



Paleogeography of the Aves Ridge and its potential role as a bio-colonization pathway linking South America and the Greater Antilles in the mid-Cenozoic

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ARTICLE INFO

Keywords:

Aves Ridge
Biogeography
Dispersal
Island-hopping
GAARlandia
Paleogeography

ABSTRACT

The Aves Ridge in the eastern Caribbean Sea is thought by many to have operated as a short-lived, mid-Cenozoic, dry-land path that was used by the ancestors of a number of South America-derived faunal groups to colonize the Greater Antilles. The idea is, however, contentious and has triggered much debate. Here, we review the various models, notably *GAARlandia*, focusing on mechanisms to account for the emergence of the Aves Ridge causeway, the time window over which it operated, where along northern South America its southern end abutted, and its portrayal in written descriptions and on maps. In response to perceived weaknesses, a new paleogeographical scenario is presented, which draws upon a sizeable body of literature including several recent publications. We suggest that from the start of the Late Middle Eocene (41.2 Mya) through to the late Early Miocene (c. 17 Mya) the Aves Ridge's crest was topped with scattered carbonate platforms and coral atolls, but these were separated from one another by 30- to 70-km-wide gaps. During this interval we find no support for high-elevation islands, with their accompanying diverse habitats. Instead, suggested analogues for what we term the 'Aves Ridge Reef Belt' are flat, atoll-like islands with limited ecospace such as those currently in the southeast Bahama Banks (western North Atlantic) and the Spratly Islands (southern South China Sea). We also address the likelihood of 'stepping-stone' colonization whereby taxa are thought to advance from a source continent to a remote landmass or archipelago via a suite of closely-spaced islands. We argue that the mechanism has a much lower probability compared with direct (over-water) dispersal, and that it played no appreciable part in seeding the Greater Antillean land-vertebrate assemblages, either via the Aves Ridge or the nearby Lesser Antilles chain. We show that phylogenies of living species support direct dispersal rather than stepping-stone transfer.

1. Introduction

Over the last three decades, one of the most discussed ideas in Caribbean biogeography concerns the role of a postulated short-lived causeway ("GAARlandia") that in the middle Cenozoic supposedly connected northern South America with the Greater Antillean islands of Puerto Rico, Hispaniola, and Cuba (the fourth major landmass in the group, Jamaica, was then thought to have been isolated by a deep-water strait). The 850- to 900-km-long pathway ran along the spine of the Aves Ridge (Fig. 1), which today is almost completely submerged beneath the waters of the eastern Caribbean Sea. In a series of publications, Manuel Iturralde-Vinent and Ross MacPhee called upon the hypothesized route to explain the colonizations that had been made by three extant or

recently-extirpated land-mammal lineages (MacPhee and Iturralde-Vinent, 1995, 2000) whose fossilized ancestors had been recovered from Lower Oligocene deposits on Puerto Rico (megalonychid sloths) and a Lower Miocene formation on Cuba (capromyid rodents, megalonychid sloths, and pitheciine primates) (see Table 1 in MacPhee and Iturralde-Vinent, 1995). At this juncture, it should be observed that the Greater Antilles' post-Eocene land-mammal assemblage comprises just five other clades, and that detailed understanding of these has largely emerged only in the last half decade. Specifically, these are (i) a chinchilloid rodent from Puerto Rico, (ii) a geomyoid rodent from Puerto Rico, (iii) a group of nesophontid insectivores on multiple islands, (iv) a pitheciine primate from Jamaica, and (v) a sigmodontine rodent from Jamaica. However, only the first has any bearing on the Aves Ridge

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<https://doi.org/10.1016/j.earscirev.2024.104823>

Received 7 February 2024; Received in revised form 13 May 2024; Accepted 27 May 2024

Available online 28 May 2024

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proposal due to it having South American origins (Marivaux et al., 2020). The second and the third crossed from North America/Central America (Springer et al., 2018; Marivaux et al., 2021). The monkey is exclusive to Jamaica (the ‘separate landmass’), plus associated molecular-clock data (Woods et al., 2018) yield a 14.9–0 Mya colonization age, which post-dates the theorized conduit. The rice rat was derived from Central America, it was present on Jamaica, and its Pleistocene arrival also renders it too young (Morgan, 1993; Percequillo et al., 2021).

Three other factors underpinned Iturralde-Vinent and MacPhee’s proposal, and these featured prominently in the early versions of its outlining. The book chapter by Holcombe and Edgar (1990) was important because a number of submarine highs along the Aves Ridge that are now at about 1-km water depths were deemed to have been close to sea level in the mid-Cenozoic. This was based on the recovery of shallow-marine accumulations in a number of dredge-haul samples. Second, the geological records of Puerto Rico, Hispaniola, and Cuba suggested that each island had only been continuously emergent since the start of the Late Eocene (see Iturralde-Vinent and MacPhee, 1999), and this placed an older limit on when the ancestors of the land-mammal clades could have arrived; after 37.7 Mya based on Walker and Geissman (2022). Third, over-water dispersal was excluded from having been involved in the colonizations because of the apparent lack of Middle Miocene-Recent faunal arrivals, that is, they had all taken place in the mid-Cenozoic. This temporal pattern was attributed to the regional surface-water currents for much of the Cenozoic being configured such that the Greater Antilles were unreachable to any South American land-mammals that found themselves adrift in the Caribbean Sea (e.g. Iturralde-Vinent and MacPhee, 1999; MacPhee and Iturralde-Vinent, 2005). As a consequence, passage to the island group via a landbridge was presented as the default explanation.

On several occasions we have questioned various biological and geological aspects of the Aves Ridge routeway proposal (Hedges, 1996a, 1996b, 2001, 2006; Ali, 2012; Ali and Hedges, 2021). A major issue impeding discussion stems from irregularities/ambiguities with elements of its definition in a suite of publications dating back to the

mid-1990s: MacPhee and Iturralde-Vinent (1994, 1995, 2000, 2005); Iturralde-Vinent and MacPhee (1999, 2023); Iturralde-Vinent (2004–5, 2006). Specifically, these concern (i) the different geophysical processes that account for it becoming sub-aerial, (ii) the period of emergence, (iii) where along the margin of South America the Aves Ridge’s southern tip was connected, and (iv) conflicts between how the model has been described in written statements and portrayed on maps. Our review examines each of these and follows with the presentation of a new paleogeographical model for the Aves Ridge and surrounding areas. Finally, we assess the practicalities of ‘stepping-stone’ colonization using phylogenetic data from extant taxa on the Greater Antilles and Lesser Antilles, and through hypothetical probabilistic scenarios. First, though, we summarize the Holcombe and Edgar (1990) publication, which appears to have underpinned the thesis of Iturralde-Vinent and MacPhee.

2. The publication of Holcombe and Edgar (1990)

Holcombe and Edgar (1990) were the first to argue, at least based on direct geological evidence, that the Aves Ridge (a remnant arc, e.g. Westbrook et al., 1984; Bouysse, 1988) was in the Cenozoic dotted with islands and these could have enabled land-locked mammals on the Greater Antilles to have crossed from South America. Their proposal arose following a detailed appraisal of dredge-sample data from various parts of the physiographic high that had been reported by Fox et al. (1971), Marlowe (1971), Nagle (1972) and Bouysse et al. (1985), which they integrated with the tectonic-plate model of Pindell et al. (1988). Through their compilation, they showed that in the Middle Eocene through Early Miocene a number of locations along the ridge that are now at 800–1200 m water-depths (on the Papagayo Seamount, Golondrina Seamount, Halcon Ridge, Alcatraz Seamount, Pelicano Seamount, Flamenco Ridge, Los Hermanos Spur, and the La Blanquilla High; Figs. 2 and 3, and Table 1) were formerly close to sea level based upon the recovery of coastal or neritic sedimentary material. In exploring the data’s significance, they argued that mammals from South America might have used the buildups to cross to the Greater Antilles, in the

