

THE INTERPRETATION OF CARIBBEAN PALEOGEOGRAPHY: REPLY TO HEDGES

ROSS D. E. MACPHEE & MANUEL A. ITURRALDE-VINENT

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Resum

La hipòtesi de GAARlàndia (Iturralde-Vinent & MacPhee, 1999) especifica que una llengua de terra, capaç d'actuar com a via de dispersió per a organismes terrestres, va connectar les futures Antilles Majors amb la vorera del nord-oest de Sud Amèrica durant un període curt cap a la transició Eocè/Oligocè. Hedges (2001) ha criticat aquesta hipòtesi sota diferents prismes, i a aquest treball tractam de replicar algunes de les seves objeccions, tenint en compte l'evidència més recent que tenim sobre les següents tres qüestions: (1) Quant ha durat la presència dels ambients terrestres actuals de la conca del Carib? (2) Quines han estat les dates d'emergència més probables per a les illes que tenen aquests ambients? (3) Quin efecte tenen les corrents de superfície marines sobre la distribució dels objectes que surten a l'àrea del Carib? Primer, en contra del que diu Hedges, encara no hi ha evidència geològica per a donar suport a una continuïtat als ambients terrestres del Carib abans de fa 37 Ma. A llavors, la pretensió d'Hedges que com a mínim algunes entitats biòtiques haurien persistit *in situ* per períodes de més de 37 Ma (la data més primerenca suportada per tal evidència), com a mínim a algunes de les illes actuals, encara no es pot mantenir sobre bases geològiques. Segon, l'esdeveniment d'importància decisiva en l'emergència de GAARlàndia no fou la baixada del nivell eustàtic de la mar, sinó l'aixecament d'un arc insular tot seguint el final de la seva fase magmàtica. A llavors, notar, com Hedges fa, que l'emergència de GAARlàndia no va estar correlacionada amb una baixada identificable principal—encara que fos correcte—no és pertinent al problema plantejat. Ni ho són les incerteses de les datacions, tant de les baixades com de l'esdeveniment d'aixecament. Finalment, encara que el moviment de les corrents de superfície marines està afectat per la força de Coriolis, el vent és molt més important per al moviment dels objectes sobre la superfície. Experiments reals revelen que aquests moviments són significativament caòtics, cosa que condueix a que el transport passiu virtualment mai esdevindrà en línia recta. Com a resultat, encara que els objectes transportats pels rius de Sud Amèrica eventualment poden embarrancar a les costes del Carib, els temps de trànsit són probablement llargs. Aquest fet, tal volta més que qualsevol altre, condueix a que les llargues estades a la mar siguin un mètode improbable de dispersió exitosa per a moltes castes d'organismes. Òbviament, les investigacions geològiques i paleontològiques no poden falsar escenaris històrics, però poden subministrar *termini ad quem* per precisament el tipus d'esdeveniments en que els biogeògrafs insulars haurien d'estar interessats, tals com quan apareixen per primera vegada a una àrea ambients desitjables per organismes terrestres, i quins organismes (representats per les seves restes) eren els primers en disposar de l'avantatge d'aquestes noves terres.

Paraules clau: Carib, biogeografia, paleogeografia, tectònica, vertebrats.

Abstract

The GAARlandia hypothesis (Iturralde-Vinent & MacPhee, 1999) specifies that a landspan, capable of acting as a dispersal conduit for terrestrial organisms, connected the future Greater Antilles with the margin of northwestern South America for a short period around the time of the Eocene/Oligocene transition. Hedges (2001) has criticized this hypothesis on various grounds, and in this paper we seek to reply to several of his objections by considering the most recent evidence bearing on these three questions: (1) How long have the present land environments of the Caribbean basin been in existence? (2) What are the likeliest emergence dates for the islands supporting those environments? (3) What effect do sea-surface currents have on the distribution of flotsam in the Caribbean area? First, *contra* Hedges, there is still no geological evidence for *continuity* in Caribbean land environments earlier than 37 Ma. Therefore, Hedges' claim that biotic entities on at least some of the present islands have persisted *in situ* for periods longer than 37 Ma (the earliest date supported by such evidence) still cannot be sustained on geological grounds. Secondly, the event of overriding importance in the emergence of GAARlandia was not drawdown in eustatic sea level, but uplift in the island arc following the termination of its magmatic phase. Therefore, noticing as Hedges does that the emergence of GAARlandia was not correlated with an identifiable major drawdown—even if correct—has no pertinence to the issue at hand. Neither do uncertainties in the dating of either drawdowns or the uplift event. Finally, although the movement of sea-surface currents is affected by the Coriolis force, wind is much more important for the motion of objects on the surface (flotsam). Actual experiments reveal that such motions are significantly chaotic, which means that passive transport will virtually never occur in a straight line. As a result, although objects carried by South American rivers may eventually wash up on Caribbean shores, transit times are likely to be long. This fact, perhaps more than any other, makes long seas journeys an improbable method of *successful* dispersal for many kinds of organisms. Among such organisms we count most land mammals, for a host of autecological and physiological reasons. For other kinds of organisms, including herps, different considerations may apply. Obviously, paleontological and geological investigations cannot falsify historical scenarios, but they can provide *termini ad quem* for precisely the kinds of events that island biogeographers should be interested in, such as when environments suitable for land organisms first appeared in an area, and what organisms (as represented by their remains) were the first to take advantage of these new lands.

Key words: Caribbean, biogeography, paleogeography, tectonics, vertebrates.

INTRODUCTION

The GAARlandia hypothesis (Iturralde-Vinent & MacPhee, 1999) specifies that, close to the Oligocene/Eocene transition, a landspan (i.e., a land "bridge" connecting a mainland to a suite of islands) formed by the spine of the emergent Aves Ridge briefly (~1 Ma? [million years]) joined northwestern South America to at least three of the present Greater Antilles (Fig. 1; the involvement of tectonic blocks that now comprise the eastern part of Jamaica is possible but unconfirmed). The GAARlandia landspan episode ended with the onset of subsidence along the Aves Ridge and, contemporaneously, with the subdivision of the Greater Antillean Ridge into tectonic blocks and terranes and therewith the creation of the islands in approximately their current form (Iturralde-Vinent & MacPhee, 1999; MacPhee *et al.*, 2003). The degree to which GAARlandia (Greater Antillean + Aves Ridges) constituted a continuous subaerial feature at any given instant cannot yet be reconstructed empirically with available data. However,

as discussed in the papers cited, the available evidence strongly indicates that much of it could have been exposed as dry land during its short existence during the Eocene/Oligocene transition. Refinements to the model continue to be made (e.g., MacPhee *et al.*, 2003), although truly decisive data will probably have to await a program of deep-sea drilling along the Aves Rise.

