted in dates of 710 000 and 650 000 years ago. With "numerous assumptions and sources of error" and characterizing the estimates as "approximations" Wendel & Percival (1990: 112) nevertheless consider their close agreement striking and declare Croizat's Galapagos *Gossypium* track "nothing more than a line drawn between points representing a long-distance dispersal event". Wendel & Albert (1992) attempt a combination of paleontological, geological, and molecular arguments to establish a global historical chronology for the cotton genus *Gossypium* (Malvaceae). With malvacous pollen being Eocene or younger, earlier continental drift events are ruled out as the mechanism for cotton distribution. An "independent assessment" is offered in the form of cpDNA sequence divergence estimates between maximally divergent lineages. For calibration Wendel & Albert (1992) turn to comparisons of plastid-encoded *rbc-L* gene sequences between taxa for which fossil records provide "reasonable estimates" of divergence times. Using the fossil record of a variety of

plant groups they estimate an initial dichotomy for *Gossypium* of 24–33 Myr. Wendel & Albert (1992: 138) acknowledge "several obvious potential sources of error" and for an estimate that is "clearly only an approximation" but "nevertheless consistent with the palynological record". In light of this 'consistency' they attribute the distribution of *Gossypium* to transoceanic dispersal and reassert long-distance dispersal for the origin of Galapagos *Gossypium*.

Schilling, Panero & Eliasson (1994) estimated the age of Galapagos daisy *Scalesia* to be 1.9–6.2 Myr while also noting that cpDNA estimates rely on a number of poorly substantiated hypotheses concerning an estimation of total sequence divergence from restriction site data and relating estimated sequence divergence to values based on *rbcL* sequence data. These problems notwithstanding, Schilling *et al.* (1994: 252) invoke dispersal of *Scalesia* and related *Pappobolus* over a 3 Myr Central American landbridge from a putative centre of origin in Mexico.

Differentiation of the mitochondrial locus encoding subunit I of the enzyme cytochrome oxidase for the flightless *Galapaganus* weevils was estimated by Sequeira *et al.* (2000) to be 10.7–12.1 Myr based on an mtDNA clock proposed by Brower (1994) for "arthropods in general". However, Brower (1994) only examined about six insect species and one crustacean species representing "recently diverged arthropod taxa" for which mtDNA sequence divergence measures were already calculated from 'known' dates of divergence. Brower (1994) did not specify the historical evidence for "dated geological events" inferred from "biogeography and paleoclimatology".

Divergence estimates of 33–48 Myr for the *Tropidurus* lizards by Lopez *et al.* (1992) were based on a 'general' rate of one immunological distance for every

0.6 Myr obtained from a combination of molecular clocks based on unspecified fossil data and a combination of "fossil and geological" information in the literature. Divergence estimates for Galapagos iguanids by Rassmann (1997) used an ungulate rate of sequence evolution, although rates of mitochondrial sequence evolution were acknowledged to likely vary among taxon groups. Rassmann (1997) addressed this problem by adopting the rate from taxa with "well-known phylogenetic relationships and divergence times". Ungulate taxa were selected by Rassmann (1997) as representing "robust groupings in previous molecular analyses" and a relatively well-documented fossil record to provide "good estimates of their separation times". In addition Rassmann (1997) considered the ungulate calibration to be "probably associated with large errors" and probably to underestimate the predicted 10.5–19.5 Myr separation of Galapagos iguanids. These internal errors are compounded by lack of information on the ungulate calibration other than the assertion that the fossil record is 'good'. Notwithstanding these uncertainties, probable errors and acknowledged underestimation, Rassmann (1997) emphasizes the DNA data are 'consistent' with immunological estimates of 15–20 Myr by Wyles & Sarich (1983). Wyles & Sarich (1983: 177) calibrated iguanid serum albumins against the fossil record to provide a "reasonably accurate molecular clock", although the criteria for defining iguanid fossils was never specified. In a discussion of conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards, Wiens & Hollingsworth (2000) suggest that cytochrome b and ND4 may give "positively misleading results" and they urge caution in estimating phylogenies based only on these particular genes.

Divergence estimates by Vineck *et al.* (1997) for the Galapagos finches were obtained by comparing the Mhc class II sequences of the pheasant and the domestic fowl "believed to have diverged 20 Mya". Group 1 finch alleles were predicted to have a common ancestor about 15 Mya ( $\pm 20\%$ ), but since Vineck *et al.* (1997: 114) accept 10 Myr as the earliest formation of the Galapagos earlier arrival was precluded. They conclude the arrival time of Galapagos finches cannot be determined precisely although 2.8 Mya was considered "acceptable" and the 5 Myr age of the current islands represented the upper limit consistent with all molecular estimates.