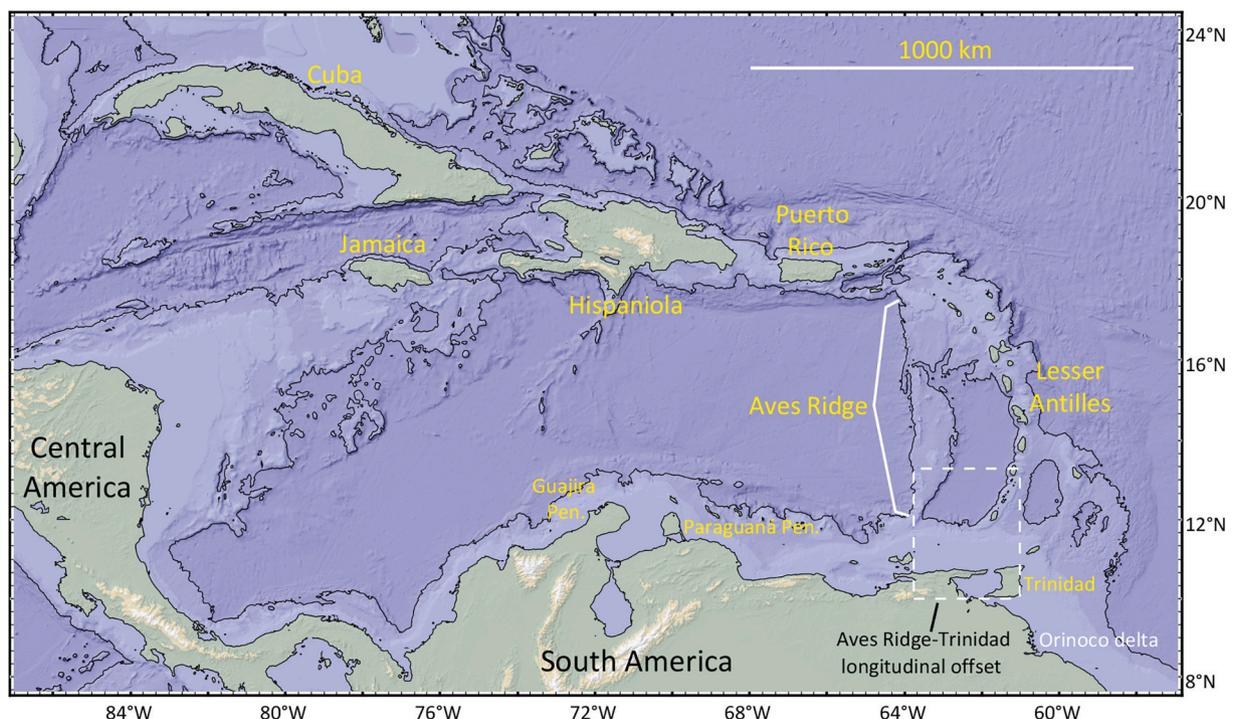


Fig. 1. Map of the Caribbean region showing the important geographical features. The base image was generated using GeoMapApp (Ryan et al., 2009). To provide insight on the bathymetry, the 2000-m isobath is also depicted.

Table 1
Details of the various sampling locations that are displayed in Fig. 3 (see text for details).

Holcombe and Edgar (1990) compilation				
Lat. (°N)	Long. (°)	Study	Study ref.	Sediment age
15.517	-64.050	Bouysse et al. (1985)	112D	Late Cret. + Middle Eocene + Late Eocene
15.000	-63.417	Nagle (1972)	None	Oligocene
14.200	-63.583	Bouysse et al. (1985)	109D	Middle Eocene
13.567	-62.950	Fox et al. (1971)	5	Middle Eocene + Late Eocene
13.550	-62.967	Fox et al. (1971)	3	Middle Eocene + Late Eocene
13.533	-63.133	Bouysse et al. (1985)	108D	Middle Eocene + Oligocene + Early Miocene
13.517	-62.983	Fox et al. (1971)	4	Early Miocene
13.500	-63.167	Marlowe (1971)	None	Oligocene + Early Miocene
13.383	-63.167	Perfit (unpubl.)	None	Eocene
13.117	-63.400	Fox et al. (1971)	9	Late Eocene
12.967	-63.600	Fox et al. (1971)	8	Early Miocene
12.967	-63.483	Fox et al. (1971)	6	Late Eocene
12.833	-63.533	Bouysse et al. (1985)	106D	Middle Eocene + Oligocene + Early Miocene
12.500	-63.500	Fox et al. (1971)	14	Early Miocene
12.117	-64.067	Nagle (1972)	17	Middle Eocene
Garroccq et al. (2021)				
Lat. (°N)	Long. (°)		Study ref.	Sediment age
14.727	-62.790		DR-GA-05-01	early Early Miocene
14.564	-62.790		DR-GA-06-02	early Early Miocene
14.529	-62.773		DR-GA-06-01	early Early Miocene
13.645	-62.936		DR-GA-10-01	early Early Miocene
13.105	-62.913		DR-GA-08-02	Late Middle Eocene to Late Eocene + early Early Miocene
12.959	-63.035		DR-GA-07-02	early Early Miocene
Church and Allison (2004) Saba Bank borehole				
Lat. (°N)	Long. (°)		Study ref.	Sediment age
17.289	-63.427		SB1	Middle Eocene to Late Eocene

process quoting Woods (1990; see below). However, inspection of the 15 relevant records from the 17 that Holcombe and Edgar (1990) listed in their Table 2 (one dredge-haul sample site from the Beata Ridge and a second from the Grenada Basin are the two that were omitted), indicates that none was proximate to an elevated landmass as evidenced by the lack of true terrigenous material, in particular volcanic detritus or coarse-grained clastics. Instead, deposition appears to have been on or close to atoll tops and carbonate mounds. It should also be observed that the footprints of each of the bathymetric highs would produce islands that were generally smaller than those of the modern-day Lesser Antilles, with the gaps between neighbouring bodies typically 30 to 70 km (Fig. 6 in Holcombe and Edgar, 1990; Fig. 2). They also mulled the possibility that Aves Ridge formed a continuous dry-land pathway, which required the sea floor down to about 2000 m to have been exposed. However, support for this was based on a single borehole

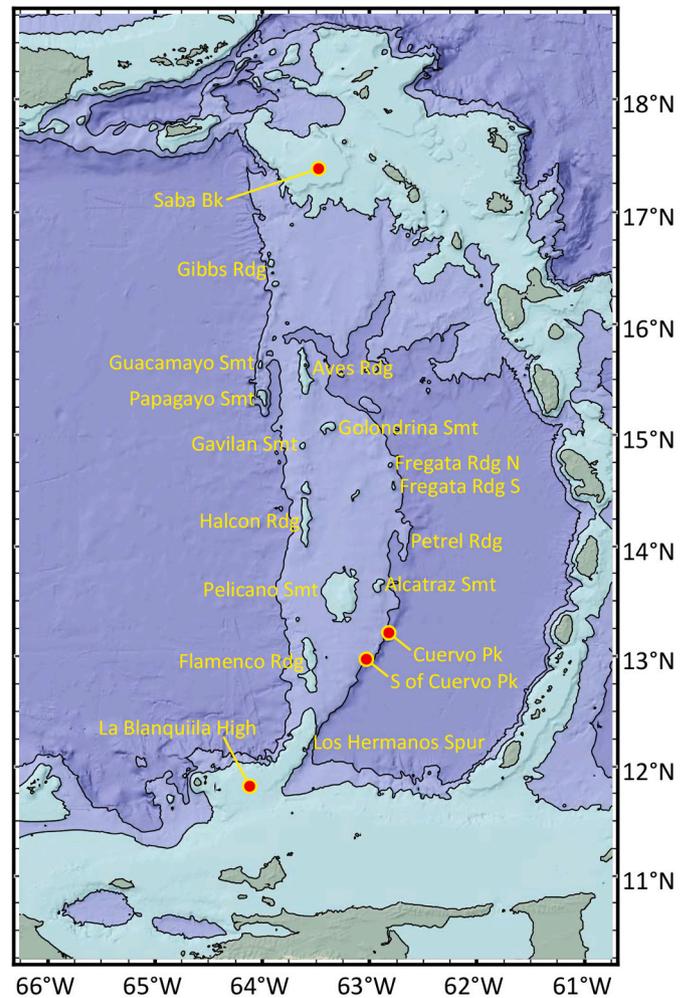


Fig. 2. Map of the Aves Ridge showing the key bathymetric highs. The base image was generated using GeoMapApp (Ryan et al., 2009). The labels are from Bouysse et al. (1985), but only a few of them are formally recognized and listed in the GEBCO Atlas (www.gebco.net).

record (SB1) from the Saba Bank towards the northern end of the sea-floor high (Bouysse et al., 1985; Figs. 2 and 3), specifically reef limestones from within a 934-m-thick Middle to Upper Eocene unit, the top of which is now at c. 1922 m below sea-level (and 1831 m below the sea floor; see Church and Allison, 2004). This signified that substantial subsidence had taken place, but the notion that it might apply to the whole of the Aves Ridge was pure speculation. Notably, the recent work by Cornée et al. (2021; see below) has falsified the suggestion.

The Caribbean-mammal specialist Charles Woods (1990) also considered the potential for the Aves Ridge providing a South America-Greater Antilles colonization path (alongside the Beata Ridge and the Lesser Antilles). Referencing Holcombe and Moore (1977) and Holcombe and Edgar (1990), he concluded that several highs were likely emergent in the Eocene through Middle Miocene. However, the two subsidence scenarios he explored, involving 600 m and 1000 m downshifts of the seabed, resulted in stepping-stone chains with numerous gaps, some >100 km (125 km and 250 km).