The GAARlandia hypothesis has generated a certain amount of controversy (cf. Graham, 2003a). Although opinion does not really divide along disciplinary lines, at present the idea seems to enjoy greater favor among paleontologists (e.g., Sánchez-Villagra *et al.*, 2000; Polcyn *et al.*, 2002) than among neontologists (e.g., Hedges, 2001; Dávalos, 2004). Hedges (2001) in particular has criticized several elements of the GAARlandia hypothesis. Our purpose here is to briefly reply to the points he raises that seem to us to be the most germane to Caribbean historical biogeography. These are:

- Permanency of land environments in the Caribbean basin
- Emergence dates for GAARlandia
- Generation of sea-surface currents and their effect on flotsam.

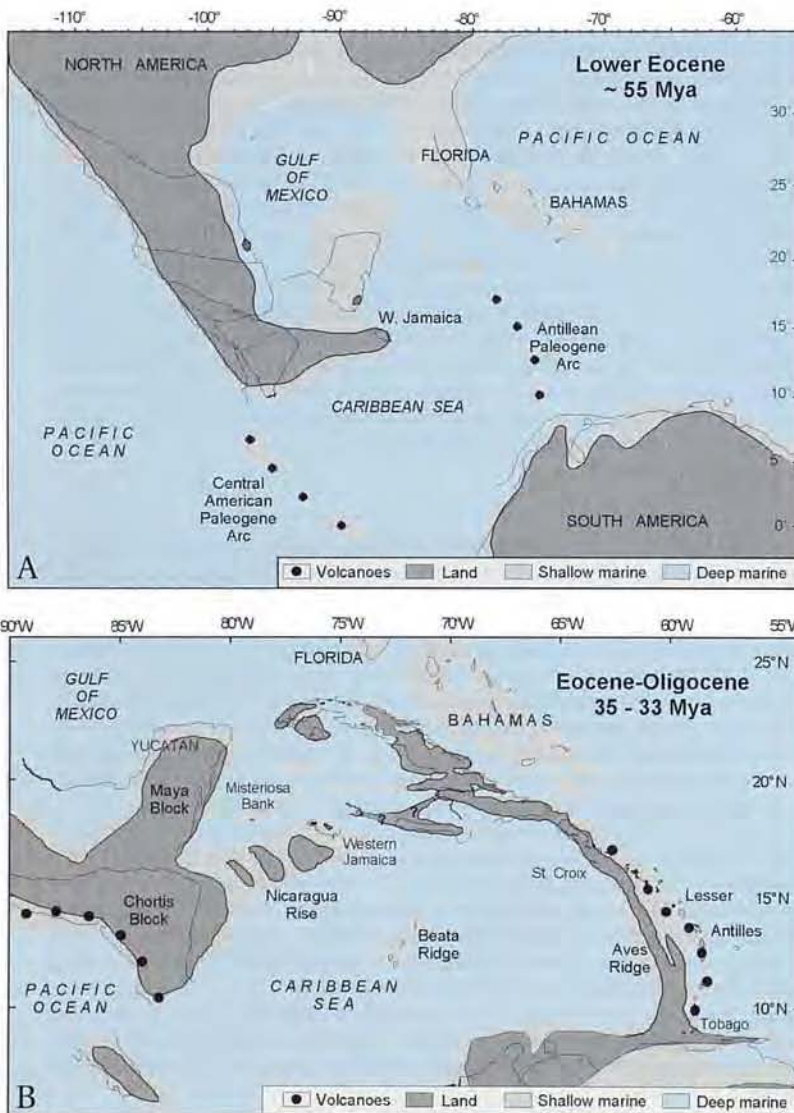


Fig. 1. Caribbean region in earlier (A) and later (B) Paleogene. In A, the small islands indicated along the spine of the Paleogene island-arc are indicated for purposes of illustration only. Although such islands doubtless existed, their disposition is not known. As part of the leading edge of the Caribbean plate, the basement of these islands would have been strongly deformed as they were incorporated into the Antillean foldbelt—the core of later GAARlandia. Note the existence of the broad Panamanian Seaway, which would have greatly influenced oceanic circulation and therewith the climate and sea-surface current patterns in the Caribbean region. In B, the GAARlandia landspan is depicted as it might have existed at its maximum extent for a short period around the time of the Eocene-Oligocene transition. For additional discussion see Iturralde-Vinent & MacPhee (1999).

Fig. 1. La regió caribenyà al Paleògen primerenc (A) i tardà (B). A la figura A, les petites illes indicades al llarg de l'espinà de l'arc insular del Paleògen només estan indicades amb finalitat il·lustrativa. Encara que indubtablement aquestes illes varen existir, la seva situació no és coneguda. Com part de la vorera capdavantera de la placa caribenyà, el basament d'aquestes illes hauria estat fortament deformat a mesura que s'incorporessin al cinturó del plegament antillà — el cor de la posterior GAARlàndia. Noteu l'existència de l'ampli canal panameny, que hauria influït en gran mesura la circulació oceànica, juntament amb els patrons de corrents superficials marines i el clima a la regió caribenyà. A la figura B, la llengua de terra de GAARlàndia es representa com podria haver existit en la seva extensió màxima durant un curt període de temps de la transició Eocè-Oligocè. Per a una discussió addicional, veure Iturralde-Vinent & MacPhee (1999).

PERMANENCY OF LAND ENVIRONMENTS IN THE CARIBBEAN BASIN

First, Hedges (2001) takes issue with our claim that existing land environments within the Caribbean Sea are of relatively recent origin (i.e., Late Eocene and later). In his view, at least some Antillean land environments have been in continuous existence for a much longer period, perhaps since the late Mesozoic. We agree that there were land environments in the Caribbean prior to the end of the Paleogene, but our view of their origin and paleogeographical history is rather different from that espoused by Hedges. In our 1999 paper we provided empirical evidence for several such environments, and in more theoretical terms we included pre-Late Eocene terrestrial facies in our general model of the paleogeographical evolution of the Caribbean and circumjacent mainlands (e.g., Iturralde-Vinent & MacPhee, 1999, fig. 12, p. 53). However, our objective was to review the available evidence for judging the *permanency*, not the mere prior existence, of such land environments. The critical point here is that there is ample stratigraphic evidence throughout the Caribbean region for repeated marine transgressions that would have swamped any islands existing during the late Mesozoic and early Paleogene. Thus these earlier land environments—whatever their nature—cannot be regarded as being connected by an unbroken succession of subaerial conditions that persisted to the present. In post-Paleogene times, by contrast, the geological record supports the view that Neogene transgressions have been less complete (except in the case of western Jamaica; cf. Iturralde-Vinent & MacPhee, 1999). Thus at least on larger islands, terrestrial deposition, soil formation, and other indications of persistent subaerial conditions can be continuously traced from approximately 37 Ma at the earliest to the present—that is, from the time during the Late Eocene when the cores of the Greater Antilles were first uplifted following the termination of active volcanism, but before they coalesced into a unitary structure (GAARlandia) over which conditions were broadly subaerial to nearly subaerial. Although our model is more elaborate than others that have been proposed for Antillean Cenozoic paleogeography (e.g., Rosen, 1975, 1985), our basic framework builds on work by others interested in making regional biological history and earth history congruent (e.g., MacFadden, 1980; Perfit & Williams, 1989).

