



COMMENTARY



Colonizing the Caribbean: is the GAARlandia land-bridge hypothesis gaining a foothold?

Understanding how the assemblage of present and recently extinct non-volant terrestrial vertebrates on the Greater Antilles (Cuba, Hispaniola, Jamaica and Puerto Rico; Fig. 1) came to be is one of the most intriguing challenges in biogeography. Until the introduction of plate tectonic theory in the 1960s, explanations were dominated by over-water dispersal (e.g. Darlington, 1938). Critical evidence included the observation that the fauna was conspicuous for its limited high-order taxonomic composition; in a number of cases, those forms that crossed to the islands underwent large adaptive radiations as a consequence of filling an array of vacant niches; South America appears to be their principal source, which is consistent with Caribbean sea-surface flow.

In the 1970s and 1980s, and riding on the back of plate tectonics, vicariance models rose to prominence (e.g. Rosen, 1975). It was argued that during the Late Cretaceous, New World animals were 'trapped' on the Greater Antilles as the proto-Caribbean plate migrated eastwards from a location corresponding to today's southern Central America (Fig. 1b; Rosen, 1975). In the early 1990s, over-water dispersal re-emerged as a result of the then newly developed molecular dating techniques being applied to the Greater Antillean faunas. Key was the discovery that the ancestors of the non-flying vertebrates, particularly the reptiles and amphibians, had arrived at ostensibly random times in the Cenozoic (e.g. Hedges *et al.*, 1992). Furthermore that the endemics were relatively young circumvented the need for these lineages to have survived the direct blast and indirect effects (tsunamis, debris clouds) of the massive Cretaceous–Tertiary boundary-age bolide impact on the nearby Yucatan Peninsula (Fig. 1a).

In 1999, the debate took another twist. Armed with a deep understanding of the Caribbean's geotectonic development, and sceptical of the efficacy of sweepstake colonization, Iturralde-Vinent & MacPhee (1999) introduced a radical explanation: the

mid-Cenozoic GAARlandia (GAAR = Greater Antilles + Aves Ridge) land bridge. They proposed that many of the Greater Antilles' non-volant terrestrial vertebrates were descended from animals that had walked to the archipelago from South America. Colonization was via a quasi-continuous causeway atop the Aves Ridge during a 1–2 Myr interval close to the Eo-Oligocene boundary, *c.* 34 Ma. The proposal has since spurred a passionate discourse (e.g. Graham, 2003; MacPhee & Iturralde-Vinent, 2005; Hedges, 2006; and references therein).

A new paper by Alonso *et al.* (2011) firmly favours GAARlandia. Their phylogenetic investigation of 10 species of the toad genus *Peltophryne* on Cuba, Hispaniola and Puerto Rico indicates that a common ancestor reached the islands *c.* 33 Ma, exactly when the purported land bridge is thought to have existed. On the basis that amphibians are largely (but not exclusively) salt-water intolerant, Alonso *et al.* (2011) argued that they could not have swum/rafted to the Great Antilles, arriving instead via the land bridge.

With the hypothesis receiving a fillip, it is timely to re-appraise GAARlandia. The first step in such a process inevitably involves evaluating the elements underpinning Iturralde-Vinent & MacPhee's (1999) model. From their knowledge of the regional geology, they argued that the Greater Antilles and the broader area experienced a 1–2 Myr period of tectonic uplift around the Eo-Oligocene boundary. Critically, the Aves Ridge (Fig. 1a) is thought to have been involved; the bathymetric high then formed the volcanic arc to the east-advancing Caribbean plate (today the ridge sits *c.* 200 km 'behind' and to the west of the active Lesser Antilles arc, which in turn, relative to North America, South America and the Greater Antilles, is *c.* 1000 km east of its Late Eocene location, see Fig. 1b). Furthermore, the up-forcing coincided with a dramatic sea-level fall due to rapid ice-sheet growth on Antarctica. Thus the combination of tectonic compression and a

lowered global ocean exposed large portions of Aves.

A second aspect that Iturralde-Vinent & MacPhee dwelt upon was the assumed surface-water circulation of the western Atlantic–Caribbean Sea–eastern Pacific during the Late Eocene–Early Oligocene and the Early to Middle Miocene. At both instants, and effectively up until the Late Miocene, they inferred that the regional flows were unsuited for over-water dispersal between South America and the Greater Antilles.

Curiously, the one feature we would anticipate from GAARlandia, namely a spike in terrestrial vertebrate arrivals at the Eo-Oligocene boundary, was never demonstrated by Iturralde-Vinent & MacPhee (1999). Alonso *et al.* (2011) have attempted to rectify this, listing various studies apparently supportive of the land-bridge model. These include investigations of non-volant terrestrial mammals, specifically megalonychid sloths, hystricognath rodents and primates, plus certain frogs, fishes, spiders and plants. However, the significance of some of the data is probably overplayed. For instance, of the listed mammals, the oldest are Early Miocene (*c.* 20 Ma) palaeontological finds, and are thus much younger than GAARlandia. Furthermore, only the rodents exist today, but they have not yet been subjected to molecular-clock dating.

