
MODERN PROCESSES AND HISTORICAL FACTORS IN THE ORIGIN OF THE AFRICAN ELEMENT IN LATIN AMERICA

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ABSTRACT

The combination of factors that account for present-day distributions of organisms is unique to individual lineages and varies over time. An observation relevant to some lineages at some point in their history is that hurricane frequency and intensity appears to be increasing with global warming. If so, then directional winds from Africa to the Caribbean region (the trade winds), from South America to Africa (the westerlies), the ocean currents they induce, and the transport of the floating islands they carry, were likely more intense during the generally warmer-than-present Tertiary Period and especially at peaks of exceptional warmth. These peaks occurred in the Paleocene/Eocene (65–45 Ma), in the early to middle Miocene (broadly between ~23–12 Ma), in the middle Pliocene (3–4 Ma), and probably extended slightly later in the lower latitudes. The Paleocene/Eocene interval includes the time when the distance between Africa and South America was one-half to two-thirds that of the present, and when the Greater Antilles island arc was first becoming emergent as increasing target areas for propagules. The second and third intervals of warming include the times when molecular evidence suggests divergence between several African and New World lineages. Thus, wind and ocean transport of organisms and propagules throughout the Tertiary, and especially at peaks of warmth, was likely a more important means of dispersal than would seem plausible under present conditions.

Key words: Africa, Caribbean, dispersal, dust transport

RESUMEN

La combinación de factores que explican la distribución actual de los organismos es única a los linajes individuales y varía a través del tiempo. Una observación relevante para algunos linajes en un cierto punto en su historia es que la frecuencia y la intensidad de huracanes parecen aumentar con el calentamiento global. De ser así, entonces los vientos direccionales desde África hacia la región del Caribe (los vientos alisios), desde América del Sur hacia África (los vientos del oeste), las corrientes oceánicas que inducen y el transporte de las islas flotantes que llevan, fueron posiblemente más intensos durante el período Terciario, generalmente más caliente que el presente, y especialmente durante los picos excepcionales de calor. Estos picos ocurrieron en el Paleoceno/Eoceno (65–45 Ma), en el Mioceno temprano a medio (ampliamente entre ~23–12 Ma), en el Plioceno medio (3–4 Ma) y probablemente se extendieron levemente más adelante a las latitudes más bajas. El intervalo de Paleoceno/Eoceno incluye el tiempo en que la distancia entre África y América del Sur era la mitad a dos tercios de la actual, y cuando el arco de las Antillas Mayores recién empezaba a emerger como área blanco para los propágulos. El segundo y el tercer intervalos de calentamiento incluyen los períodos en que la evidencia molecular sugiere divergencia entre varios linajes africanos y del Nuevo Mundo. Así, el transporte de los organismos y propágulos por viento y océano durante el Terciario, y especialmente durante los picos de calor, fue probablemente un medio más importante de dispersión de que parecería plausible en condiciones actuales.

An increasing number of plants with African affinities is being recognized in the Gulf/Caribbean and adjacent region. For example, the American Lythraceae genera *Crenea* Aubl. and *Ginoria* Jacq. have African origins (S. Graham, 2002). The Dominican amber has long been regarded as a product of the legume *Hymenaea* L., but Hueber and Langenheim (1986) have shown that rather than being produced by the widespread New World species *H. courbaril* L., its spectral pattern is most similar to the African *H. verrucosa* Gaertn. In the pteridophytes there are an

estimated 114 species showing relationships between Africa/Madagascar and the Neotropics of which 27 are common to both areas and 87 are species pairs. Migration seems to have been primarily from South America to Africa, but, as the authors note (Moran & Smith, 2001; Smith, pers. comm., 2004), the direction of movement is not always clear, and extinctions may have obscured the pattern. In a study of 123 species of *Elaphoglossum* Schott ex J. Sm. (Elaphoglossaceae), Rouhan et al. (2004) concluded on the basis of molecular evidence that at least 21 long-distance

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dispersal events occurred between the African-Indian Ocean region and the Neotropics. Renner (2004) further lists 110 angiosperm genera with species on both sides of the tropical Atlantic Ocean.

The principal explanation for the origin of biotic affinities between Africa and the Americas at the level of family or \pm distantly related genera is vicariance dating to the separation of the New and Old World continents in Jurassic and Cretaceous times (Nelson & Rosen, 1981; Wiley, 1988). For more recently evolved taxa, one option is direct overland migration available until about the middle Eocene (see below). After that time, long-distance dispersal (LLD: Cain et al., 2003; Renner & Givnish, 2004) becomes progressively more important for those capable of crossing significant marine barriers; for example, for the 14 polypodiaceous families (*sensu lato*) listed by Moran and Smith (2001) as appearing primarily in the Tertiary.