Nevertheless, Hedges (2001) argues that in the case of Hispaniola and Puerto Rico there is evidence that permanent land environments have existed much longer than we allow. In support of his position he cites two papers, one by Larue (1994) and the other by Donnelly (1992). As Larue's paper does not contradict any aspect of the GAARlandia model, including the time of uplift of Puerto Rico, we cannot explain why Hedges (2001) cited it. Indeed, Larue summarizes the late Paleogene history of Puerto Rico in terms that are entirely consistent with ours: "Cessation of volcanism, uplift of several kilometers, deformation and rotation of the arc massif in the late Eocene to middle Oligocene in Puerto Rico..." (Larue, 1994: 161; see also Larue & Ryan, 1998).

Donnelly (1992), by contrast, argued that parts of the

Greater Antilles Arc (specifically Hispaniola and Puerto Rico) have been subaerial since the Albian (ca. 100-110 Ma), "and in these places emergence persisted to the present." Hedges (2001) fails to note, however, that Donnelly's argument for continuous emergence is not based on stratigraphic evidence *per se*, but on considerations of isostasy (as laid out by Donnelly [1990]). The scale of this approach, however, is far too gross to be useful in the present context. Relative buoyancy of crustal material is determined by mass relationships within the lithosphere, and has nothing to do with ambient sea level. If it did, then light, positive continental areas would not be subject to marine transgression. (The repeated appearance of epicontinental seas in North and South America during the Phanerozoic [cf. Hallam, 1989] is sufficient evidence to the contrary.)

True, crust becomes thicker and lighter—and, in consequence, more buoyant—during island-arc evolution. Indeed, this is why any island arc will experience general uplift immediately subsequent to the termination of volcanism, as one consequence of the exhaustion of magmatic chambers and the crystallization of large plutons beneath it (Iturralde-Vinent & MacPhee, 1999). In the case of the Cretaceous and Paleogene Caribbean arcs, on stratigraphic grounds we were able to document general uplift for short periods during latest Campanian-Maastrichtian and Middle-Late Eocene. Each phase of arc uplift was followed by later subsidence and major transgressions, also determined by stratigraphic evidence. In the case of the Cretaceous arc, no terrane has yet been identified by our methods that remained above sea level up to the present. In the case of the Paleogene arc, there is abundant evidence of continuous emergence only after magmatic extinction in the Middle Eocene. Thereafter, extinct arc segments were generally exposed from the late Eocene onwards, even during times of significant marine invasion of lowland areas.

During the last decade, one of us (MIV) has visited all the localities referred to by Donnelly (1992) as well as others of a similar nature in Cuba to obtain relevant samples for the purpose of verifying age and paleoenvironmental contexts. Results are collated, with the recent observations of many other workers, in table 1 of our paper (Iturralde-Vinent & MacPhee, 1999). In sum, this evidence shows that marine rocks of virtually every stage from Early Cretaceous through Late Eocene are well developed in the volcanic arc portions of present-day Puerto Rico, Hispaniola, Cuba and Jamaica. Terrestrial conditions certainly existed from time to time, but in our investigations older land indicators were everywhere succeeded by younger marine beds, indicating that any islands which existed were transitory.

Some heights-of-land may have avoided inundation during the pre-Late Eocene transgressions just mentioned, surviving as small islands until a later period. This is suggested by the occurrence in stratigraphic records of coarse-grained terrestrial conglomerates and montane plant fossils, both suggestive of elevated topography (Iturralde-Vinent & MacPhee, 1999, appendix 1; Graham, 2003b). However, the handful of late Paleogene island environments that have been investigated suffered later inundation and are therefore not examples of continuous survival (e.g., Cretaceous island masses

exposed near Canal Paso Bonito a Cruces in Cuba; Iturralde-Vinent & MacPhee, 1999, p. 24; Eocene Guy Hill Fm terrestrial sandstone in Jamaica, op. cit., p. 39; and section diagrams in op. cit., appendix 1). In the few places where it has been possible to build up a good regional paleogeographic record, as in the case of the Havana area and the Sierra Maestra (Bresznyszki & Iturralde-Vinent, 1978, 1985), land and marine indicators establish that there were many instances of emergence/submergence/reemergence of land during the later Mesozoic and early Paleogene. Such events had to have had a substantial effect on any terrestrial biota that managed to reach whatever islands there were prior to the Late Eocene (e.g., Donnelly, 1990, p. 607). In our view that effect would have been extinction.

Hedges (2001) does not discuss the fact that Donnelly (e.g., 1988: 26ff) also presented arguments to the effect that, during some part of the Paleogene, the northern Greater Antilles may have formed a continuous landmass; that island-island vicariance, affecting animals and plants resident thereon, might have occurred along this axis (Donnelly, 1990: 606); and that, most tellingly in view of the present discussion, a topographic high "either on the site of the present Aves Ridge, or along the present Lesser Antilles" formed a barrier to deep-water circulation between the Pacific and the Atlantic beginning "about 45 million years ago and was essentially complete at about 35 million years." (Donnelly, 1990: 601-602).

It should not be concluded from preceding paragraphs that Donnelly either presaged or would now accept the idea of GAARlandia as we present it. Indeed, Donnelly (e.g., 1989) even doubts the existence of a Caribbean "plate" as a rigid, coherent body, and situates the Greater and Lesser Antilles more or less where they are now for all of the Cenozoic. He is also everywhere careful to say that there is no persuasive evidence for a continuous landbridge/landspan on the spine of the Aves Ridge or that the ridge was ever connected to South America. On the other hand, a fair reading of the geological evidence does not lead him to reject all such possibilities out of hand, which is the point we wish to make here.