Divergence estimates of 2.3 and 1.3 Myr between the Galapagos finches and the closely related *Tiaris* by Sato *et al.* (2001) were calibrated against the divergence estimates proposed for birds by Shields & Wilson (1987) and mammals by Irwin, Kocher & Wilson (1991) with the observation, "Both rates have been widely used". Calibration of MtDNA evolution for geese

by Shields & Wilson (1987) was based on fossils with the claim that fossil geese "have been relatively well preserved and studied" without providing information on the criteria for assigning fossils to the modern geese genera central to the divergence estimates. Similarly, Irwin *et al.* (1991) claim ungulates have a "good fossil record" and several divergences within artiodactyls have "well-established divergence dates from the fossil record", without specifying criteria for the reliability of fossil data or their representation of actual divergence events for mammalian lineages.

A molecular study by Caccone *et al.* (1999) analysed three mainland South American species of *Geochelone* as the 'best' candidates for the closest living relative of the Galapagos tortoises (*G. nigra*). Using a 50% majority rule consensus tree for maximum parsimony generated from cytb and 16S rRNA, a sister species relationship was proposed between *G. nigra* and *G. chilensis*. A divergence date between 6 and 12 Mya was based on "published mtDNA rates estimated from turtles and other vertebrate ectotherms". The authors provide no evidence other than to cite previously published work on other groups – Avise *et al.* (1992), Caccone *et al.* (1997) and Rand (1994). Avise *et al.* (1992) emphasize the slow rate of turtle divergence derived from geographic correlations with inferred biogeographic events while noting the speculative character of biogeographic histories and phylogenetic relationships. Similarly, Caccone *et al.* (1997: 127) acknowledge calibration of the molecular clock against absolute time is controversial and also point out that while dates based on fossils should provide both minimum and maximum dates these depend on the degree of fossil resolution. They also point out the problem of accurately associating geological events with particular historical scenarios. Rand (1994) emphasized the influence of metabolic rate resulting in variation in the absolute rate of mtDNA evolution. Caccone *et al.* (1999) did not specify how they applied the data and problems presented in these papers.

Molecular calibrations that rely on the fossil record as an accurate or realistic estimator of lineage duration and divergence generally fail to consider or acknowledge the oldest fossil records as the minimal phylogenetic age of a lineage (cf. Croizat, 1964; Rosen, 1976; Craw *et al.*, 1999). In addition, fossils may even lack the full repertoire of phylogenetic characters necessary for their taxonomic placement with respect to modern groups. Divergence calibrations based on calibrations for other lineages removes the procedure from immediate verification other than accepting the authority of the sources as being accurate and precise. These problems suggest molecular techniques, while emphasizing the antiquity of Galapagos taxa relative to the age of the modern islands are methodologically suspect, or at the very least problematic, and do not

constrain with any reliability the upper phylogenetic age of the Galapagos lineages.

With the earliest geological formation of the Galapagos hotspot 90 Mya, the temporal geological window for island-arc colonization of the Galapagos ranges from late Cretaceous through early and mid-Tertiary time. Falling well within this time frame is the 33–48 Myr molecular divergence estimate for *Tropidurus* based on “geological” as well as fossil information. Biogeographic correlation of distributions and tectonic patterns provide an alternative, and perhaps more accurate estimation of phylogenetic age than fossil-based methods (Craw *et al.*, 1999). Five of the American *Galapaganos* species, for example, are confined to the Piñón terrane (Craw *et al.*, 1999) – a geological system with an estimated accretion period between late Cretaceous and Eocene time (Feininger, 1987; Kellogg & Vega, 1995). It may be possible in the future to develop a statistical test of association between Galapagos endemics and their relatives by comparing endemic and non-endemic Galapagos taxa and their track relationships with respect to allochthonous terranes.