3. Inconsistencies/ambiguities with various aspects of the GAARlandia proposals

3.1. Geophysical processes invoked to explain the Aves Ridge's emergence

The geophysical processes that have been called upon by Iturralde-

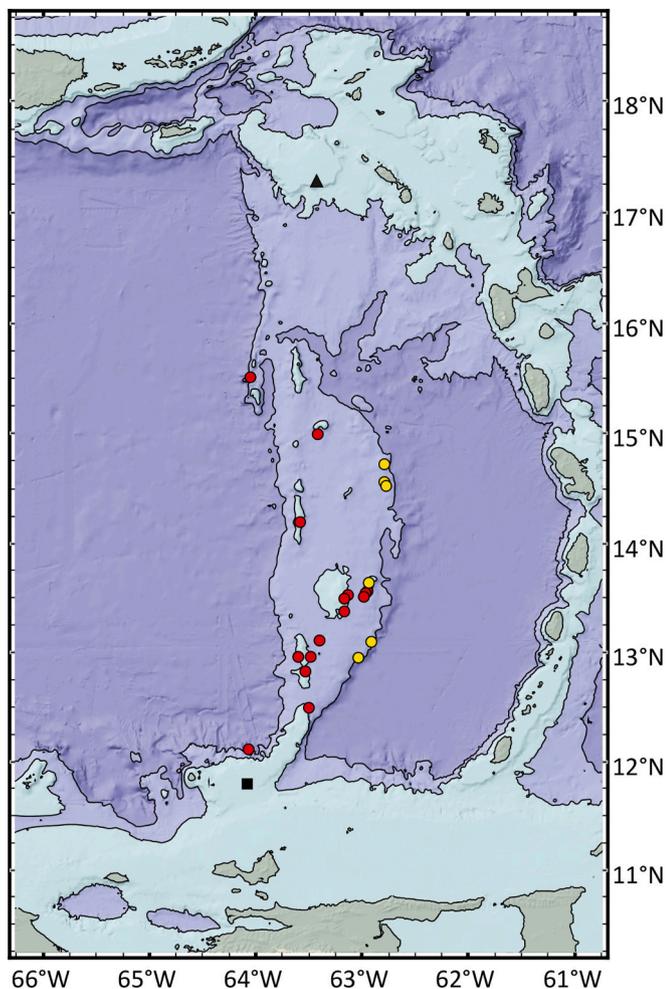


Fig. 3. Map of the Aves Ridge showing important study sites. The base image was generated using *GeoMapApp* (Ryan et al., 2009). Table 1 provides details on the various locations. Red and yellow circles are dredge-sample locations where coastal or neritic sedimentary rocks were recovered and reported in the compilation of Holcombe and Edgar (1990) or by Garroq et al. (2021). The position of the SB1 borehole into the Saba Bank is shown by the black triangle. The black square on the La Blanquilla High indicates the area where a seismic line in Clark et al. (2008) is interpreted as having Cretaceous-age basement that is unconformably overlain by Middle Miocene sediments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Vinent and MacPhee to explain the Aves Ridge's emergence have not always been the same. In their first publication (MacPhee and Iturralde-Vinent, 1994), uplift of the Aves Ridge alongside a major fall in sea level were cited. The mechanism for the former was thought to be related to arc-splitting, a tectonic process that is associated with many of the marginal basins that are found in and adjacent to the western Pacific Ocean (e.g. Karig, 1974; Clift, 1995). The idea was that subduction-related magmatism along the Aves Arc at the eastern edge of the Caribbean plate continued until the Late Eocene (n.b., today, it is widely accepted that magmatism terminated in the Late Paleocene, e.g. Aitken et al., 2011; Garroq et al., 2021; Allen et al., 2019). This was followed by arc splitting with the Aves Ridge becoming the remnant arc and the Lesser Antilles the active arc with the Grenada (back-arc) Basin developing to fill the intervening space. The breakup was thought to have caused the Aves Ridge to rise, although the driving mechanism was not stated. Crucially, arc splitting per se would have led to subsidence due to the arc crust being thinned that in turn would reduce its buoyancy. Hence, a substantial input of heat would be required to account for the

upward vertical motion, which would cause an expansion of the crust and thus induce its raising. The second element involved a supposed c. 160 m fall in sea-level at the Early/Late Oligocene boundary that Haq et al. (1987) had reported. Together, the two processes produced “continuous land or groups of very closely spaced islands from western Cuba through to northern South America.” Termination of the routeway was thought to result from rising sea levels in the Late Oligocene. Revising the various dates to the time-scale of Walker and Geissman (2022) results in a window of opening of c. 37.7 to 27.8 Mya.

Within 13 months, MacPhee and Iturralde-Vinent (1995) had re-tooled their original hypothesis plus they introduced ‘GAARlandia’ as a label for their landspan. Interestingly, uplift of the Aves Ridge related to arc-splitting was not mentioned nor even inferred. Furthermore, the sea level fall at the Early/Late Oligocene boundary was dismissed because the conduit's termination was regarded as too young due to it conflicting with the paleontological data (MacPhee and Iturralde-Vinent, 1995, pp. 19–20). Instead, the ridge's exposure was now deemed to result solely from regional uplift as the Caribbean Plate was forced between the west-migrating North American and South American plates. The primary evidence was the widespread occurrence of Upper Eocene-Lower Miocene conglomerates on Cuba, Hispaniola and Puerto Rico (Fig. 10 in MacPhee and Iturralde-Vinent, 1995), signifying ground raising and concomitant erosion. Additionally, the apparent lack of Oligocene accumulations on the Aves Ridge deduced from the dredge-sampling study of Fox et al. (1971), i.e. negative evidence, was taken to indicate its sub-aerial exposure. In building their argument, MacPhee & Iturralde-Vinent (1995 p. 18) emphasized “worldwide Pyrenean phase of tectogenesis”. The term ‘tectogenesis’, which is today largely redundant, refers to regionally-developed deformation structures (see Aubouin, 1965) that are associated with ‘geosyncline’ theory (e.g., Haarmann, 1930; Longwell, 1945; Belousov, 1961), the now-defunct framework for viewing Earth's dynamic outer shell. Importantly, the notion of linking similar-age orogenic belts that are separated by two or more plate boundaries, as is the case with the Caribbean and Pyrenean systems, is something most modern geoscientists would reject; they are nothing more than temporal coincidences.

Unlike their two previous publications, which were concerned primarily with the presentation of palaeontological information, Iturralde-Vinent and MacPhee (1999) focused instead on the Caribbean's geographical development. Again, the “Pyrenean phase” of regional uplift was central. Furthermore, they latched upon a major global sea-level fall at the Eocene-Oligocene boundary that Miller et al. (1996) had identified that was explained by the rapid build-up of large-scale ice sheets on Antarctica. Incidentally, the more recent work by Miller et al. (2024) shows that this shift was close to 80 m, from around +72 m to –8 m with respect to the present datum (Fig. 4). Concerning the tectonic component, Iturralde-Vinent & MacPhee (pp. 28–30), drew attention to the many stratigraphic sections from across the region that lacked Upper Eocene-Lower Oligocene marine deposits. In their place were either sedimentary hiatuses, or red-bed packages, including coarse-grained conglomerates. However, there was no detailed documentation of structural evidence (i.e. thrusts, reverse faults, folds, angular discordances etc.) that might convincingly support the idea of tectonic uplift. Therefore, the sedimentary record could simply reflect the downward eustatic shift that triggered widespread erosion (see De Lira Mota et al., 2023). Alternatively, the sediment shedding could be a more localized phenomenon and related to strike-slip faulting (Burke et al., 1984; Stephan et al., 1990), with deposition in pull-apart basins, as the Caribbean plate moved eastwards relative to North America shortly before as well as subsequent to Cuba's docking with Florida and the Bahama Banks.

Later outputs in the twenty-noughties (MacPhee and Iturralde-Vinent, 2000, 2005, and Iturralde-Vinent, 2004–5, Iturralde-Vinent, 2006) reiterated the idea. However, after a nearly two-decade break Iturralde-Vinent and MacPhee (2023) re-joined the debate, incorporating ideas that had been presented by Church and Allison (2004), Sawyer and Mann (2004), Clark et al. (2008), Philippon et al. (2020),

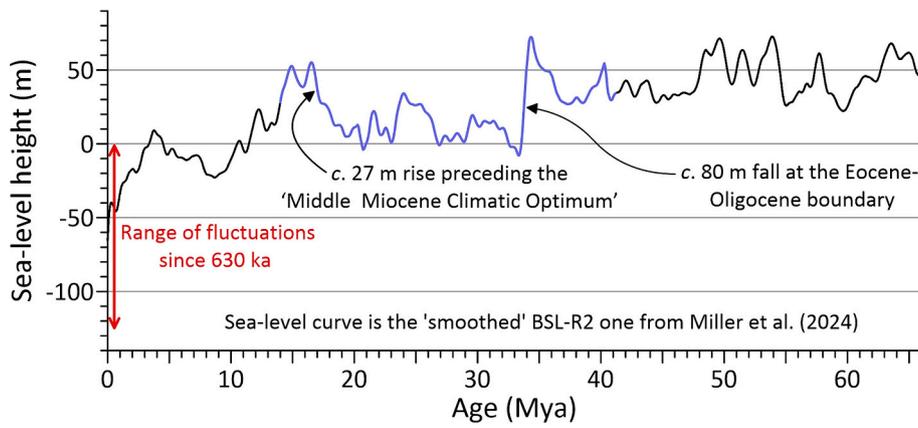


Fig. 4. Global sea-level record spanning the start of the late Middle Eocene (41.2 Mya) to end of the Early Miocene (16.0 Mya) based on Miller et al. (2024). For reference, also shown are the extremes in eustatic fluctuations that have taken place over the last 630 kya (e.g. Bintanja et al. (2005).