Whilst the *Peltophryne* toad study (Alonso *et al.*, 2011) adds support for GAARlandia, I remain unconvinced about the causeway's role in shaping Greater Antillean biogeography. With a geology–geophysics background, my prime concern is the lack of ocean-floor drilling data demonstrating the extent to which Aves was sub-aerial in the mid-Cenozoic. Insights can, however, be gleaned from active island arcs around the globe, e.g. Marianas–Bonin (Western Pacific), Scotia (South Atlantic), Kermadec–Tonga (south-west Pacific), Sangihe (Molucca Sea), Luzon (western Philippine Sea), as well as the Lesser Antilles. cursory inspection of these archipelagos renders it highly improbable that the Aves

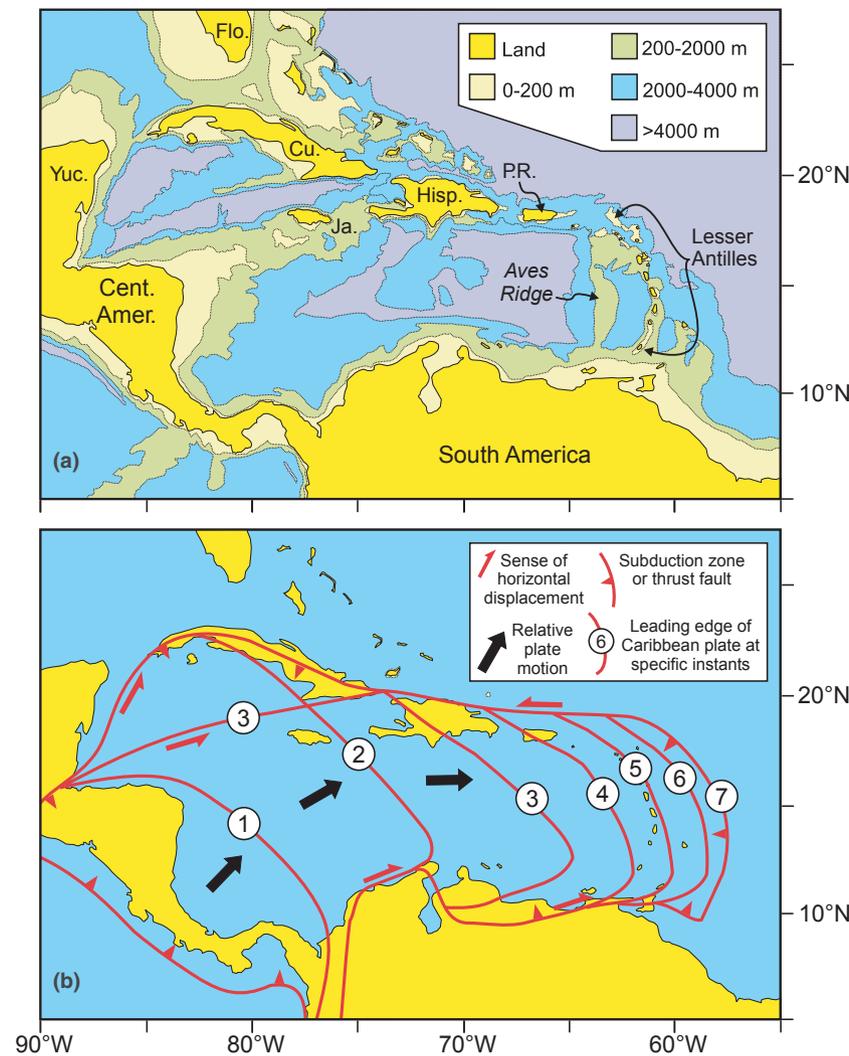


Figure 1 Maps of the Caribbean and adjacent regions showing (a) simplified bathymetry and (b) schematic development of the Caribbean plate during the Late Cretaceous and Cenozoic. Abbreviations: Cu., Cuba; Ja., Jamaica; Hisp., Hispaniola; P.R., Puerto Rico; Yuc., Yucatan Peninsula. Panel (b) depicts the Caribbean plate’s eastward migration relative to North and South America (based on Escalona & Mann, 2011). Solid red lines represent the inferred leading edge of the Caribbean plate during: 1, mid–Late Cretaceous, *c.* 80 Ma; 2, Middle Palaeocene, *c.* 60 Ma; 3, Middle Eocene, *c.* 44 Ma; 4, mid–Oligocene, *c.* 30 Ma; 5, Middle Miocene, *c.* 14 Ma; 6, Early Pliocene, *c.* 5 Ma; and 7, Present.

volcano chain ever formed an unbroken land bridge between South America and the Greater Antilles. None forms anything close to a continuous area of emergent land; even a major sea-level drop associated with a glacial maximum (say *c.* 130 m) would change the patterns only slightly. Indeed, if the system with the closest-spaced islands is used as a guide (curiously, the Lesser Antilles), then the largest gaps were *c.* 60 km, with many others of a similar magnitude. Such an arrangement must have acted as a strong impediment to gene flow along Aves; investigation of the frog *Leptodactylus validus* on northern South America,

Trinidad, Tobago and the southern Lesser Antilles provides a pertinent example (Camargo *et al.*, 2009), as does Henderson’s (2004) wider-ranging snake survey.