## CONCLUSIONS

- (1) Panbiogeography re-introduces the question of geographic distribution into the analysis of Galapagos origin and evolution. Existence of standard tracks intersecting at the Galapagos and comprising taxa of both ‘good’ and ‘poor’ means of dispersal emphasizes the need for development of a comprehensive biogeography to assess the relative merits of geologically or biologically mediated mechanisms of Galapagos colonization and evolution.
- (2) Colonization biogeography fails to meet the Galapagos challenge because it is incapable of yielding new insights into the evolutionary history of the islands. Panbiogeographic methodology is independent of geological history so its capacity to accurately predict new geological facts provides a better test of its explanatory power than measuring its conformity with any accepted historical scenario (Craw & Weston, 1984; Craw & Page, 1988; Craw *et al.*, 1999). Panbiogeographic analysis of Galapagos demonstrates the liability of biogeographic and evolutionary history being retrofitted onto popular or preferred historical geological reconstructions that are themselves only narratives or theories constructed by geologists analysing geological characters and homologies, and therefore subject to subsequent revision or replacement.
- (3) Galapagos biogeography remains as important for modern evolutionary theory as it was historically significant for Darwin and Hooker. The colonization model reduces the Galapagos to a special case under the umbrella of ‘island’ biogeography through sweepstakes and waif dispersal (Cox & Moore, 2000; Grant, 1998). Colonization biogeography maintains its general methodological applicability by distinguishing between ‘oceanic’ origin for Galapagos and ‘continental’ origin for mainland biota (Craw *et al.*, 1999). Panbiogeographic reconstructions suggest the origin and evolution of Galapagos biota involve the same general processes of earth history that also influenced the origin and evolution of ‘continental’ biotas.
- (4) Pacific basin biogeography is predicted to represent a significant component of the geological and biological history involved with the origin and composition of the Galapagos biota. Croizat’s (1958) successful prediction of a major tectonic formation associated with Galapagos confirms the panbiogeographic method as both useful and productive.
- (5) The panbiogeographic reconstruction presented here for the Galapagos does not fall into the classic ‘dispersal’ *versus* ‘vicariance’ dichotomy favored by traditional biogeographers (Stace, 1989; Brown & Lomolino, 1998; Cox & Moore, 2000; Cox 1983). Ancestral distributions are not specified other than to define the track links for the descendants. With the highly mobile Pacific geology, it is suggested dispersal ability and topography acted together in a reciprocal relationship as taxa moved over landscapes now lost to modern geography. Under these historical constraints notions of vicariance and dispersal are inadequate concepts for analysing spatio-temporal evolution of earth and life.
- (6) The preponderance of ‘good’ dispersal ability is not necessarily evidence for Galapagos colonization through the ability of organisms to disperse. Dispersal characteristics of the Galapagos biota may be correlated with the constraints of ecological survival on small, geologically unstable islands (Hooker, 1851b; Croizat, 1952: 168; Croizat 1964: 36; Craw 1978; Craw *et al.*, 1999). As small, emergent, outcrops these islands support a biota characteristic of marine rock stacks with few mammals and large vertebrates (with the exception of sea-birds), and a contrasting abundance of lizards, invertebrates, and seed-plants dominated by herbs and shrubs, often with a weedy or pioneer ecology (Heads, 1990: 579). In a historical or evolutionary context: “If anything were ever left of a whole continent the chance is that its last remnant in the shape of an oceanic rock would still be tenanted by breeding birds of the sea, perhaps a lizard, a bug and a few enduring weeds”. (Croizat 1958 I: 722).