Cerpa et al. (2021), Escalona and Mann (2011), Garroq et al. (2021) and Padron et al. (2021), plus responding to critical commentaries by Ali (2012) and Ali and Hedges (2021). Notably, Iturralde-Vinent and MacPhee (2023) refuted some of the interpretations of the seismic stratigraphy that had been made by Garroq et al. (2021), suggesting instead that the shallower parts of the Aves Ridge, for instance along profile BOL-30 where it crosses the southern end of the Flamenco Ridge (Fig. 2) were sub-aerial prior to the start of the Miocene. Based on Church and Allison (2004), they also argued for the Saba Bank being exposed

between the Cretaceous and Pliocene; Cornée et al. (2021) provides a more nuanced vertical-motion history of the massif and nearby areas, which is summarized below in a section on recent studies. Iturralde-Vinent and MacPhee (2023) also cited Clark et al. (2008), who argued that the La Blanquilla High (Figs. 2 and 3) has a Cretaceous basement that is overlain unconformably by Middle Miocene and younger deposits, implying a protracted period of emergence. Interestingly, however, no mention was made of the major global sea-level fall at the Eocene–Oligocene boundary (Fig. 4; Miller et al., 2020; De Lira Mota

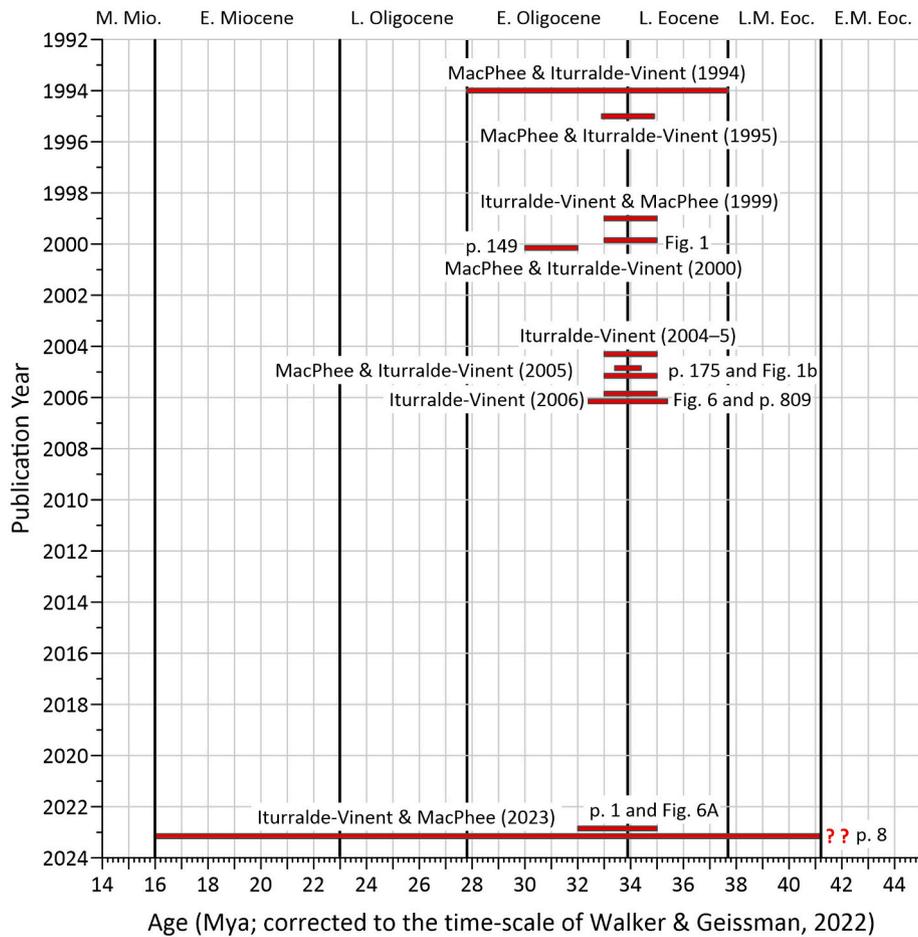


Fig. 5. Aves Ridge emergence periods according to different publications by Ross MacPhee and Manuel Iturralde-Vinent. Due to refinements in the geological time-scale, the ages have been corrected to Walker and Geissman (2022). For instance, MacPhee & Manuel Iturralde-Vinent (1994) drew upon the one in Haq et al. (1987), where the Eocene-Oligocene boundary was set at 36.0 Mya; today, its numerical age is 33.9 Mya.

et al., 2023; see also Miller et al., 2024).

3.2. Period of emergence of the Aves Ridge

The second concern regarding the Aves Ridge hypothesis arises from the vagaries of the interval over which the feature was purportedly emergent (acknowledging changes to the various applied geological time-scales, for instance Haq et al., 1987, as compared to Walker and Geissman, 2022). Although the general perception is for the route to have operated for a 2–3 Myr period around the Eo-Oligocene boundary (for some time this has been dated as 33.9 Mya; Luterbacher et al., 2004; Walker and Geissman, 2022), inspection of the various associated publications indicates that this was not the case. The first paper (MacPhee and Iturralde-Vinent, 1994) had the pathway open for c. 10 Myr (Fig. 5). Furthermore, from the Year 2000 onwards all but one of the associated works (i.e. Iturralde-Vinent, 2004–5) made internally contradictory statements on the matter (Fig. 5). For example, Fig. 1 in MacPhee and Iturralde-Vinent (2000) used 35–33 Mya, whereas the text on p. 149 gives a window of 32–30 Mya; MacPhee and Iturralde-Vinent (2005) mentioned a 1 Myr duration on p. 175, but 35–33 Mya was shown on

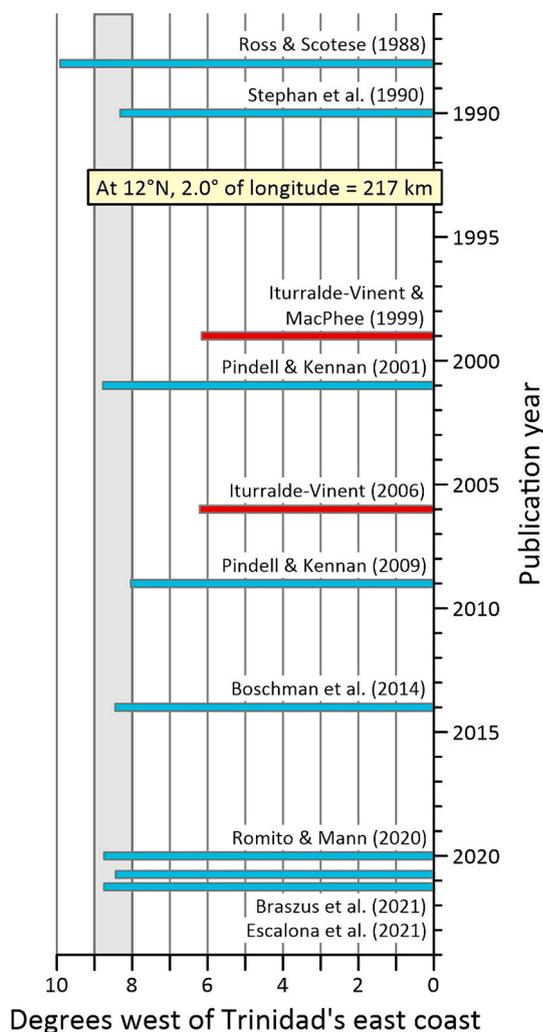


Fig. 6. Angular longitudinal offset between the Aves Ridge's southern end and the eastern coast of Trinidad Island in various plate tectonic/paleogeographical reconstructions (Fig. 1). This is for the Eocene-Oligocene boundary (33.9 Mya), and in some cases the values have been calculated using age-based interpolations/extrapolations. Concerning the Trinidad marker, the 'busy' part of the Orinoco delta a short distance to the south is a useful support guide (see Fig. 1).

Fig. 1b. Curiously, the most recent publication (Iturralde-Vinent and MacPhee, 2023) has in the caption to Fig. 6A the landspan dating from 35 to 32 Mya, which tallies with statements made in their abstract on p. 1 ("Here we reaffirm that GAARlandia was exposed above sea level between late Eocene and early Oligocene"). However, on p. 8 they declare that "... the Aves ridgecrest, including the Saba Bank and La Blanquilla High, was a structural high, and most probably land, during middle Eocene-early Miocene times." Based on their Fig. 6 (A and B), plus other statements in the text, we interpret this to mean from the start of the Late Middle Eocene (41.2 Mya) through to the end of the Early Miocene (16.0 Mya), that is, >25 Myr.

3.3. Placement of Aves Ridge's southern end against South America

A third issue with the Aves Ridge proposals concerns the positioning of the pathway's southern end against northern South America; we suggest that it is too far to the east by at least 200 km (details below). To demonstrate this, we make use of two geographical reference markers, one on the western side of the Aves Ridge close to where the La Blanquilla High and the Los Hermanos Spur meet (Figs. 2 and 3), the other on the N–S aligned coastline of eastern Trinidad. With Iturralde-Vinent and MacPhee (1999) and Iturralde-Vinent (2006) the angular longitudinal separation is c. 6.2° (Fig. 6; estimated to two decimal places, reported to one; unfortunately, an estimation cannot be made for Iturralde-Vinent and MacPhee, 2023, because the relevant map lacks latitude and longitude markers). However, in a series of publications by other workers spanning 30-plus years the separations ranged from 8.0° to 8.8° (note that some of the values are age-based interpolations/extrapolations to the age of the Eocene-Oligocene boundary, 33.9 Mya). The specific offsets are: Stephan et al. (1990): 8.3°; Pindell and Kennan (2001): 8.8°; (2009): 8.0°; Boschman et al. (2014): 8.5°; Romito and Mann (2020): 8.8°; Braszus et al. (2021): 8.8°; Escalona et al. (2021): 8.4°; even greater is Ross and Scotese (1988): 9.9°. Furthermore, Meschede and Frisch (1998), Mann (1999), and Müller et al. (1999) concur, although it is not possible to extract angular values because their charts either lack latitude-longitude ticks, or they do not extend far enough east to include Trinidad. The 1.8° to 2.6° discrepancy (at 12°N, a difference of between 196 and 283 km respectively) is significant because a number of the studies indicate that the more westerly connection area on South America, which is close to the Paraguayan Peninsula (Fig. 1), had complex land-sea patterns due to the sub-region then being tectonically active (e.g., Stephan et al., 1990; Pindell and Kennan, 2001, 2009; Escalona and Mann, 2011; Romito and Mann, 2020; Escalona et al., 2021).