Furthermore, and like Hedges (2006), I am sceptical about Iturralde-Vinent & MacPhee’s (1999) inferences regarding Caribbean surface-water currents being incorrectly configured to permit South America–Greater Antilles over-water dispersal. Their assertions concerning land–sea distributions, bathymetry and atmosphere–ocean interactions seem overly simplistic. Moreover, their analysis failed to incorporate computer-based palaeoceanographic

simulations. Thus their original and re-stated view (Iturralde-Vinent & MacPhee, 1999; MacPhee & Iturralde-Vinent, 2005) that sweepstake colonization was highly unlikely is questionable. In fact, ocean–atmosphere modelling for various points in the Cenozoic invariably shows currents flowing from northern South America to the Greater Antilles (e.g. Huber & Caballero, 2003).

Whilst GAARlandia might explain some of the biological data, I contend that the overwhelming majority of terrestrial vertebrates on the Greater Antilles have ancestors that arrived as over-water dispersalists; possibly a small number of forms are relictual (Cuban night lizard, solenodontid mammals: Hedges, 2006). As many others have recognized (e.g. Darlington, 1938; Hedges, 2006), the key question is, why do we not observe in both extant taxa and the fossil record a broad range of orders and families? Instead we see a restricted high-order taxonomic composition, plus at the lower levels several broad adaptive radiations due to species exploiting a wide range of unoccupied niches (e.g. ground sloths, capromyid rodents, eleutherodactyline frogs, and anoline and sphaerodactyline lizards). A second critical point concerns the estimated arrival times not clustering at *c.* 34 Ma (e.g. fig. 6 in Hedges, 2006). To provide perspective, since South America connected with Central and North America *c.* 3 Ma, there has been a massive biotic exchange between the two continents; based on GAARlandia, a not too dissimilar pattern, or at least influx, must be anticipated for the Great Antilles back in the mid-Cenozoic. In conclusion, GAARlandia is a thought-provoking hypothesis, but appreciably more data (geological, biological and to a lesser extent palaeoceanographical) are required before I will be persuaded of its importance in explaining Caribbean biogeography.

JASON R. ALI

Department of Earth Sciences,
University of Hong Kong,
Pokfulam Road, Hong Kong,
China
E-mail: jr.ali@hku.hk

ACKNOWLEDGEMENTS

I thank R.J. Whittaker for inviting me to write this commentary, M. Huber for sharing information, J.C. Aitchison and P. Cunich for reviewing various drafts, and A. de Queiroz and an anonymous referee for their constructive critiques.

REFERENCES

- Alonso, R., Crawford, A.J. & Bermingham, E. (2011) Molecular phylogeny of an endemic radiation of Cuban toads (Bufonidae: Peltophyne) based on mitochondrial and nuclear genes. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2011.02594.x.
- Camargo, A., Heyer, W.R. & de Sá, R.O. (2009) Phylogeography of the frog *Leptodactylus validus* (Amphibia: Anura): patterns and timing of colonization events in the Lesser Antilles. *Molecular Phylogenetics and Evolution*, **53**, 571–579.
- Darlington, P.J. (1938) Origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. *The Quarterly Review of Biology*, **13**, 274–300.
- Escalona, A. & Mann, P. (2011) Tectonics, basin subsidence mechanisms, and paleogeography of the Caribbean-South American plate boundary zone. *Marine and Petroleum Geology*, **28**, 8–39.
- Graham, A. (2003) Geohistory models and Cenozoic paleoenvironments of the Caribbean region. *Systematic Botany*, **28**, 378–386.
- Hedges, S.B. (2006) Paleogeography of the Antilles and the origin of West Indian terrestrial vertebrates. *Annals of the Missouri Botanical Garden*, **93**, 231–244.
- Hedges, S.B., Hass, C.A. & Maxson, L.R. (1992) Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proceedings of the National Academy of Sciences USA*, **89**, 1909–1913.
- Henderson, R.W. (2004) Lesser Antillean snake faunas: distribution, ecology, and conservation. *Oryx*, **38**, 311–320.
- Huber, M. & Caballero, R. (2003) Eocene El Niño: evidence for robust tropical dynamics in the “hothouse”. *Science*, **299**, 877–881.
- Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, **238**, 1–95.
- MacPhee, R.D.E. & Iturralde-Vinent, M.A. (2005) The interpretation of Caribbean paleogeography: reply to Hedges. *Proceedings of the International Symposium on Insular Vertebrate Evolution: the Palaeontological Approach* (ed. by J.A. Alcover and P. Bover), *Monografies de la Societat d'Història Natural de les Balears*, **12**, 175–184.
- Rosen, D.E. (1975) A vicariance model of Caribbean biogeography. *Systematic Zoology*, **24**, 431–464.

Editor: John Lamshead