With regard to Hedges' molecular evidence for very long existence (since ?late Mesozoic) of a small number of herp lineages in the Caribbean basin, we (Iturralde-Vinent & MacPhee, 1999) note in our figure 9 and accompanying text that there is too much inherent uncertainty in his supporting arguments to accept that a molecular clock used to date phylogenetic divergences can be directly used to date colonization events (for exhaustive review of the methodological issues involved, see Crother & Guyer, 1996). It is well appreciated in the literature that there are a host of issues in linking divergence estimates, with their typically large CIs (95% credibility intervals), with specific events in earth history (for a pertinent West Indian example, see Roca et al. [2004]). By making various assumptions about tectonic scenarios and rates of molecular evolution, Crother & Guyer (1996) show that as little as 30% and as much as 90% of the available ID (immunological distance) data on herp lineages can be made to conform with one or another Antillean vicariance model. (These authors, who con-

cluded that continent-island vicariance probably played a substantial role in determining Antillean vertebrate distributions, did not consider the GAARlandia hypothesis as an alternative explanation for concordant dispersal.) If, for example, the interpretation of the ID data for the endemic Cuban xantusiid *Cricosaura typica* by Hedges *et al.* (1992) is to be accepted at face value, it would be necessary to conclude that the lineage represented by this terminal taxon has been permanently resident in the same "place" since the Santonian (~87-83 Ma). This seems unlikely in view of the fact that "Cuba" did not exist as such at that time. Since Santonian time the components of the present Cuban foldbelt have been tectonically transported, stacked, and also transgressed at least once during each of the Campanian, Maastrichtian, Paleocene, and Eocene Stages/EPOCHS, all of which would have had dramatic effects on their topography.

Hedges *et al.* (1992) refer to one other mega-event, the giant tsunamis that would have been produced by the impact that struck Chicxulub in Yucatan at the K/T boundary, but they claim survival should still have been possible for some species (e.g., those distributed in montane areas). At least in the case of the Caribbean region, the most recent work (Bralower *et al.*, 1998; Tada *et al.*, 2000; Kiyokawa *et al.*, 2003; Tada *et al.*, 2004) on the magnitude of the impactor's effects seem to us to militate against survival of any terrestrial taxa (but see Crother & Guyer, 1996). In any case, impactor scenarios, no matter how violent, only address the matter of proximate cause. For the biota the knock-on consequences of the impactor event, in terms of catastrophic climatic and environmental change, were just as important (if not more so) than the event itself.

The case for Mesozoic origin of some lineages living in the Greater Antilles has recently been augmented by the work of Roca *et al.* (2004). Using molecular evidence, these authors showed that the divergence of *Solenodon* from other placentals is consistent with a calibrated origination date for the former of 76 Ma (95% CI, 72-81 Ma). Since solenodons occur nowhere else than the Greater Antilles, and since the sister-group of Solenodontidae remains persistently uncertain (Asher *et al.*, 2002), it is tempting to conclude that these insectivores have essentially always been where they are now. This temptation is redoubled if the xantusiid datum noted above is viewed as a sort of independent corroboration of very early land-vertebrate colonization of landmasses in the Caribbean Sea. However, divergence dates and colonization dates are two quite different things, and in the absence of relevant fossil evidence (for either group, in this case), there is no warrant for conflating the two. The lemurs of Madagascar are equally unique biogeographically, but to our knowledge no one has suggested that this clade originated vicariantly in the mid-Jurassic, when Madagascar and eastern Africa parted company (cf. Yoder *et al.*, 1996).

Clearly, this aspect of the debate will have no resolution without some new data, and the nature of the data needed are obvious. If there was a pre-Cenozoic Antillean fauna, then surely it consisted of more than a few herp taxa. If so, where was it and where are the fossils to document it?

EMERGENCE DATES FOR GAARLANDIA

A second group of Hedges' (2001) criticisms concerns our methodology for revising the emergence time of GAARlandia. Hedges makes two observations: (1) Originally, MacPhee & Iturralde (1994) defined the emergence date of GAARlandia as falling within the range 30–27 Ma, but later on they (Iturralde-Vinent & MacPhee, 1999) used another, older interval of 35–33 Ma for the same emergence event. (2) The reason for the change was that a sloth fossil from Puerto Rico, dated to the Early Oligocene on the basis of invertebrate faunas in associated beds (MacPhee & Iturralde-Vinent, 1995), was too "early" for the first emergence interval. Accordingly, the interval was altered to make sure that the emergence of GAARlandia preceded the deposition of the fossil. Hedges (2001) concluded that Iturralde-Vinent & MacPhee therefore biased their interpretations to make their geological sequences conform to their fossil discoveries.

Hedges (2001) is correct in noting the change, but incorrect in his characterization of the rationale for it. In the early 1990s, when we first considered the possibility of a dryland route to the large islands, the uplift event that is the fundamental basis for the GAARlandia hypothesis was very poorly constrained. Recognizing this, we originally said (MacPhee & Iturralde-Vinent, 1994, p. 10) that "a possible optimum for colonization [of the Greater Antilles] occurred between the end of the Middle Eocene and the beginning of the Late Oligocene" in concert with the Pyrenean orogenic event. We went on to hazard the possibility that the point of greatest landspan emergence might turn out to be centered on the Early/Late Oligocene boundary, since a major sea level drop, dated to 29 Ma by Haq *et al.* (1987), occurred at about that time. With further work over the next few years we were able to verify that the uplift event was actually centered several million years earlier than this, around the time of the Eocene/Oligocene transition. This was the consideration that put the 29 Ma drawdown out of contention.

It is also relevant to note that the estimated chronometric position of the Eocene/Oligocene boundary was also in a state of flux through the early 1990s, with estimates ranging from nearly 38 Ma to about 32 Ma (Prothero & Swisher, 1992). Clearly, it would have been an excess of refinement to settle on a particular chronometric estimate until a consensus on the boundary emerged. The estimate that we use presently for the Eocene/Oligocene boundary is 33.9 Ma, which is the geomagnetic polarity time scale value published by the Geologic Time Scale 2004 project (Gradstein *et al.*, 2004). The Yauco sloth, which has not been dated chronometrically, is and will remain Early Oligocene age on the basis of biostratigraphic associations. Its relative age, accordingly, will always be younger than the Eocene/Oligocene boundary, whatever its estimated absolute date may be now or in the future.

In further criticism of our 1999 paper Hedges (2001, p. 28) goes on to say that "However, the sea level drop shown by Miller *et al.* (1996) at 35 mya was not a redating of the major Oligocene drop (Haq *et al.*, 1987) used by MacPhee & Iturralde (1994), now considered to be 32.2 mya (Miller *et al.*, 1996), but rather another sea level drop altogether. This inconsistent use of evidence shows that their paleo-

geographical model was influenced by their biogeographical model (i.e., the need to have the land bridge in place before the sloth fossil date)."