3.4. Geographical configuration of the Aves Ridge pathway

The fourth area of confusion arises from written proclamations on, and pictorial representations of the Aves Ridge pathway's geographical configuration. In several publications, Iturralde-Vinent and MacPhee were careful to state that the route comprised either a completely connected path or one with closely spaced islands, or words to that effect (e.g. MacPhee and Iturralde-Vinent, 1994, p. 8; MacPhee and Iturralde-Vinent, 1995, p. 18; MacPhee and Iturralde-Vinent, 2000 p. 149; Iturralde-Vinent and MacPhee, 1999 p. 31). Indeed, the most recent publication takes this even further by backing away from the ridge forming a simple continuous causeway: "Whatever the fine details of its subaerial history, Aves Ridge operated as a filter, not as a wide-open corridor for the unimpeded dispersion of land biota of all kinds from South America into the Greater Antilles." The problem, though, is that each of the paleogeographical maps they have published has always depicted the routeway as fully emergent (MacPhee and Iturralde-Vinent, 2000, Fig. 1; MacPhee and Iturralde-Vinent, 2005, Fig. 1B; Iturralde-Vinent and MacPhee, 1999 Fig. 6; Iturralde-Vinent and MacPhee, 2023, Fig. 6; Iturralde-Vinent, 2004–5, Fig. 8; Iturralde-Vinent, 2006, Fig. 6); only in the caption for the 1999 publication is there any indication that it might

have contained gaps.

4. Insights from recent investigations

The recent studies by Cornée et al. (2021), Garroq et al. (2021), and Tejada et al. (2024) provide key insights into the Aves Ridge's development. The first focused on the Saba Bank-northern Lesser Antilles, while the second was concerned with Grenada Basin and the eastern Aves Ridge, with both integrating information from numerous seismic lines and large geological datasets. Tejada et al. (2024) integrated information from those two studies in particular to produce a paleogeographic model.

Fig. 16 in Cornée et al. (2021) comprises temporal snapshots that summarize the sub-region's geophysical evolution. From the start of the Late Middle Eocene (41.2 Mya) through to the end of the Early Miocene (16 Mya) the Saba Bank was fully emergent. It was then deep marine ($\geq 200\text{-m}$ -water depths) until c. 5 Mya (Middle Miocene to early Pliocene) before acting as a shallow-water carbonate platform through to the present. Importantly, however, throughout this 40-plus million-year interval the adjoining parts of the Aves Ridge to the south were always deep marine.

As part of their presentation, Garroq et al. (2021) argued, based on Wright and Wyld (2011), that the Aves Ridge formed an active arc at the eastern edge of the Caribbean Plate from c. 75 Mya up until c. 59 Mya. Arc-splitting and the opening up of the Grenada Basin, with the subduction system below migrating eastwards with the Lesser Antilles, was followed by subsidence along the Aves Ridge remnant arc. However, during the Eocene through Early Miocene the sinking rates were subdued and this allowed carbonate platforms to establish and persist atop of a number of scattered basement highs (Figs. 2 and 3; Fregata Ridge, Petrel Ridge, Alcatraz Seamount, Pelicano Seamount, Cuervo Peak). However, by the Middle Miocene the downward rates of movement had increased to the point where the atolls were pulled beneath the photic zone and subsequently drowned. Incidentally, at c. 17 Mya (late Early Miocene) there was a rapid 15- to 27-m raising of global sea-level that preceded the Mid-Miocene Climatic Optimum (Fig. 4; Rohling et al., 2022; Miller et al., 2024). As will be seen below, we suggest it played a significant part in terminating the reef growth.

A second piece of important information provided by the Garroq et al. (2021) study concerns the region's deformation record. The seismic work they reported revealed three structural elements that were labelled "F1", "F2" and "F3". The first two were caused by rifting (extension) in the Late Paleocene-Early Eocene that preceded the Grenada Basin's opening, the F1 set being primary NE-SW striking normal faults that are found across the region, whereas the F2 set are reactivated discontinuities with N-S trends that are confined to a narrow latitudinal band at c. 13.5°N (Fig. 10 in Garroq et al., 2021). In contrast, the F3 structures were induced by compression and comprise reverse faults, thrusts and folds that date from about the Oligocene-Miocene boundary (23 Mya). The features are variably aligned, from NNE-SSW to NE-SW in the northern half of Grenada Basin to E-W in the south. Presumably, this reflects the localized stress fields in the Caribbean Plate's frontal part as it interacted with the major plates and the minor crustal blocks that bounded it (see also Cerpa et al., 2021; Montheil et al., 2023b). Conspicuously, there are no reported structures that might be related to the GAARlandia shortening event (e.g. Iturralde-Vinent and MacPhee, 1999).

Tejada et al. (2024) presented a suite of land-sea maps (as part of their Fig. 1) based largely on Cornée et al. (2021) and Garroq et al. (2021). Although the figures lacked detail, many locations along the Aves Ridge were shown as emergent in two temporal snapshots at 35 and 15 Mya, the full exposure window being 37 to 13.8 Mya. Also, they suggested that these landmasses played a critical role in the sloth-clade colonization.

5. Differences between Iturralde-Vinent and MacPhee (1999) and Iturralde-Vinent and MacPhee (2023)

Relative to the older GAARlandia proposals, in particular Iturralde-Vinent and MacPhee (1999), the recent one of Iturralde-Vinent and MacPhee (2023) includes several important changes (Fig. 7). Two areas of high-elevation land have been added to the map, a small one on the La Blanquilla High, and a large one in the Virgin Islands area. The sub-aerial parts of the Aves Ridge have been pared down and are narrower by c. 40–50%. The Grenada Basin and the area to the north is wider with a larger expanse of deep water, although it appears not to be fully opened (c.f. Garroq et al., 2021). The former land connection between the northern and southern halves of Hispaniola is now shown as "shallow marine" and with a question mark. Additionally, there are other substantive changes to the inferred geography, although none is directly relevant to the Aves Ridge pathway proposal. Specifically, a shallow-water spur to the west of the southern Cuba has been extended, and along-strike from it is an elongate ridge with a small island; a sea-floor mound that was positioned to the east of southern Hispaniola has been removed; the southern tip of Florida is now submerged.

6. Introducing the 'Aves Ridge Reef Belt'

Having critiqued various elements of the Aves Ridge landspan proposals, we thought it appropriate to construct our own paleogeographical model for the feature and the neighbouring areas. Before outlining the scenario, it is important for us to acknowledge the contribution of Holcombe and Edgar (1990), specifically their suggestion that the elevated parts of the bathymetric highs that are now at c. 1000 water depths were once close to sea level (see above). We also note that their basic idea was reaffirmed and developed by the more recent studies of Cornée et al. (2021), Garroq et al. (2021) and Tejada et al. (2024). Our proposed scenario is applicable for the Late Middle Eocene (41.2 Mya) through late Early Miocene (c. 17.0 Mya). The start time could, however, date from the Early Middle Eocene (47.8 to 41.2 Mya), but then the Greater Antilles were largely submerged (Woodring, 1954; Stephan et al., 1990; Iturralde-Vinent and MacPhee, 1999); the end time is more exactly defined due to its surmised tie to the eustatic rise that is associated with the onset of the Middle Miocene Climatic Optimum (also see above). The case is illustrated through two land-sea maps, one for the Eocene-Oligocene boundary (33.9 Ma; Magnetochrons C15–C13, see Ogg, 2020), and a second for the mid-Early Miocene (19 Mya) (Fig. 8). Both depict the approximate positions of the shorelines and the tops of the carbonate growth structures. It is emphasized, however, that no attempt has been made to categorize land areas as 'low' or 'high' elevation (for which a widely recognized value does not exist), nor the sea into 'shallow' and 'deep', which is generally defined as 200 m below sea level (e.g. Thistle, 2003). Crucially, data for the latter do not exist for us to be able to confidently portray such information. Also, from a biogeographical perspective it is relatively unimportant.

The plate tectonic reconstructions that were presented as Figs. 17 and 21 in Pindell and Kennan (2009) provide the base-map stencils. However, an adjustment is made to the southern end of the Aves Ridge in the vicinity of the La Blanquilla High and the adjoining part of the Los Hermanos Spur (Fig. 2). This involves straightening the bent portion of the Aves Ridge into a N-S alignment to remove the shearing rotation the area experienced in the Neogene as the Caribbean Plate migrated eastwards relative to South America (e.g. Pindell et al., 1988; Escalona and Mann, 2011).