- (7) Molecular clock calibrations of Galapagos endemics are methodologically problematic, particularly for their uncritical reliance on pre-existing calibrations that also tend to treat the fossil record as accurate and precise with respect to phylogenetic position and temporal appearance. Uncritical use of fossils in calibration may severely underestimate phylogenetic age (cf. *Craw et al.*, 1999 on fossils), and attempts by geneticists to dismiss spatial biogeographic reconstructions for their incongruence with molecular estimates (e.g. *Trewick*, 2000) are premature. Geographic correlation between tracks and tectonic patterns provides an alternative measure of phylogenetic origin for the Galapagos that should be incorporated into molecular studies.
- (8) While many modern Galapagos organisms, including some endemics, are no doubt derived from ancestors dispersing over-water from the modern America, the prevailing view that this is the only viable historical mechanism is no longer biogeographically or geologically tenable. Panbiogeographic approaches enhance the role of Galapagos in evolutionary theory by demonstrating how even 'oceanic' islands can evolve through the same kind of co-evolutionary relationship with geological history characteristic of a 'continental' biota. This evolutionary correspondence suggests that while distinctions between 'oceanic' and 'continental' may be satisfactory as a descriptive technique, the contrast is questionable as an analytical tool for evolutionary biology (cf. *Craw et al.* 1999).
- (9) Future consideration of earth history for Galapagos will need to examine both the broad issue of geotectonic relationships spanning the Pacific and the paucity of good phylogenetic and geographic information for the evolutionary relationships of the Galapagos biota. Scientific funding agencies charged with responsibility for the science of evolution should prioritize systematic and biogeographic studies of Galapagos biota and related taxa to capitalize on a major evolutionary resource before ongoing environmental devastation obliterates much of the region's biogeographic and evolutionary record.

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#### REFERENCES

- Acton GD, Galbrun B, King JW. 2000.** Paleolatitude of the Caribbean plate since the late Cretaceous. *Proceedings of the Ocean Drilling Program, Scientific Results* **165**: 149–173.
- Ahn K, Ashe JS. 1996.** A revision of *Rothium* Moore and Legner (Coleoptera: Staphylinidae: Aleocharinae) with a discussion of its phylogenetic relationships. *Journal of the Kansas Entomological Society* **69**: 234–256.
- Avisé JC, Bowen BW, Lamb T, Meylan AB, Bermingham E. 1992.** Mitochondrial DNA evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in the testudines. *Molecular Biology and Evolution* **9**: 457–473.
- Axelrod DI. 1972.** Ocean-floor spreading in relation to ecosystematic problems. *University of Arkansas Occasional Paper* **4**: 15–68.
- Bahlburg H, Hervé F. 1997.** Geodynamic evolution and tectonostratigraphic terranes of northwestern Argentina and northern Chile. *Geological Society of America Bulletin* **109**: 869–884.
- Baptista LF, Trail PW. 1988.** On the origins of Darwin's finches. *The Auk* **105**: 663–671.
- Belles X. 1992.** Sistemática, historia natural y biogeografía del genero *Pitnus* Gorham, 1880 (Coleoptera, Ptinidae). *Eos* **68**: 167–192.
- Bernardello LM. 1986.** Revisión taxonómica de las especies sudamericanas de *Lycium* (Solanaceae). *Boletín de la Academia Nacional de Ciencias, Córdoba* **57**: 173–356.
- Bickel DJ, Sinclair BJ. 1997.** The Dolichopodidae (Diptera) of the Galápagos islands with notes on the New World fauna. *Entomologica Scandinavica* **28**: 241–270.
- Bowman RI, Berson M, Leviton AE. 1983.** *Patterns of evolution in Galapagos organisms*. California: Pacific Division, AAAS, San Francisco.
- Brower AVZ. 1994.** Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 6491–6495.
- Brown JH, Lomolino MV. 1998.** *Biogeography*. Sunderland, Massachusetts: Sinauer Associates.
- Brown JW, Donahue JP, Miller SE. 1991.** Two new species of geometrid moths (Lepidoptera: Geometridae: Ennominae) from Cocos Island, Costa Rica. *Natural History Museum of Los Angeles County Contributions to Science* **423**: 11–18.
- Caccone A, Milinkovitch MC, Sbordoni V, Powell JR. 1997.** Mitochondrial DNA rates and biogeography in European newts (Genus *Euproctus*). *Systematic Biology* **46**: 126–144.