In the earlier days of biogeography, long-distance transport essentially constituted a non-theory because it was invoked to explain how any organism could get anywhere given enough time. This was countered by the equally fatuous view that vicariance was the means of dispersion, and that dispersal biogeography was "a science of the improbable, the rare, the mysterious, and the miraculous" (Nelson, 1978). As noted elsewhere, vicariance, as thus proclaimed, has certain mystic qualities of its own (Graham, 1999: 318). More balanced hypotheses tailored to the age, morphological features, and systematic relationships of individual lineages have been proposed (Givnish & Renner, 2004) within a context of temporally better-defined tectonic events and climatic conditions (Graham, 2003a, b; present symposium).

It is also increasingly recognized that patterns of biotic affinities are immensely complicated, and that their origin is not likely resolvable by single-factor explanations. The most satisfactory models will be based on a systems approach, wherein a broad spectrum of factors varying in kind and degree, and in different combinations over time, form the basis for models accounting for the presence of identical or closely related organisms in distant geographic regions. The requisite information includes: (1) a taxonomy that accurately reflects real affinities and the level of relationship; (2) a knowledge of the dispersal processes (Higgins et al., 2003); (3) the principal transporting vectors (directional atmospheric and ocean currents, animal migration routes); (4) an adequate fossil record broadly establishing the probable time, place, and migration history of the lineage; (5) a knowledge of the relevant geologic events and landscape configurations during the existence of the lineage; and (6) a knowledge of the climates and climatic change, at the relevant times,

across the area being transgressed. The North Atlantic land bridge became progressively discontinuous from the south (the Thulean route) to the north (the Svalbard route) after about the middle Eocene (Tiffney, 1985; Graham, 1999: 61–64), and this was at about the same time that global climates at the high latitudes were trending from the generally tropical hothouse interval of the Paleogene toward the temperate icehouse conditions of the Neogene. The Panama land bridge connecting North and South America was discontinuous until ~ 3.5 Ma (Ma = million years, millions of years ago), continuous but with lowland habitats suitable for tropical elements until ~ 2.5 Ma (Coates, 1997), and continuous with scattered upland habitats available for more temperate elements after that time (Graham, 1992; Burnham & Graham, 1999). Thus, the relevancy of these routes to a particular lineage depends on when the migration took place and the ecological requirements of the migrants. It is obvious that much of the information necessary for documenting migration routes and the origin of disjunct distributions is unknown for most organisms, for most places, for most of geologic time. Consequently, information that increases the range of feasible dispersal opportunities is useful in building a database commensurate with the complexity of the problem.

An observation particularly apparent in the satellite era is that large amounts of dust, bacteria, diatoms, phytoliths, fungi, spores, and probably lichen fragments are blown into the Caribbean region each year via the northeast and southeast trade winds from the Sahara Desert and the Sahel, the drought-plagued region south of the Sahara in Africa (BioBriefs, 1991; Reid et al., 1996; Cadée, 1998; Arimoto, 2001; Harrison et al., 2001; Kohfeld & Harrison, 2001; Prospero, 2001; Prospero & Lamb, 2003; Ryan, 2001; Griffin et al., 2002; Garrison et al., 2003; Toon, 2003). The amounts are impressive—13 million tons/yr. (Griffin et al., 2002), depositing one pound of phosphate/yr./acre into the Amazon Basin. The phenomenon has been recognized since the time of Darwin, who complained that it was "dirtying everything on board [the Beagle] and even hurting people's eyes" (Cadée, 1998: 16). Studies on the atmospheric transport of dust are primarily concerned with the climatic effects, the bleaching of corals, the spread of pathogens, and human health, but the potential for disseminating small propagules is obvious, if remote under present conditions.

However, conditions change, and another observation is that possibly the frequency (Trenberth, 2005) and certainly the intensity of hurricanes in the Atlantic Ocean and elsewhere has increased in recent decades (Moreno et al., 2002; Otvos, 2002; Emanuel,

2005). There has been an estimated two-fold increase in the number of hurricanes over the past six years compared to the previous 24 years, and the number of major hurricanes has increased 2.5 times (Bengtsson, 2001; Goldenberg et al., 2001; Hoyos et al., 2006; Webster et al., 2005). The suspected cause is global warming (Knutson et al., 1998; Goldenberg et al., 2001), and the change has been induced by an estimated global rise of only 0.6°C for the past century and 0.2°C–0.3°C in the last 40 years. An association not widely noted in the current literature is that this brings the observation on modern hurricanes into the realm of paleontological interest, because throughout the Tertiary temperatures were generally warmer than at present (see global paleotemperature curve; e.g., Graham, 1999: 89), and there have been times in the geologic past when they were much warmer than at present.