This passage displays confusion on several levels, not least over the interpretation of sea level position (several major fluctuations occurred during the later Eocene and Early Oligocene). What we (Iturralde-Vinent & MacPhee, 1999, p. 27) actually said was that "general tectonic uplift coincided with a major eustatic sea level drop at ca. 35 Ma (Miller *et al.*, 1996). As a result, subaerial exposure within the Caribbean basin was probably more extensive than at any other time in the Cenozoic, including the late Quaternary." This passage has nothing to do with the mid-Oligocene drawdown, which we had already discarded as too late. Instead, we were making the point that, because of the scale of uplift, the correlated drawdown at ca. 35 Ma would have led to a relatively greater amount of subaerial exposure in the Caribbean basin than at any other time. This is not implausible. Perhaps it needs to be re-emphasized for non-geologists that, because the Caribbean basin is and always has been an active tectonic region, earth movements may outstrip the rate of eustatic sea level change. Thus it is rather dangerous to rely too heavily on the latter for reliable paleogeographic information. Instead, we consistently based our reconstructions on stratigraphic considerations, using well-defined and well-understood land and marine indicators documented for specific time intervals in multiple rock sections (Iturralde-Vinent & MacPhee, 1999, appendix 1). We only noted correspondences with the eustatic sea-level curve when the correlation seemed especially interesting.

As we repeatedly emphasize in our paper (Iturralde-Vinent & MacPhee, 1999; see also Iturralde-Vinent, 2003), the most significant land indicators for the inferred exposure of GAARlandia around the time of the Eocene/Oligocene boundary is the widespread occurrence of depositional hiatuses and the so-called "conglomerate event" that we see registered in sections throughout the Caribbean basin and its North and South American margins. *Uplift, on a geographically massive scale, is the only conceivable interpretation of this evidence.* The eustatic sea-level curve is not in conflict with this interpretation, because by definition it excludes relative changes in sea level due to local coastline subsidence or elevation.

In summary, with continuing refinements due to discoveries and reanalysis in many different areas, we expect to be able to shed additional light on the timing and consequences of the GAARlandia hypothesis. Far from being "inconsistent" with the evidence, we find ourselves fully in accord with the scientific method that treats relevant new facts and interpretations as useful occasions to test old ideas, including our own.

SEA-SURFACE CURRENTS AND THEIR EFFECT ON FLOTSAM

Finally, Hedges (2001) criticizes our modeling of sea-surface currents during the mid- and late Cenozoic. As in previous papers (e.g., Hedges, 1996a, b), Hedges (2001) continues to emphasize the overarching importance of

the Coriolis force for imposing direction on the drift of flotsam, and repeats his earlier statement that "because the Caribbean always has been north of the equator during geological history, the Coriolis Force would have produced the same clockwise current flow in the past, even while a water connection to the Pacific was in existence" (Hedges, 1996b, p. 118). Because of this, he argues, the movement of flotsam will always be from the southeast toward the northwest in the Caribbean and adjacent tropical Atlantic, and this phenomenon (alone or in combination with powerful storms) can completely explain the origin of the Antillean fauna by overwater transport. This viewpoint was recently repeated without comment or modification by Hower & Hedges (2003): "If this clade [*Ameiva*] were an ancient product of proto-Antillean vicariance, the divergence time estimate between it and mainland species should be greater (e.g., 70–80 Mya) than we observe (25–30 Mya). Therefore, the West Indian Clade [of *Ameiva*] most likely arose by a single fortuitous dispersal event over water on floating debris (flotsam)." It is not made clear, or even addressed, why overwater dispersal is "most likely" when the landspan phase of GAARlandia existed at much the same time and could have provided a dryland route. Indeed, given inherent errors in both geological and molecular methods of estimating elapsed time—Hedges' earlier immunological distance estimate for the appearance of the *Ameiva* clade in the West Indies was ~36 Mya (Hedges *et al.*, 1992)—this near-approximation by investigators using quite different techniques must be regarded as little short of astounding.

Hedges gives no more than passing attention to several critical factors that might have appreciably influenced sea-surface currents in the Caribbean region during the Cenozoic, such as alterations in sea-bottom topography, presence or absence of submarine or sub-aerial topographic barriers, interoceanic connections, and climate change. Several of these issues were discussed by us previously (Iturralde-Vinent & MacPhee, 1999) and we continue to believe that they are important. Further, we continue to regard explanations that simply assume overwater transport under all conditions to be overstated as to the significance of the Coriolis force on "current flow" and simplistic as to the implied constancy of direction of motion of flotsam. We will close this paper with some additional observations on these two matters, which to us appear to go to the core of the "high" likelihood of overwater transport in the Caribbean region:

1. Generation of sea-surface currents. In discussing "current flow" in the Caribbean Sea and adjacent Atlantic, Hedges pays virtually no attention to the role of variables such as wind force and direction in the generation of surface currents. Wind and water currents that are attributable to the Coriolis force (plus the horizontal pressure gradient) are generally denoted as "geostrophic," in contrast to "surface" winds and currents whose direction and patterns are influenced by temperature gradients, the earth's surface relief, atmospheric pressure differentials, local climate, and other factors that induce or modify frictional forces (Levitus, 1982; Pickard & Emery, 1990; Berggren & Hollister, 1974). In the case of atmospheric motion, it is crucial to note that geostrophic

winds are generally found at altitudes above 1000 m, and because of this are little influenced by the earth's surface except in montane areas. By contrast, surface winds are significantly influenced by ground- and sea-surface conditions, and these will in turn affect prevailing wind direction at such surfaces.

We cannot provide here the relevant data on wind mapping and wind power density estimates for surface winds in the Caribbean, but we can refer the reader to useful on-line wind energy resource atlases for the Dominican Republic and Puerto Rico (Elliott *et al.*, 2002; also follow links at <http://rredc.nrel.gov/>). Information for Cuba is contained in the *Atlas Nacional de Cuba* (1970). Windrose directional information indicates that, at the level of the sea surface, winds may come in from virtually any direction during the course of the year on these islands. However, by far the commonest direction recorded at coastal and near-coastal recording stations is either ENE or due E. This is tangent to the inertial effect provided by the Coriolis force rather than parallel to it, and prevailing sea-surface wind direction is unlikely to have been different in the Caribbean region in the past (except to the degree to which local relief will considerably affect winds in the immediate vicinity of islands as they blow onto, or off of, emergent land).

These observations do not necessarily diminish the strength of Hedges' argument regarding the pre-eminence of overwater transport, as long as it is reasonable to believe that animal-bearing flotsam could travel toward the Antilles from positions that lie to the E or ENE of these islands. To evaluate this, we must now consider the flotsam contribution of large South American rivers.