- Caccone A, Gibbs JP, Ketmaier V, Suatoni E, Powell JR. 1999.** Origin and evolutionary relationships of giant Galapagos tortoises. *Proceedings of the National Academy of Sciences of the United States of America* **96**: 13223–13228.
- Carlquist S. 1965.** *Island life*. Garden City, New York: The Natural History Press.
- Carson HL. 1992.** The Galapagos that were. *Nature London* **355**: 202–203.
- Christie DM, Duncan RA, McBirney AR, Richards MA, White WM, Harpp KS, Fox CG. 1992.** Drowned islands downstream from the Galapagos hotspot imply extended speciation times. *Nature London* **355**: 246–248.
- Connor EF, Simberloff D. 1978.** Species number and compositional similarity of the Galápagos flora and avifauna. *Ecological Monographs* **48**: 219–248.
- Constantino R. 1998.** Catalog of the Living Termites of the New World (Insecta: Isoptera). *Arquivos de Zoologia* **35**: 135–230.
- Contreras-Mendoza R, Luna Vega I, Morrone JJ. 1999.** Biogeographic analysis of the genera of Cycadales and Coniferales (Gymnospermae): a panbiogeographic approach. *Biogeographica* **75**: 145–162.
- Cook J, Howden HF, Peck SB. 1995.** The Galapagos islands' genus *Neoryctes* Arrow (Coleoptera: Scarabaeidae: Dynastinae). *The Canadian Entomologist* **127**: 177–193.
- Cox A. 1983.** Ages of the Galapagos Islands. In: Bowman RI, Berson M, Leviton AE, eds. *Galapagos Organisms*. San Francisco: AAAS, 11–23.
- Cox CB, Moore PD. 2000.** *Biogeography: An ecological and evolutionary approach*. Oxford: Blackwell Scientific Publications.
- Craw RC. 1978.** Two biogeographical frameworks: implications for the biogeography of New Zealand. A review. *Tuatara* **23**: 81–114.
- Craw RC. 1979.** Generalized tracks and dispersal in biogeography: a response to R.M. McDowall. *Systematic Zoology* **28**: 99–107.
- Craw RC. 1982.** Phylogenetics, areas, geology and the biogeography of Croizat: a radical view. *Systematic Zoology* **31**: 304–316.
- Craw RC. 1983.** Panbiogeography and cladistics: are they truly different? *Systematic Zoology* **32**: 431–438.
- Craw RC. 1984.** Biogeography and biogeographic principles. *New Zealand Entomologist* **8**: 49–52.
- Craw RC. 1988.** Panbiogeography: Method and synthesis in biogeography. In: Myers AA, Giller PS, eds. *Analytical Biogeography*. London, Chapman & Hall, 405–435.
- Craw RC. 1989.** Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. *Systematic Zoology* **37**: 291–310.
- Craw RC, Page R. 1988.** Panbiogeography: Method and metaphor. In: Ho M-W, Fox S, eds. *Evolutionary Processes and Metaphors*. Chichester, UK: John Wiley & Sons, 163–189.
- Craw RC, Weston P. 1984.** Panbiogeography: a progressive research programme? *Systematic Zoology* **33**: 1–13.
- Craw RC, Grehan JR, Heads MJ. 1999.** *Panbiogeography: Tracking the history of life*. New York: Oxford University Press.
- Crisci JV, Morrone JJ. 1992.** Panbiogeografía y biogeografía cladística: paradigmas actuales de la biogeografía histórica. *Ciencias* **6**: 87–97.
- Croizat L. 1952.** *Manual of Phytogeography*. The Hague, Junk.
- Croizat L. 1958.** *Panbiogeography*. Caracas: Published by the author.
- Croizat L. 1961.** *Principia Botanica*. Caracas: Published by the author.
- Croizat L. 1964.** *Space, Time, Form: The Biological Synthesis*. Caracas: Published by the author.
- Croizat L. 1976.** Biogeografía Analítica y Sintética ("Panbiogeografía") de las Américas. *Biblioteca de la Academia Ciencias Físicas Matemáticas y Naturales* **15**: 1–454.
- Croizat L. 1981.** Biogeography: Past, present, and future. In: Nelson G, Rosen DE, eds. *Vicariance biogeography: A critique*. New York: Columbia University Press, 501–523.
- Darwin C. 1871.** *The origin of species by means of natural selection*. London: John Murray.
- Davis DR. 1994.** Neotropical Tineidae, V: The Tineidae of Cocos Island, Costa Rica (Lepidoptera: Tineoidea). *Proceedings of the Entomological Society of Washington* **96**: 735–748.
- De Marmels J. 2000.** The larva of *Allopetalia pustulosa* Selys, 1873 (Anisoptera: Aeshnidae), with notes on aeshnoid evolution and biogeography. *Odonatologica* **29**: 113–128.
- De Queiroz K. 1987.** Phylogenetic systematics of iguanine lizards: a comparative osteological study. *University of California Publications in Zoology* **118**: 1–203.
- Di Marco G. 1994.** Les terrains accrés du sud du Costa Rica: Evolution tectonostratigraphique de la marge occidentale de la plaque Carabe. *Mémoire de Géologie* **20**: 135–166.
- Dixon JR. 1973.** *Phyllodactylus* Gray: Leaf-toed geckos. In: Powell R, ed. *Catalogue of American Amphibians and Reptiles. American Society of Ichthyologists and Herpetologists* **141**: 1–2.
- Donnelly TW. 1989.** Geologic history of the Caribbean and Central America. In: Bally AW, Palmer AR, eds. *The Geology of North America; an Overview*. Boulder, Colorado: The Geological Society of America.
- Duncan RA, Hargraves RB. 1984.** Plate tectonic evolution of the Caribbean region in the mantle reference frame. *Geological Society of America Memoir* **162**: 81–93.
- Durnham JW. 1985.** Movement of the Caribbean plate and its importance for biogeography in the Caribbean. *Geology* **13**: 123–125.
- Elisens WJ. 1992.** Genetic divergence in *Galvezia* (Scrophulariaceae): evolutionary and biogeographic relationships among South American and Galapagos species. *American Journal of Botany* **79**: 198–206.
- Emerson AE. 1969.** A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera). *American Museum Novitates* **2359**: 1–57.