With the vertical dimension, for the Aves Ridge, we overlay the environmental-setting interpretations of Fox et al. (1971), Marlowe (1971), Nagle (1972), Bouysse et al. (1985), Holcombe and Edgar (1990), Clark et al. (2008), Escalona and Mann (2011), Cornée et al. (2021), Garroq et al. (2021), BouDagher-Fadel et al. (2023), and Montheil et al. (2023a) (see Fig. 3 and Table 1). For the broader region, the 34 Mya scenario is based largely on Fig. 6A in Iturralde-Vinent and

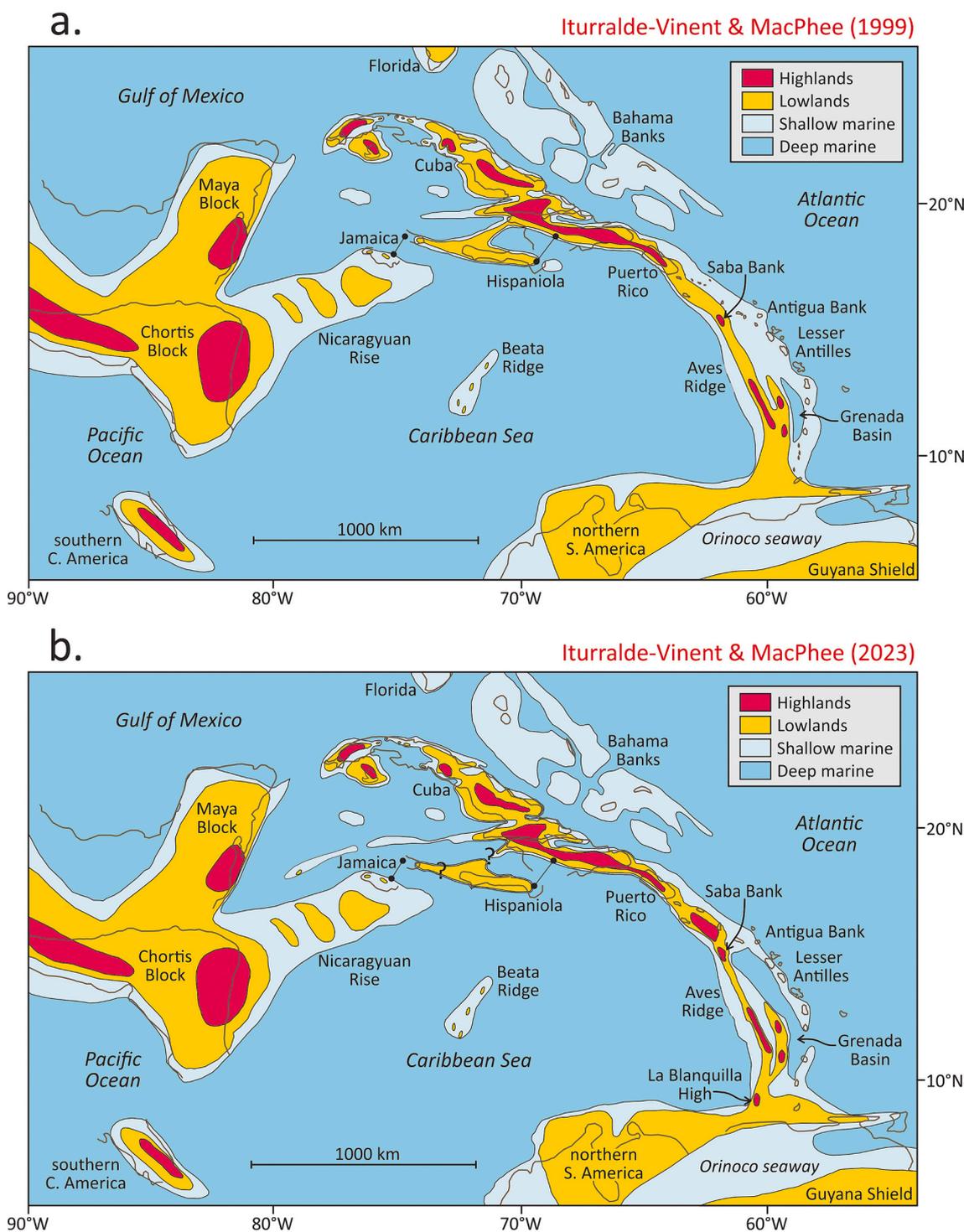


Fig. 7. Paleogeographical maps of the eastern Caribbean at the Eocene-Oligocene boundary when Iturralde-Vinent and MacPhee have proposed that the Aves Ridge was emergent. Respectively, Panels (a) and (b) are re-drafts of Fig. 6 in Iturralde-Vinent and MacPhee (1999), and Fig. 6A in Iturralde-Vinent and MacPhee (2023), with the colour scheme adopted from the older publication. Key differences between the two are explained in the text.

MacPhee (2023) with detail on northern South America from Fig. 18E in Escalona and Mann (2011). The 19 Mya reconstruction draws largely from Fig. 3 in Woodring (1954) with small modifications (e.g. southeast Cuba) adopted from Fig. 6B in Iturralde-Vinent and MacPhee (2023). For both instants, the paleogeographical maps of Weeks (1948), Stephan et al. (1990) and Hoorn et al. (2010) provide extra control.

The data suggest that at both times parts of the La Blanquilla High (in the south) and the Saba Bank (in the north) were fully emergent (see Clark et al., 2008; Cornée et al., 2021). However, the former appears to

have been separated from South America by substantial marine barriers (Fig. 18 in Escalona and Mann (2011), while the latter may have been intermittently linked to Puerto Rico, first in the late Middle Eocene and then in the Late Oligocene (Fig. 16 in Cornée et al., 2021). The main part of the Aves Ridge, spanning c. 540 km, was rather different and included a number of irregularly positioned coral atolls (e.g. Alcatraz, Gavilan, Golondrina and Papagayo seamounts) and larger carbonate mounds (e.g. Flamenco and Halcon ridges, Los Hermanos Spur, and Pelicano Seamount) that had grown upwards from extinct, and likely greatly

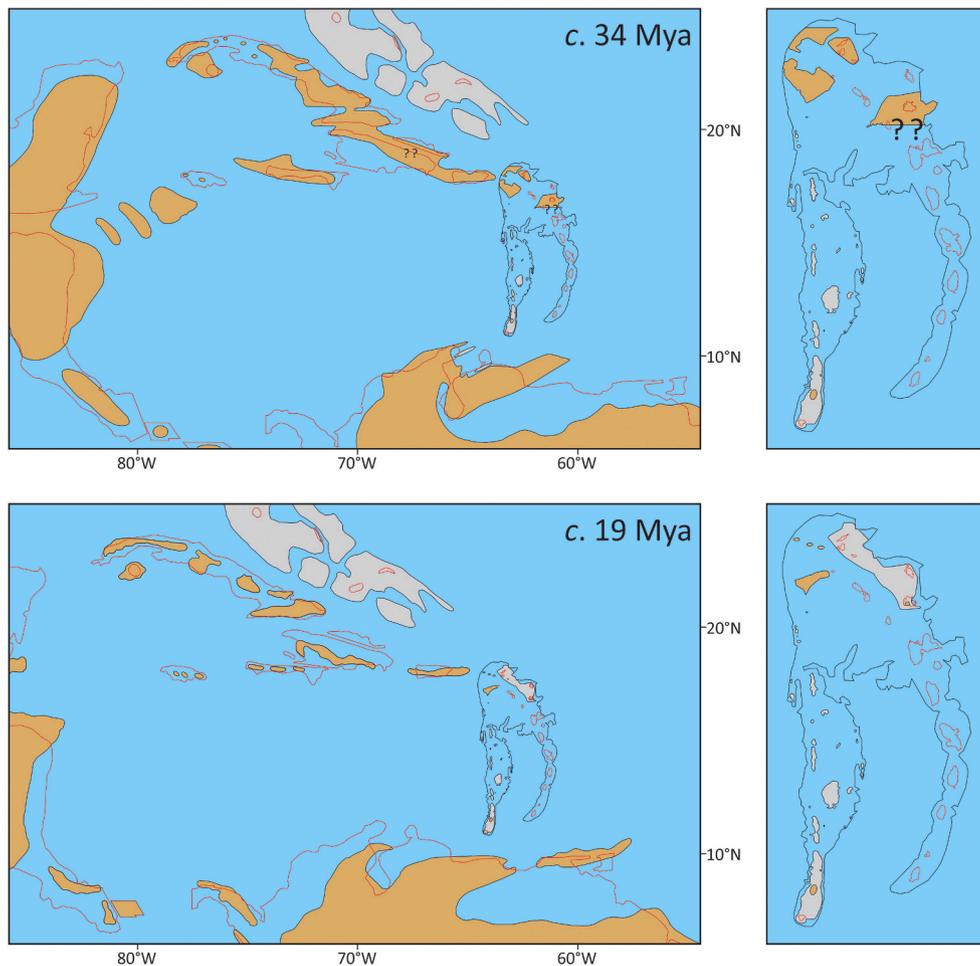


Fig. 8. Newly hypothesized land-sea maps for the Caribbean and the Aves Ridge area at approximately the time of the Eocene-Oligocene boundary (c. 34 Mya; top row) and mid-Early Miocene (19 Mya; bottom row). Land areas are pale brown, sea/ocean surface is pale blue, the tops of various carbonate platforms/atolls, which are close to sea-level, are pale grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

eroded, volcanic highs along the remnant arc (Fox et al., 1971; Marlowe, 1971; Nagle, 1972; Bouysse et al., 1985; Holcombe and Edgar, 1990; Garroq et al., 2021; BouDagher-Fadel et al., 2023). Based on Holcombe and Edgar (1990), we use the 1000 m isobath to delimit the approximate aerial extents of these biological super structures. The tops of the carbonate bodies would have been at or just below sea-level, although each may have had patches of true dry land composed of reef debris that had been piled up during storms, which in some areas they may have been capped with sand dunes. Typically, these would be no higher than 5 to 10 m above sea level, but on some of the larger platforms perhaps a few tens of metres (e.g., Carew and Mylroie, 2001). Importantly, the aforementioned absence in any of the dredge-sample reports (Table 1) of volcanogenic detritus or coarse-grained clastics suggests that there were no ‘high’ islands, nor periods when the Aves Ridge crest was substantially emergent. To avoid the feature being conflated with ‘GAARlandia’, we label the structure (see also Holcombe and Edgar, 1990; Tejada et al., 2024) the ‘Aves Ridge Reef Belt’, and suggest that it looked a lot like the modern-day southeast Bahama Banks in the western North Atlantic (Carew and Mylroie, 1997) (Fig. 9), or the Spratly Islands in the southern South China Sea (Hancox and Prescott, 1995; Hutchison and Vijayan, 2010) (Fig. 10). Notably, in the modelled scenario the deep-water gaps separating adjoining carbonate buildups are typically 30–70 km, and these are similar to those in the modern-example systems.