2. Flotsam formation and travel times. In our paper we showed that the largest Cenozoic river systems in northern South America were never particularly well situated for sending propagules into the Caribbean, before or after the closing of the Panamanian isthmus. Hedges (2001, p. 26) criticized us for concentrating on "the rivers of northwestern (rather than northeastern) South America...because, even today, they are less likely to be major contributors of flotsam to the Greater Antilles." The major rivers in question—Demarara, Berbice, Courantyne, Oyapock, and several others—are all quite short, with lengthy flood plains, and small annual discharges in comparison to that of the Amazon or Orinoco. These rivers are well south of the usual tracks followed by hurricanes at the present day. Thus any variation in discharge rate is likely to be essentially seasonal, with large storms having only occasional effects. Nevertheless, according to Hedges (2001, p. 26), the important point is that flotsam coming out of these rivers would always have been pushed relatively northwestward due to the Coriolis force, and therefore "at least some flotsam from northeastern South America would have been deposited on the Aves land bridge (i.e., part of the Antilles) and directly on the Greater Antilles."

We agree. Generalizing from the drift bottle experiments we cite in our paper (Iturralde-Vinent & MacPhee, 1999), the evidence is clear that flotsam in this region will go practically everywhere—eventually. Time, however, is the central problem. Whatever capacities herp species may have for surviving long-distance overwater transport,

mammals such as insectivores and primates (let alone rodents and sloths) are unlikely to match them, especially when travel requires long periods in the open sea. Indeed, a primary reason for our suspecting that there must be a mechanism other than overwater transport to account for most Antillean land mammal distributions is the nature of the physiological constraints operating on small mammals. As Lindstedt (1980, p. 163) noted, "...the smallest animals are first to experience the effects of perturbations in their microclimate as their body temperatures are more directly affected by the physical environment (wind, radiation, temperature, etc.) than are those of larger animals." For a *Nesophontes*-sized animal, it is hard to contemplate a microclimatic perturbation more severe than spending a long time on a small natural raft (for interesting speculations regarding the ability of monkeys to survive long sea journeys, see Houle, 1999).

It is reasonable to infer from the information presented on prevailing surface winds that flotsam originating from rivers draining the Guiana Highlands must first travel northward before there is much chance of it being sent into the Caribbean. The named current that is the likeliest transporter of flotsam northward along the Atlantic coast of northeastern South America is the North Brazil (or Guiana) Current, although Hedges (2001) does not name it as such. One of the distinctive features of the North Brazil Current is that it produces very large (~400 km) anticyclonic eddies or "rings" that continually spin off from the main trunk of the current in the region of 6–8°N, i.e., along the coasts of the Guianas (Fratantoni, 2001). These rings, whose origin is not well understood, remain intact for long periods, passing roughly northwestward where they eventually decay. Because of their potential importance for transporting upper-ocean water across the equatorial-tropical gyre boundary into the Atlantic, ring formation and translation is being intensively studied by physical oceanographers using drifters and satellite imagery (Fratantoni, 2001; Fratantoni & Glickson, 2002). Drifters are submersible buoys that travel at operator-determined depths and relay various kinds of data (position, current speed, temperature, pH, etc.) on a specific schedule to monitoring satellites. Although there are no data on the effect of rings on the movement of the kind of flotsam of interest here, the fact that phytoplankton distribution is affected by these massive eddies suggests that other kinds of surface objects will be as well (Muller-Karger & Aparicio Castro, 1994). In one series of experiments monitored in 1998–2000 (Fratantoni, 2001; Fig. 2), drifters released at positions between approximately 9°N and 7°N (approximately the latitude of the mouths of the Orinoco and of Georgetown, Guyana), well away from the continental shelf. The most frequent drift pattern seen was lengthy entrapment in an eddy, with eventual release northwards (see fig. 2 and movie clip at http://science.whoi.edu/users/dfratantoni/NBC%20Rings/drifter_car.mov). Some drifters were caught in Atlantic surface currents that took them away from land, to eddy in positions east of Bahamas for the period of the experiment (fig. 2A, C). Others (not shown) actually went east, evidently caught by the Atlantic Equatorial Countercurrent which extends several degrees north of the equator because of the northern offset of the

warmest tropical water. Still others—those of greatest interest—passed into the Caribbean Sea through inter-island channels (i.e., between individual islands in the Lesser Antilles, or between the northern Greater Antilles and Bahamas/Turks and Caicos Islands). Transit times varied greatly (fig 2B, D), but the majority of drifters that entered Caribbean waters took *weeks to months* to cover the distance between their release point and the inter-island channel providing egress

As noted, for very small mammals with high metabolic rates living in the tropics, it is the capacity to withstand high temperatures that often determines survival (Vogel, 1980; Churchfield, 1990). Although metabolic rates are relatively lower in tropical as compared to temperate shrews (Vogel, 1980), we judge that a *Nesophontes*-sized insectivore would stand no chance of surviving a sea journey of more than a few hours in the Caribbean, because heat stress, exposure, and lack of food would surely kill it. Although it is a popular view that rodents are constitutionally more likely to survive a rafting event than are most other small mammals, this is unsupported assumption. Spennemann (1997), minutely reviewing the distribution of *Rattus rattus* and *R. norvegicus* in the Marshall Islands, concludes that these species have only invaded successfully when individuals managed to disembark along ropes and planks from moored vessels. Spennemann (1997) was unable to find any evidence of successful colonization from shipwrecks, as rats do not swim well enough to negotiate the surf. Like any anecdote-based argument, this conclusion can be challenged. However, it is surely germane to consider how difficult even short trips must necessarily be for most small mammals.

The fact that oryzomyin sigmodontines outside of the West Indies were also able to attain the Galápagos (Steadman, 1986) and Fernando da Noronha (Carleton and Olson, 1999) without any evident assistance from tectonics is a relevant counterclaim to our position, but such cases should not be overemphasized. In our view, physiological limits on propagules, whether actual or estimated, provide the only avenue for constraining the automatic appeal to rafting as nearly the sole (> 99%) mechanism of vertebrate faunal formation in the Antilles. If some kinds of reptiles can survive for long periods on rafts, as may be possible (e.g., Guadeloupean green iguanas rafting for ~ 1 month before reaching Anguilla; Censky *et al.*, 1998), then perhaps no constraint is feasible for this group. For mammals, we suspect that journeys of this length are normally out of the question. Finding a way of empirically verifying such a view, without appeal to mere anecdote, is the next challenge of Caribbean vertebrate biogeography.