- Feininger T. 1987.** Allochthonous terranes in the Andes of Ecuador and northwestern Peru. *Canadian Journal of Earth Science* **24**: 266–278.
- Finston TL, Peck SB, Perry RB. 1997.** Population density and dispersal ability in Darwin's darklings: flightless beetles of the Galápagos Islands. *Pan-Pacific Entomologist* **73**: 110–121.
- Frost DR. 1992.** Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (*Iguana*: Tropicuridae). *American Museum Novitates* **3033**: 1–68.
- Gay FJ. 1975.** An Australian species of *Incisitermes* Krishna (Isoptera: Kalotermitidae). *Journal of the Australian Entomological Society* **14**: 395–398.
- Gertsch WJ, Peck SB. 1992.** The pholcid spiders of the Galapagos Islands, Ecuador (Araneae: Pholcidae). *Canadian Journal of Zoology* **70**: 1185–1199.
- Grant PR. 1998.** *Oceanic Islands*. Oxford: Oxford University Press.
- Grehan JR. 1991.** A panbiogeographic perspective for pre-Cretaceous angiosperm-Lepidoptera evolution. *Australian Systematic Botany* **9**: 91–110.
- Grehan JR. 2001.** Panbiogeography from tracks to ocean basins: evolving perspectives. *Journal of Biogeography* **28**: 413–429.
- Grinnell G. 1974.** The rise and fall of Darwin's first theory of transmutation. *Journal of the History of Biology* **7**: 259–273.
- Hauff F, Hoernle K, Schminke H-U, Werner R. 1997.** A mid-Cretaceous origin for the Galapagos hotspot: volcanological, petrological and geochemical evidence from Costa Rican oceanic crustal segments. *Geologische Rundschau* **86**: 141–155.
- Heads M. 1990.** Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *New Zealand Journal of Zoology* **16**: 549–585.
- Heads M. 1999.** Vicariance biogeography and terrane tectonics in the South Pacific: analysis of the genus *Abrotanella* (Compositae). *Biological Journal of the Linnean Society* **67**: 391–432.
- Heywood VH. 1993.** *Flowering Plants of the World*. New York: Oxford University Press.
- Holden JC, Dietz RS. 1972.** Galapagos Gore, NazCoPac Triple Junction and Carnegie/Cocos Ridges. *Nature London* **235**: 266–269.
- Hooker JD. 1851a.** An enumeration of the plants of the Galapagos Archipelago; with descriptions of those which are new. *Transactions of the Linnean Society* **20**: 163–234.
- Hooker JD. 1851b.** On the vegetation of the Galapagos Archipelago, as compared with that of some other tropical islands and of the continent of America. *Transactions of the Linnean Society* **20**: 235–262.
- Irwin DM, Kocher TD, Wilson AC. 1991.** Evolution of the cytochrome b gene of mammals. *Journal of Molecular Evolution* **32**: 128–144.
- Katinas L, Morrone JJ, Crisci JV. 1999.** Track analysis reveals the composite nature of the Andean biota. *Australian Systematic Botany* **47**: 111–130.
- Jackson MH. 1993.** *Galapagos: a natural history*. Calgary: University of Calgary Press.
- Keast A. 1991.** Panbiogeography: Then and now. *Quarterly Review of Biology* **66**: 467–471.
- Kellogg JN, Vega V. 1995.** Tectonic development of Panama, Costa Rica, and the Colombian Andes: Constraints from global positioning system geodetic studies and gravity. *Geological Society Special Paper* **295**: 75–80.
- Kimura G, Sakakibrara M, Okamura M. 1994.** Plumes in central Panthalassa? Deductions from accreted oceanic fragments in Japan. *Tectonics* **13**: 905–916.
- Laj C, Mitouard P, Roperch P, Kissel C, Mourier T, Megard F. 1989.** Paleomagnetic rotations in the coastal areas of Ecuador and northern Peru. In: Kissel C, Laj C, eds. *Paleomagnetic Rotations and Continental Deformation*. Dordrecht: Kluwer Academic Publishers, 489–511.
- Landry B, Rindge FH. 1995.** Additions to the Geometridae (Lepidoptera) of the Galapagos Islands, Ecuador, including a new species of *Eupithecia*. *American Museum Novitates* **3118**: 1–9.
- Lanteri AA. 1992.** Systematics, cladistics and biogeography of a new weevil genus, *Galapaganus* (Coleoptera: Curculionidae) from the Galapagos Islands, and coasts of Ecuador and Perú. *Transactions of the American Entomological Society* **118**: 227–267.
- Lapierre H, Bosch D, Dupuis V, Polvé M, Maury RC, Hernandez J, Monié P, Yeghicheyan D, Jaillard E, Tardy M, Mercier de Lépinay B, Mamberti M, Desmet A, Keller F, Sénebier F. 2000.** Multiple plume events in the genesis of the peri-Caribbean Cretaceous oceanic plateau province. *Journal of Geophysical Research* **105**: 8403–8421.
- Lomize MG, Zakharov VS. 1999.** The global asymmetry of island arc distribution and the breakup of Pangea. *Geotectonics* **33**: 89–101.
- Lopez TJ, Hauselman ED, Maxson LR, Wright JW. 1992.** Preliminary analysis of phylogenetic relationships among Galapagos Island lizards of the genus *Tropidurus*. *Amphibia-Reptilia* **13**: 327–339.
- Lourenço WR. 1998.** Panbiogéographie, les distributions disjointes et le concept de famille relictuelle chez les scorpiens. *Biogeographica* **74**: 133–144.
- Mann P. 1995.** Preface. In: Mann P. ed. *Geologic and tectonic development of the Caribbean plate boundary in southern Central America*. Boulder, Colorado: Geological Society of America Special Paper 295, xi–xxxii.
- Mathis WN, Wirth WW. 1978.** A new genus near *Canaceoides* Cresson, three new species and notes on their classification (Diptera: Canacidae). *Proceedings of the Entomological Society of Washington* **80**: 524–537.
- Mattson PH. 1984.** Caribbean structural breaks and plate movements. *Geological Society of America Memoir* **162**: 131–152.
- Mauffret A, Leroy S. 1997.** Seismic stratigraphy and structure of the Caribbean igneous province. *Tectonophysics* **283**: 61–104.
- Mayr E. 1982.** Vicariance biogeography (review). *Auk* **99**: 618–620.
- Meschede M, Frisch W. 1998.** A plate tectonic model for