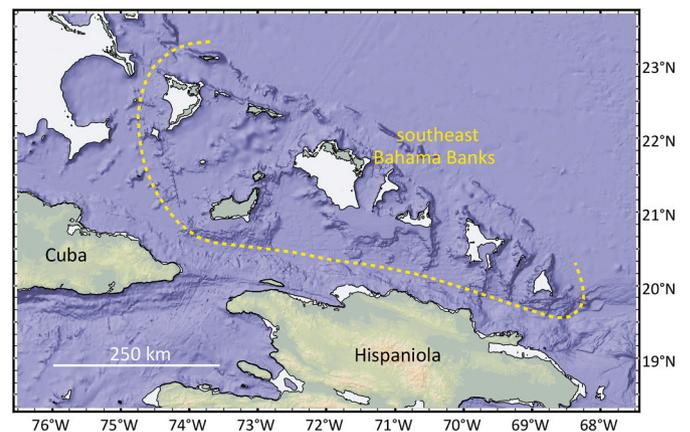


Fig. 9. Map of the southeast Bahama Banks area showing a number of coral atolls and carbonate platforms, each of which is separated from the others by deep water. The image was generated using *GeoMapApp* (Ryan et al., 2009). Alongside the Spratly Islands (Fig. 10), the region is a proposed analogue for the main part of the Aves Ridge in the late Middle Eocene through Early Miocene (Fig. 8), that is buildup size and spacing plus the overall extent of the system.

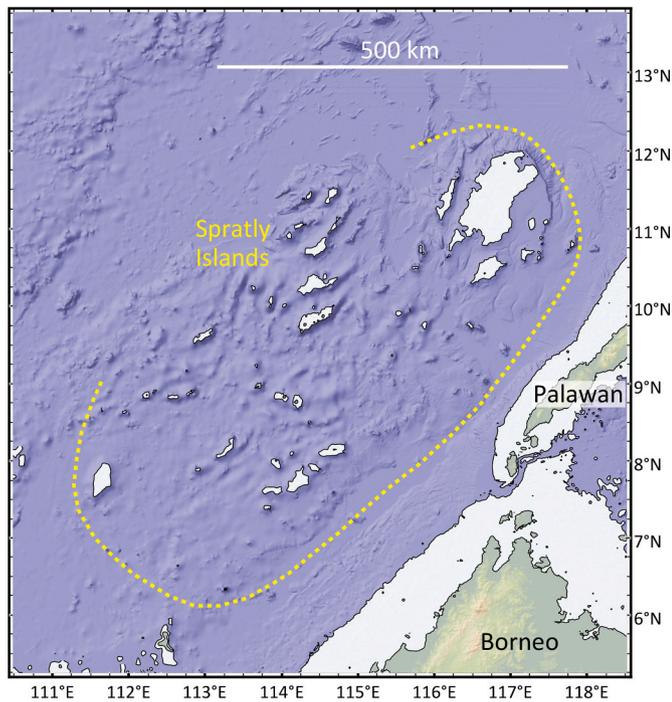


Fig. 10. Map of the Spratly Islands area, showing a number of coral atolls and carbonate platforms, each of which is separated from the others by deep water. The image was generated using *GeoMapApp* (Ryan et al., 2009). Alongside the southeast Bahama Banks (Fig. 9), the region is a proposed analogue for the main part of the Aves Ridge in the late Middle Eocene through Early Miocene (Fig. 8), that is buildup size and spacing plus the overall extent of the system.

7. Feasibility for the Aves Ridge Reef Belt to have enabled land-bound vertebrates on South America to colonize the greater Antilles

In the sub-sections below, we explore the challenges that are involved with a taxon or clade making an island-hopping colonization from South America to the Greater Antilles.

7.1. Insights provided by the advance of South America-derived land-vertebrate clades within the Lesser Antilles

For more than three decades, efforts to determine when the different Greater Antillean land vertebrate clades arrived has been estimated using molecular methods (Hedges et al., 1992). Such data are pivotal for evaluating various sorts of colonization mechanisms, for instance vicariance, over-water dispersal, or along land bridges (reviewed in Ali and Hedges, 2021). For that purpose, relatively sparse sampling of Antillean groups has been sufficient. However, denser sampling of species by DNA sequencing in recent years has resulted in larger, more comprehensive phylogenetic trees and timetrees that has the potential to facilitate a more nuanced form of investigation.

Island-hopping dispersal has been proposed many times for the Lesser Antilles (e.g., Holcombe and Edgar, 1990; Woods, 1990; Ricklefs and Bermingham, 2002; Ricklefs, 2010; Jowers et al., 2021; Iturralde-Vinent and MacPhee, 2023; Veltjen et al., 2023). A key prediction with such a model is for each clade's phylogenetic tree to exhibit progressive 'nesting', from the closest relative in South America at the tree base, with a ladder-like branching along islands going northward with the final 'twig' or branch cluster marked by the species that are on the Greater Antilles (Fig. 11a). The GAARlandia model should lead to a similar outcome, with monophyletic Puerto Rico-Hispaniola-Cuba clades nested within lineages from the northern Lesser Antilles (MacPhee & Iturralde-Vinent, 2023), but without the ladder-like basal aspect (because the Aves Ridge land areas are now submerged).

To evaluate the idea, we reviewed the literature for 35 clades of terrestrial vertebrates of Caribbean islands (nomenclature from Hedges et al., 2019 and Ali and Hedges, 2021). However, 28 of the groups cannot be used in a test due to them not being sourced from South America (e.g. *Solenodonta* giant shrews, *Tarentola* wall geckos), or not having representatives on the Lesser Antilles (e.g. Caribbean monkeys, ground sloths, and hutia rodents), or there being a lack of genetic information (e.g. *Phyllodactylus* geckos, Antillean two-lined skinks and chinchilloid caviomorphs). The first of the seven 'applicable' clades is the *Anolis roquet* group of anole lizards, whose members are confined to the southern Lesser Antilles (they have advanced only as far as Martinique; Nicholson et al., 2012). A second anole lineage, the *Anolis bimaculatus* group, is confined to Dominica and the islands to the north, but it is

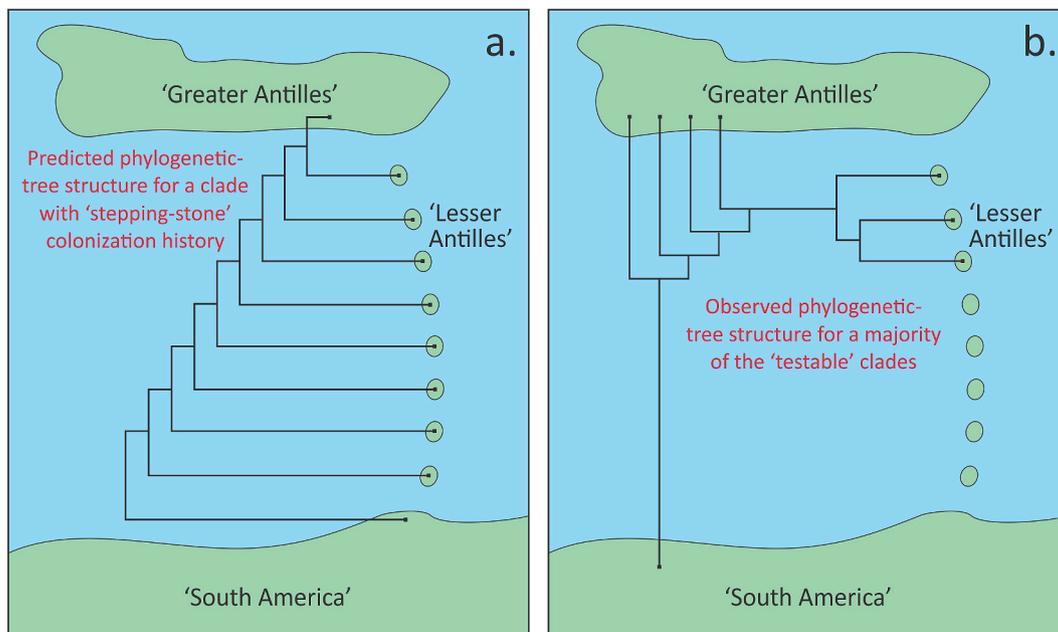


Fig. 11. Schematic diagram showing (a) the predicted phylogenetic-tree structures associated with island-hopping along the Lesser Antilles islands towards the Greater Antilles, and (b) the observed patterns.

nested within a large Greater Antillean clade (Fig. 11b), with the closest relatives on the Puerto Rican Bank islands (Nicholson et al., 2012). Significantly, the typhlopoid blindsnakes (Hedges et al., 2014), ground lizards (Tucker et al., 2017), racer snakes (Hedges et al., 2009), Antillean four-lined skinks (Hedges and Conn, 2012), and terraranan frogs (Heinicke et al., 2007; Hedges et al., 2008) all show near-identical tree structures, i.e. sourcing from the Greater Antilles, specifically the Puerto Rican Bank, with a subsequent colonization of the northern Lesser Antilles.