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Fig. 2. Tracks of five drifters based on data originally compiled for Fratantoni's (2001) investigation of massive eddies in the North Brazil Current. The ones selected (out of several dozen released) for representation here were chosen to show diversity in the nature and direction of passive drift and in travel times between start/finish. Actual motion of drifters is considerably more complex than shown in the artist's renditions. "Origin area" refers to general area in which drifters were released from shipboard, at varying distances from NE coast of Brazil (for specific locations see movie clip noted in text). Colors indicate speed of drifters along different sections of their route (see scale). Four positions (in year/month/day format) are detailed for each drifter, to provide a sense of elapsed time en route. Original data grouped in ~10 day parcels, which is therefore the limit of precision. In all cases, "1" is point at which clock started for depicted drifter (and is never the same as actual release date, which is earlier by days or even weeks); "4" is point at which clock stopped (because drifter stopped transmitting, or because data collecting for this project ended in May 2000). Points "2" and "3" were chosen arbitrarily to give some idea of position vs. elapsed time along intermediate parts of each drifter's route. Examples chosen are average with respect to direction of drifter movement and speed. Although the general sense of movement is toward the NW, over short distances each drifter's track appears to be chaotic (unpredictable), involving frequent changes in direction and lengthy periods of slow or even retrograde motion.

Panel A, illustrating drifter bypassing Lesser Antilles and continuing into central Atlantic NE of Bahamas. 1, 1999/03/28—1999/04/08; 2, 1999/08/03—1999/08/13; 3, 2000/03/24—2000/04/03; 4, 2000/05/08—2000/05/18. Total elapsed time: beginning of April 1999 to mid-May 2000 (~13 months). Drifter passed close to northern Lesser Antilles, but left the region by August 1999 without coming close to any of them.

Panel B, illustrating two rather different drifter tracks involving central Caribbean Sea. The first drifter passed around the Lesser Antilles to enter the Caribbean Sea through the Mona Passage, eventually passing into the Gulf of Mexico and thence along the E side of Florida before leaving the monitoring area. 1, 1999/03/23—1999/04/01; 2, 1999/09/07—1999/09/17; 3a, 1999/08/01—1999/08/10; 3b, 1999/11/03—1999/11/13; 4, 2000/04/01—2000/04/11 (drifter continued N off map). Passage from origin along the Lesser Antilles chain and thence to Mona Passage took ~5 months. Thereafter drifter passed into a complicated series of eddies in the central Caribbean for two months, then traveled relatively quickly through the western Caribbean and along Yucatan coast. Changed direction to E to pass through Strait of Florida.

The second drifter passed almost directly westwards through the Lesser Antilles, across the Caribbean and thence into the Gulf of Mexico, terminating near the Mississippi delta. 1, 1999/03/23—1999/04/01; 2, 1999/12/15—1999/12/25; 3a, 1999/10/07—1999/10/16; 3b, 1999/12/21—1999/12/31; 4a, 2000/02/08—2000/02/18; 4b, 2000/05/08—2000/05/18. Total elapsed time: beginning of April 1999 to mid-May 2000 (~13 months). Like the first drifter, the second drifter was caught in eddies (not shown) in the central Caribbean for a considerable period (October–December 1999) before being passed through the western Caribbean to the Yucatan Channel. From there it moved rapidly N (instead of E), crossing the Gulf of Mexico in ~2 weeks to eddy at its end point.

Panel C, illustrating route of drifter caught for ~3 months in a series of large rings propagating off NW coast of South America and continuing along E side of Lesser Antilles. 1, 1999/02/08—1999/02/18; 2, 1999/03/19—1999/03/28; 3, 1999/05/03—1999/05/12; 4, 1999/06/21—1999/07/01 (hereafter drifter followed path similar to one depicted in panel A, and remained in central Atlantic until end of experiment). Although drifter speed was comparatively high within rings, actual distance traveled along a straight line was much less.

Panel D, illustrating drifter passing into the Caribbean Sea and terminating off NW coast of Puerto Rico. 1, 1999/02/07—1999/02/17; 2, 1999/03/09—1999/03/19; 3, 1999/04/08—1999/04/17; 4, 1999/06/10—1999/06/20 (ceased transmitting). Total elapsed time: mid-February to mid-June 1999. From origin to passage through the Lesser Antilles took approximately one month. However, travel to point of termination off Puerto Rico took an additional 3 months because of eddying in central Caribbean. Thus despite this route's apparent "directness", the trip took 4 months—a long time for a terrestrial mammal, at least, to be at sea.

Fig. 2. Rastres de cinc boies basats en dades originalment agrupades per la recerca de Fratantoni (2001) sobre remolins massius a la Corrent Nord Brasileira. Les que s'han seleccionat (d'algunes dotzenes llençades), per a la seva representació aquí, varen ser triades per mostrar la diversitat en la natura i direcció de la deriva passiva i en la durada del viatge entre el començament i el final. El moviment real de les boies és considerablement més complex que el que es mostra a les recreacions artístiques. L'àrea d'origen es refereix a l'àrea general en la qual les boies varen ser llençades des d'un vaixell, a distàncies variables de la costa NE de Brasil (per a veure les localitzacions exactes, moure el tros de pel·lícula indicat al text). Els colors indiquen la velocitat de les boies al llarg de diferents seccions de les seves rutes (veure escala). Es detallen quatre posicions (en format any/mes/dia) per a cada boia, per subministrar una idea del temps transcorregut en ruta. Les dades originals estaven agrupades en parcel·les de devers 10 dies, el qual és, a llavors, el límit de precisió. En tots els casos "1" és el punt en que el relloge va començar a funcionar per a la boia representada (i mai és el mateix que la data real de llençament, la qual és uns dies o àdhuc unes setmanes anterior); "4" és el punt en que el relloge es va aturar (degut a que la boia va deixar de transmetre o degut a que l'obtenció de dades per aquest Projecte va acabar el Maig del 2000). Els punts "2" i "3" varen ser triats arbitràriament per tenir alguna idea de la posició vs. el temps transcorregut al llarg d'indrets intermedis de la ruta de cada boia. Els exemples triats són el promig respecte la direcció del moviment i la velocitat de les boies. Encara que el sentit general del moviment és NW, sobre distàncies curtes el rastre de cada boia sembla ser caòtic (impredictible), amb canvis freqüents en direcció i llargs períodes de moviment lent, o fins i tot retrògrad.