- the Mesozoic and early Cenozoic history of the Caribbean plate. *Tectonophysics* **296**: 269–291.
- Meuffels HJG, Grootaert P. 1984.** Dolichopodidae (Diptera) from Papua New Guinea I: The genus *Cymatopus* Kertész with a discussion on *Abatetia* Miller and *Cemocarus* gen. nov. *Indo-Malayan Zoology* **1**: 141–158.
- Mitchell AH, Reading HG. 1969.** Continental margins, geosynclines, and ocean floor spreading. *The Journal of Geology* **77**: 629–646.
- Montgomery H, Pessagno EA, Lewis JF, Schellekens J. 1994.** Paleogeography of Jurassic fragments in the Caribbean. *Tectonics* **13**: 725–732.
- Moore EM. 1998.** Ophiolites, the Sierra Nevada, “Cordillera”, and orogeny along the Pacific and Caribbean margins of North and South America. *International Geology Review* **40**: 40–54.
- Morrone JJ. 1996.** Austral biogeography and relict weevil taxa (Coleoptera: Nemonychidae, Belidae, Brentidae, and Caridae). *Journal of Comparative Biology* **1**: 123–128.
- Morrone JJ, Crisci JV. 1995.** Historical biogeography: Introduction to methods. *Annual Review of Ecology and Systematics* **26**: 373–401.
- Mourier T, Laj C, Megard F, Roperch P, Mitouard P, Farfan MA. 1988.** An accreted continental terrane in north-western Peru. *Earth and Planetary Science Letters* **88**: 182–192.
- Nur A, Ben-Avraham Z. 1977.** Lost Pacifica continent. *Nature London* **270**: 41–43.
- Nur A, Ben-Avraham Z. 1989.** Oceanic plateaus and the Pacific Ocean margins. In: Ben-Avraham Z, ed. *The Evolution of the Pacific Ocean Margins*. Oxford Monograph of Geology and Geophysics 8. Oxford: Clarendon, 7–19.
- Page RDM. 1987.** Graph theory and generalized tracks: quantifying Croizat’s panbiogeography. *Systematic Zoology* **37**: 250–274.
- Peck SB. 1994.** Diversity and zoogeography of the non-oceanic Crustacea of the Galapagos Islands, Ecuador (excluding terrestrial Isopoda). *Canadian Journal of Zoology* **72**: 54–69.
- Peck SB. 1996.** Origin and development of an insect fauna on a remote archipelago: The Galapagos Islands, Ecuador. In: Keast A, Miller SE, eds. *The Origin and Evolution of Pacific Island Biotas, New Guinea to eastern Polynesia: Patterns and Processes*. Amsterdam, The Netherlands: SPB Academic Publishing, 91–122.
- Pindell JL. 1993.** Regional synopsis of Gulf of Mexico and Caribbean evolution. *GCSSEPM Proceedings*, July 1, 1993: 251–274.
- Pindell JL, Barrett SF. 1991.** Geological evolution of the Caribbean region; A plate-tectonic perspective. In: Dengo G, Case JE, eds. *The Caribbean region*. Boulder, Colorado: The Geological Society of America, 405–432.
- Platnick NI. 2000.** The World Spider Catalog, Version 2.0. American Museum of Natural History, available online at <http://research.amnh.org/entomology/spiders/catalog81-87/index.html>
- Porter DM. 1983.** Vascular plants of the Galapagos: Origins and dispersal. In: Bowman RI, Berson M, Leviton AE, eds. *Galapagos Organisms*. San Francisco: AAAS, 33–96.
- Pulawski WJ. 1986.** *Tachysphex peruanus*, a new species related to *Tachysphex galapagensis* Williams (Hymenoptera: Sphecidae). *Pan-Pacific Entomologist* **62**: 95–98.
- Rand DM. 1994.** Thermal habit, metabolic rate and the evolution of mitochondrial DNA. *Trends in Ecology and Evolution* **9**: 125–131.
- Rassmann K. 1997.** Evolutionary age of the Galapagos iguanas predates the age of the present Galápagos islands. *Molecular Phylogenetics and Evolution* **7**: 158–172.
- Révillon S, Hallot E, Arndt NT, Chauvel C, Duncan RA. 2000.** A complex history for the Caribbean plateau: petrology, geochemistry, and geochronology of the Beata Ridge, South Hispaniola. *The Journal of Geology* **108**: 641–661.
- Reynaud C, Jaillard E, Lapierre H, Mamberti M, Mascle GH. 1999.** Oceanic plateau and island arcs of south-western Ecuador: their place in the geodynamic evolution of north-western South America. *Tectonophysics* **307**: 235–254.
- Ridgely RS, Tudor G. 1989.** *The Birds of South America. Volume 1 The Oscine Passerines*. Austin, Texas: University of Texas Press.
- Rieppel O. 1999.** Phylogeny and Paleobiogeography of Triassic Saurpterygia: problems solved and unresolved. *Paleo Geography, Climatology, Ecology* **153**: 1–15.
- Rosen D. 1976.** A vicariance model of Caribbean biogeography. *Systematic Zoology* **24**: 431–464.
- Sallarès V, Dañobeitia JJ. 2001.** Lithospheric structure of the Costa Rican isthmus: effects of subduction zone magmatism on an oceanic plateau. *Journal of Geophysical Research* **106**: 621–643.
- Sato A, Tichy H, O’Huigin C, Grant PR, Grant BR, Klein J. 2001.** On the origin of Darwin’s finches. *Molecular Biology and Evolution* **18**: 299–311.
- Sequiera A, Lanteri AA, Scatagliani MA, Confalonieri V, Farrell B. 2000.** Are flightless *Galapaganus* weevils (Curculionidae: Entiminae) older than the Galápagos Islands that they inhabit? *Biological Journal of the Linnean Society* **85**: 20–29.
- Shields G, Wilson AC. 1987.** Calibration of mitochondrial DNA evolution in geese. *Journal of Molecular Evolution* **24**: 212–217.
- Schilling EE, Panero JL, Eliasson UH. 1994.** Evidence from chloroplast DNA restriction site analysis of the relationships of *Scalesia* (Asteraceae: Heliantheae). *American Journal of Botany* **81**: 248–254.
- Simkin T. 1984.** Geology of the Galápagos Islands. In: Perry R, ed. *Key Environments: Galapagos*. Oxford: Pergamon Press, 15–41.
- Sinton CW, Duncan RA, Storey M, Lewis J, Estrada JJ. 1998.** An oceanic flood basalt province within the Caribbean plate. *Earth and Planetary Science Letters* **155**: 221–235.
- Sites JW, Davis SK, Guerra T, Iverson JB, Snell HL. 1996.** Character congruence and phylogenetic signal in molecular and morphological data sets: a case study in the living iguanas (Squamata, Iguanidae). *Molecular Biology and Evolution* **13**: 1087–1105.
- Smith AD, Lewis C. 1999.** The planet beyond the plume hypothesis. *Earth Science Reviews* **48**: 135–182.