That six of the seven groups available for addressing the biogeographic question exhibit the same basic pattern is particularly important. Firstly, the results almost unequivocally reject the phylogenetic tree structures that are predicted by both the Lesser Antillean- and GAARlandia-advancement models. Secondly, they indicate that direct over-water transport from South America to the Greater Antilles occurred, to Hispaniola or Puerto Rico, and this was followed by secondary dispersals, either east to the northern Lesser Antilles or west towards Cuba. The recent discovery of a former landmass on the northeast corner of the Caribbean Plate, dubbed GrANola (Philippon et al., 2020; Cornée et al., 2021), is noteworthy as it could have provided a largely continuous dry-land path that allowed taxa on the Puerto Rican Bank to advance into the northern Lesser Antilles.

7.2. Colonization involving a single long-distance overwater dispersal event versus multiple 'short-hop' events: hypothetical scenarios

In thinking about the Greater Antilles land-vertebrate colonizations, it is useful to consider hypothetical probabilistic scenarios (others who have explored the general idea include Matthew, 1915; Darlington, 1938, 1957; and Simpson, 1952). In the first instance, we consider a situation in which two 'rafts', A and B, have just been washed off a continent, each with a sufficient number of land-vertebrate species' members to establish a remote sub-population, for instance a group of mixed-sex individuals, a fertilized female, or even a clutch of viable eggs (for amphibians or reptiles). Assuming the relative probability (P_R) of Raft A finding its way to a sub-circular high island that is 60-km-distant and, incidentally, 40-km in diameter, is 10^{-2} , while the journey for Raft B directly to the 'destination' archipelago 900 km away is a hundred thousand times less ($P_R = 10^{-7}$) (Fig. 12a). For Raft A's lineage members to then systematically 'hop' to the target landmass via seven more similarly spaced and similarly sized islands has a P_R of 10^{-2} raised to the power of 9, or 10^{-18} (to provide context on the magnitude of this value, Earth formed approximately 1.436×10^{17} s ago). An alternative model involves a three-step passage (Fig. 12b). In this case, we assign $P_R = 10^{-4}$ for each of the journeys, which results in a total-journey probability of

10^{-12} (10^{-4} to the power of 3). Obviously, such scenarios are hugely simplistic, and a multitude of alternative numbers could be applied, but they nevertheless highlight the limitations of the stepping-stone colonization mechanism despite it being regularly invoked or at least offered as an option (e.g. Woods et al., 2001; Iturralde-Vinent and MacPhee, 2023; Tejada et al., 2024). Moreover, the process had to be completed within a finite period, which with most of Iturralde-Vinent & MacPhee's proposals was 2–3 Myr.

7.3. Challenges associated with step-wise colonization via a series of just-above-sea-level carbonate platform tops

As explained in Ali and Hedges (2023), for land-vertebrates that have evolved over millions of generations in continental settings, surviving on just-above-sea-level sub-tropical islands is a major challenge due to the paucity of suitable habitats. Importantly, such systems have elevated salt levels, limited supplies of freshwater, high temperatures, and are frequently inundated during storms. Amphibians and mammals are especially vulnerable to these stressors. Reptiles, although being appreciably hardier, are still strongly filtered. Additionally, the assemblages appear to experience high rates of turnover as most taxa are only marginally distinctive from the sister group they were derived from; they have not been present for long enough to have differentiated from the source-pool stock. For example, the level of endemism in the Bahamas is low compared with that of the Greater Antilles (Hedges, 1996a). Concerning the atolls in the SW Indian Ocean (Europa, Juan de Nova, and Glorieuses Islands etc.), none host native amphibians or land-bound mammals and the few reptile species that are present (Sanchez et al., 2019) are again all only slightly evolved from their mainland relatives indicating that each arrived relatively recently.

Notably, Tejada et al. (2024) suggested that vertebrate taxa are/were able to survive on low-elevation islands, and that exposed parts of the Aves Ridge (Fig. 1h and g in Tejada et al., 2024) might have facilitated the arrival of the Greater Antillean sloth clade. In building their argument, they drew upon the extant fauna on Sombrero Island (northern Lesser Antilles), as well as the extinct faunas on the Balearics (western Mediterranean), and the southern and central Ryukyus (northwest Pacific). However, none of these landmasses are/were active reef-crown systems at the time of the faunal occupations, the substrates instead comprising uplifted lithified rock that for some time prior had been subject to weathering and erosion (see Christman, 1953; Auffenberg, 1967; Ogden et al., 1985; Fornós et al., 2002; van der Geer et al., 2010a, 2010b; Watanabe et al., 2023). Thus, they are quite unlike the Aves Ridge 'islands' we envisage and should not be considered as analogous.

A second issue relates to the idea of a clade of land-vertebrates

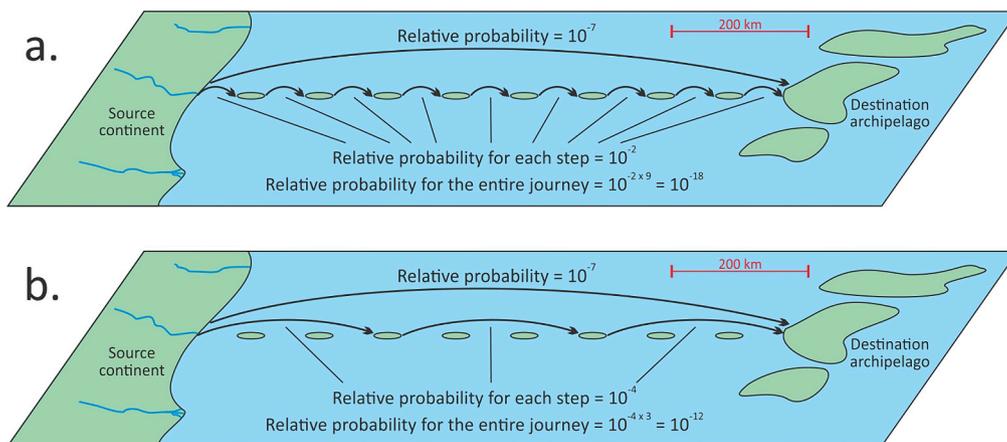


Fig. 12. Schematic diagrams showing the advancement of a taxon or a clade via a group of closely spaced islands from a continental source to a destination landmass/archipelago as compared to one resulting from a single long-distance over-water dispersal event. In the first (a) eight stopovers are made, whereas in the second (b) there are just two. See text for details.

making repeated short-distance over-water dispersal colonizations to advance along a string of low-elevation coral islands, which we suggest is highly suspect. Such landmasses lack vegetation that might provide suitable rafts (large mats, sizeable trees), the shoreline plants being dominated by scrub (e.g. Fosberg, 1949; Gibson and Phillipson, 1983; Boulet et al., 2018). Furthermore, moving dislodged plants out to the edge of the reef and in to the open water is a significant test, and then they need to be carrying passengers that might populate a carbonate island elsewhere. This contrasts with 'high' islands, which in tropical and temperate settings are typically well-vegetated and can thus spawn flotsam. Furthermore, they provide a variety of environments and are thus able to accommodate a range of faunal elements that are carried to their shores.

8. Conclusions

As part of this review, we examined important issues related to the GAARlandia landspan model, which supposedly explains how a number of terrestrial vertebrates from South America colonized the Greater Antillean islands in the middle Cenozoic. However, since the idea was first put forward in the mid-1990s, significant confusion has arisen over various statements on the feature, in particular the mechanisms that led to its emergence, the period when it operated, where along the margin of South America its southern end connected, and conflicts with its geographical configuration as described using words and on charts. In response, we have presented a new paleogeographical model, which builds upon Holcombe and Edgar (1990), Cornée et al. (2021), Garroq et al. (2021) and Tejada et al. (2024), that is applicable for the late Middle Eocene through Early Miocene inclusively (41.2 to 17.0 Mya). We posit that during this interval the spine of the Aves Ridge had growing up from it a smattering of coral reefs and carbonate platforms, the tops of which were at sea level, with small portions of them that were fully emergent. Importantly, however, the buildups were separated by considerable gaps of 30 to 70 km. Also, there were probably no 'high' islands that might have hosted a range of habitats as evidenced by the lack of relevant detritus in the numerous dredge-sample reports (see Table 1). That said, tracts of elevated ground were present in the northern Lesser Antilles (Philippon et al., 2020; Cornée et al., 2021). However, from a biogeographical perspective the phylogenetic data refute the idea that the ancestors of the extant land-vertebrate clades on the Greater Antilles arrived via these massifs.

Suggested analogues for the 'Aves Ridge Reef Belt' are the southeast Bahama Banks and the Spratly Islands. However, as a consequence of ecological mismatches and statistical improbabilities, it is extremely unlikely that the colonizer-ancestors of the land mammals, amphibians, and a large fraction of the reptile types on the Greater Antilles stepping-stone hopped along this feature from South America. Instead, the passages to the island group likely involved direct over-water dispersal. That said, it is conceivable that the ancestors of some of the small-bodied lizard clades used the ridge to cross, but likely with just one or two stopovers.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

We are grateful to Jonathan Aitchison, Alejandro Escalona, Uwe Fritz, Jean-Frederic Lebrun, Paul Mann, Kenneth Miller and Michael

Perfit for sharing information. We thank the two anonymous reviewers for their constructive critiques and Christopher Fielding for his editorial guidance.

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