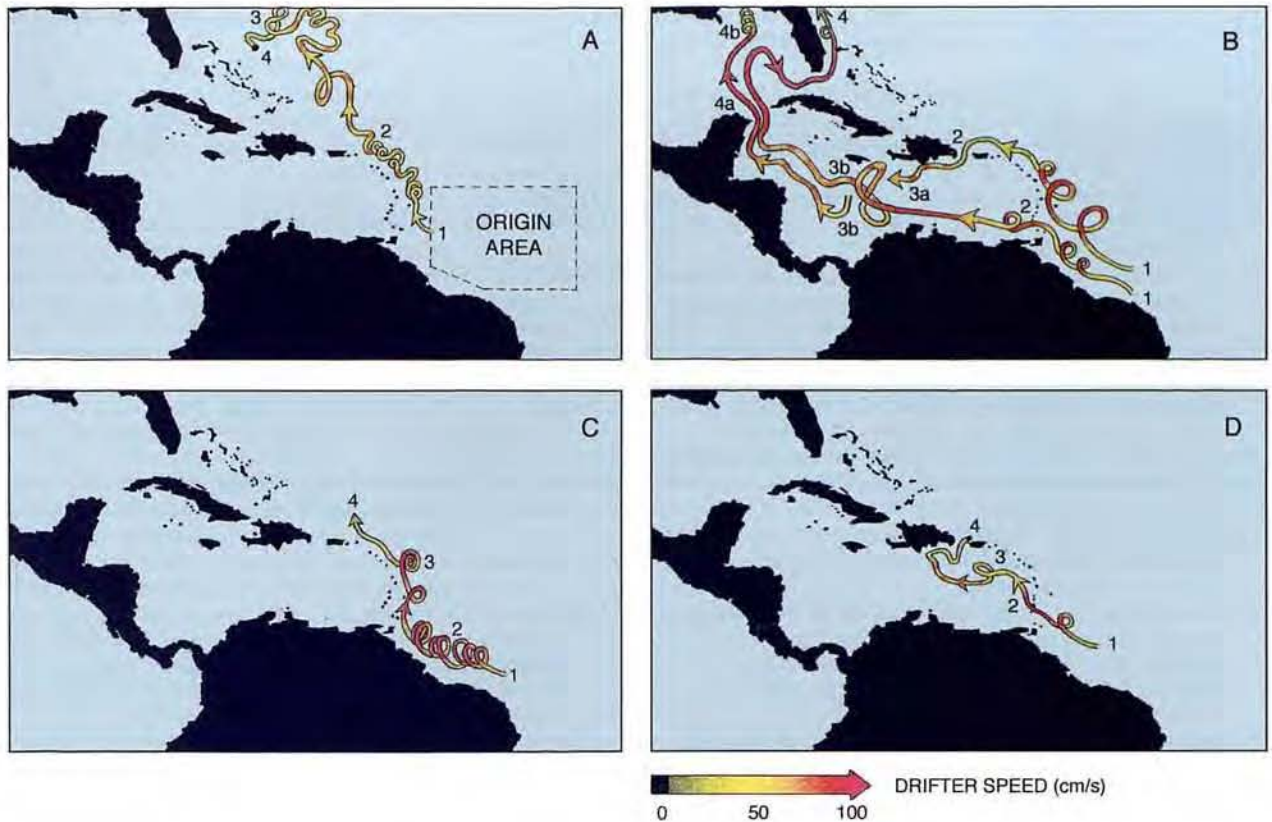
El **Panel A** il·lustra el pas de la boia per les Antilles Menors i la seva continuació cap a l'Atlàntic central, NE de Bahames. 1, 1999/03/28—1999/04/08; 2, 1999/08/03—1999/08/13; 3, 2000/03/24—2000/04/03; 4, 2000/05/08—2000/05/18. Temps total emprat: començaments d'abril de 1999 fins a mitjans maig 2000 (devers 13 mesos). La boia va passar prop de les Antilles Menors septentrionals, però va deixar la regió l'agost de 1999, sense tornar-s'hi apropiat.

El **Panel B** il·lustra dos rastres de boia més aviat diferents, afectant la Mar del Carib central. La primera boia va passar al voltant de les Antilles Menors per entrar a la Mar del Carib a través del Pas de Mona, passant al Golf de Mèxic i d'aquí al llarg de la costa E de Florida abans de deixar l'àrea de control. 1, 1999/03/23—1999/04/01; 2, 1999/09/07—1999/09/17; 3a, 1999/08/01—1999/08/10; 3b, 1999/11/03—1999/11/13; 4, 2000/04/01—2000/04/11 (la boia continuà cap al N del mapa). El pas des de l'origen al llarg de la cadena de les Antilles Menors i d'aquí al Pas de Mona va durar devers 5 mesos. A llavors la boia va passar per una sèrie de remolins complicats al Carib central durant dos mesos, a llavors va viatjar relativament aviat a través del Carib occidental i la costa del Yucatán. Va canviar de direcció cap a l'Est per passar a través de l'estret de Florida.

La segona boia va passar quasi directament cap a l'oest a través de les Antilles Menors, creuant el Carib i d'aquí cap al Golf de Mèxic, acabant prop del delta del Mississipi. 1, 1999/03/23—1999/04/01; 2, 1999/12/15—1999/12/25; 3a, 1999/10/07—1999/10/16; 3b, 1999/12/21—1999/12/31; 4a, 2000/02/08—2000/02/18; 4b, 2000/05/08—2000/05/18. Temps total transcorregut: des de començaments d'abril de 1999 fins a mitjans maig del 2000 (devers 13 mesos). Igual que la primera boia, la segona boia va ser capturada per remolins (no mostrat) a l'àrea central del Carib durant un període de temps considerable (d'octubre de 1999 a desembre de 1999) abans de passar a través del Carib occidental al Canal de Yucatán. Des d'aquí es va moure ràpidament cap al N (en lloc de cap a l'Est), creuant el Golf de Mèxic en devers dues setmanes, fins a arremolinar-se en el seu punt final.

El **Panel C** il·lustra la ruta d'una boia capturada durant devers tres mesos a una sèrie d'anells que es propagaven lluny de la costa NW de Sud-Amèrica i continuaven al llarg del costat E de les Antilles Menors. 1, 1999/02/08—1999/02/18; 2, 1999/03/19—1999/03/28; 3, 1999/05/03—1999/05/12; 4, 1999/06/21—1999/07/01 (a partir d'aquí la boia va seguir un camí similar a un representat al **Panel A**, i va restar a l'Atlàntic central fins el final de l'experiment). Tot i que la velocitat de la boia va ser relativament alta dintre dels anells, la distància real recorreguda en línia recta va ser molt més petita.

El **Panel D** il·lustra el pas d'una boia al Carib central i acabant lluny de la costa NW de Puerto Rico. 1, 1999/02/07—1999/02/17; 2, 1999/03/09—1999/03/19; 3, 1999/04/08—1999/04/17; 4, 1999/06/10—1999/06/20 (va deixar de transmetre). Temps total transcorregut: des de mitjans de febrer fins mitjans juny de 1999. Des de l'origen fins el seu pas a través de les Antilles Menors va transcórrer aproximadament un mes. No obstant això, viatjar fins al punt final lluny de Puerto Rico va implicar una duració addicional de tres mesos, degut als remolins del Carib central. Per això, tot i la semblança d'una ruta directa, el viatge va durar 4 mesos—un temps com a mínim massa llarg com per a que un mamífer terrestre estigui a la mar.



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