- Stace CA. 1989.** Dispersal versus vicariance – no contest! *Journal of Biogeography* **16**: 201–202.
- Steadman DW, Ray CE. 1982.** The relationships of *Megaryzomys curioi*, an extinct cricetine rodent (Muroidea: Muridae) from the Galápagos Islands, Ecuador. *Smithsonian Contributions to Paleobiology* **51**: 1–23.
- Stockert B, Maresch WV, Bix M, Kaiser C, Toetz A, Kluge R, Kruckhans-Lueder GK. 1995.** Crustal history of Margarita Island (Venezuela) in detail: Constraints on the Caribbean plate-tectonic scenario. *Geology* **23**: 787–790.
- Sutton DA. 1988.** *A revision of the tribe Antirrhineae*. London and Oxford: Oxford University Press.
- Thomas RA. 1997.** Galápagos terrestrial snakes: biogeography and systematics. *Herpetological Natural History* **5**: 19–40.
- Thornton I. 1971.** Darwin's Islands. *A natural history of the Galápagos*. Garden City, New York: The Natural History Press.
- Trewick SA. 2000.** Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *Journal of Biogeography* **27**: 1189–1200.
- Vandel A. 1968.** Isopodes terrestres. In: Leleup N, Lelup J, eds. *Mission Zoologique belge aux isles Galapagos et en Ecuador 1964–1965*. Institut Royal des Sciences Naturalles de Belge, 37–168.
- Van Soest RWM, Hooper JNA. 1993.** Taxonomy, phylogeny and biogeography of the marine sponge genus *Rhabderemia* Topsent, 1890 (Desmospongiae, Poecilosclerida). *Scientia Marina* **57**: 319–351.
- Van Steenis GGGJ, Van Balgooy MMJ. 1966.** Pacific plant areas volume 2. *Blumea Supplement* 5.
- Vincek V, O'Huigin C, Satta Y, Takahata N, Boag PT, Grant PR, Grant BR, Klein J. 1997.** How large was the founding population of Darwin's finches? *Proceedings of the Royal Society of London B* **264**: 111–118.
- Vinton KW. 1951.** Origin of life on the Galapagos Islands. *American Journal of Science* **249**: 356–376.
- Webster JD, Webster JR. 1999.** Skeletons and the genera of sparrows (Emberizinae). *The Auk* **116**: 1054–1074.
- Wendel JF, Albert VA. 1992.** Phylogenetics of the cotton genus (*Gossypium*): character-state weighted parsimony analysis of chloroplast-DNA restriction site data and its systematic and biogeographic implications. *Systematic Botany* **17**: 115–143.
- Wendel JF, Percival AE. 1990.** Molecular divergence in the Galapagos Islands–Baja California species pair, *Gossypium klotzschianum* and *G. davidsonii* (Malvaceae). *Plant Systematics and Evolution* **171**: 99–115.
- Wendel JF, Schnabel A, Seelanan T. 1995.** An unusual ribosomal DNA sequence from *Gossypium gossypoides* reveals ancient, cryptic, intergenomic introgression. *Molecular Phylogenetics and Evolution* **4**: 298–313.
- Weins JJ, Hollingsworth BD. 2000.** War of the iguanas: conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. *Systematic Biology* **49**: 143–159.
- Wyles JS, Sarich VM. 1983.** Are the Galapagos iguanas older than the Galapagos? In: Bowman RI, Berson M, Levington AE, eds. *Patterns of evolution in Galapagos organisms*. San Francisco: AAAS, 177–186.
- Wittmer W. 1984.** Über die gattungen *Ablechrus* Waterh. und *Tucumanius* Pic (Coleoptera, Malachiidae) 37. Beitrag zur Kenntnis der neotropischen Fauna. *Entomologica Brasiliensia* **9**: 226–243.
- Wright JW. 1983.** The evolution and biogeography of the lizards of the Galapagos archipelago: evolutionary genetics of *Phyllodactylus* and *Tropiduris* populations. In: Bowman RI, Berson M, Levington AE, eds. *Patterns of evolution in Galapagos organisms*. San Francisco: AAAS, 123–155.
- Wyles JS, Sarich VM. 1983.** Are the Galapagos iguanas older than the Galapagos? Molecular evolution and colonization models for the archipelago. In: Bowman RI, Berson M, Levington AE, eds. *Patterns of evolution in Galapagos organisms*. San Francisco: AAAS, 177–186.
- Yeakley JA, Weishampel JF. 2000.** Multiple source pools and dispersal barriers for Galápagos plant species distribution. *Ecology* **81**: 893–898.