After the asteroid impact at the end of the Cretaceous Period 65 Ma, climates began to warm and reached a threshold between the early Paleocene (65 Ma) and the early Eocene (45 Ma) termed the LPTM (late Paleocene thermal maximum) and EECL (early Eocene climatic optimum), when temperatures were as high or higher than at anytime in the Phanerozoic Era (Pomeroy & Premoli-Silva, 1986; Prothero, 1994; Huber et al., 2000; Schmitz et al., 2000). There was a rise in the early Miocene and extending into the middle Miocene (23–12 Ma with a peak at 18–14 Ma), and in the Middle Pliocene (3–4 Ma; Wrenn et al., 1999). The temperature values were ~12°C–15°C, 4°C–8°C, and 3°C–4°C warmer than at present, respectively, in the high latitudes (Graham, 1999: 89), and these periods of unusual warmth probably extended somewhat later in the mid-latitudes. If global warming is part of the cause for the modern rise in global temperatures, then warmer times of the past, and particularly these exceptionally warm intervals, should have witnessed an enhanced flow of directional winds and ocean currents between Africa and the Caribbean region, depending on the altered continental configurations (mostly in the Eocene) and the distribution of high and low pressure systems.

Two other observations are relevant to the kinds and amount of biological debris arriving from Africa during past warmer times, and especially during peaks of warmth. One is that at the time of the LPTM and EECL, the distance between Africa and the South America/Caribbean region was one-half to two-thirds that of the present. Intervening land may have been available along the mid-Atlantic Ridge, or above hot spots as at present on the Tristan da Cunha Group (oldest of the present islands is Nightingale Island at ~18 Ma fide www.btinternet.com) in the path of the opposite-flowing westerlies from South America to

Africa. The other is that it was in the Eocene that the Greater Antilles began their principal period of emergence (Graham, 2003a, b), providing increased target areas for new arrivals.

There is considerable information available from projects such as PRIDE (Puerto Rico Dust Experiment) on the chemical composition, source, and configuration of dust particles being transported under present conditions, and these particles average 30µ–40µ in size (Colarco et al., 2003; Maring et al., 2003; E. Reid et al., 2003; J. Reid et al., 2003; R. Reid et al., 1996; Prospero et al., 2005). However, the maximum size and density of particles recovered is not tabulated, although it is probably about 100µ (or less fide Prospero, pers. comm., 2004). Silica minerals greater than 75µ have been found in the atmosphere and in water columns transported from eastern Asia across the Pacific Ocean (Betzer et al., 1988). These minerals and mineral aggregates are far heavier than the less dense and often more aerodynamically suited biological material, and it may be speculated that biological debris to a maximum size of 300µ–500µ is occasionally transported under present conditions (and rarely even larger material; see Renner, 2004: S31); probably larger material arrives under hurricane conditions (perhaps as much as 500µ–700µ); and still larger material was likely transported more frequently during times of maximum warmth and greater wind velocities in the LPTM and EECL (65–45 Ma), the early to middle Miocene (23–12 Ma), and the middle Pliocene (3–4 Ma; ?700µ–1200µ). Obviously, additional information is needed on the nature and maximum size and density of material presently being transported, as well as comparable data on relevant modern dissemules, especially during times of maximum wind velocity.

The point is that, collectively, these factors in the geologic past afforded greater possibilities for the introduction of a broader array of plants from Africa into the Caribbean region, possibly in the opposite direction at lower latitudes, across the Pacific Ocean, between Patagonia and Antarctica and beyond (Iriondo, 2000; Muñoz et al., 2004), and perhaps in other parts of the world, via wind, water, and drift than would seem plausible under modern conditions. As taxonomic relationships become better defined, the number of organisms recognized with African-New World affinities will likely increase, and the above observations of enhanced hurricane intensity, shorter distances, and increasing target areas should be considered in developing multi-faceted models to explain the introduction of some of them. This is particularly true for those with means of long-distance dispersal (Givnish & Renner, 2004), such as pieces of lichen, the spores of bryophytes and ferns, vegetative

reproductive fragments, and flowering plants with minute, plumose, and/or floating seeds such as in the Bromeliaceae (Givnish et al., 2004), *Ginorea* (Lythraceae; S. Graham, 2002), some Myrtaceae (Sytsma et al., 2004), Orchidaceae, Piperaceae, and others. Fossil and/or molecular evidence also suggests correspondence between times of introduction and the exceptional warm intervals of the Tertiary Period centered around 65–45 Ma, 23–12 Ma, and 3–4 Ma. In addition to some Melastomataceae and Lemnaceae (*Wolffiella* Hegelm.) estimated to have dispersed between Africa and South America 10–11 Ma (Renner, 2004, table 2), Tremetsberger (pers. comm., 2004) provides the following examples of plants with Old World–New World relationships, and estimates of the time of separation corresponding to ~3–4 Ma:

Evidence for long distance dispersal across the Atlantic Ocean has been documented in *Senecio* sect. *Senecio* L. (Asteraceae; two inferred dispersals from the Old to the New World; Coleman et al., 2003). The Mediterranean and southern African floras were not distinguishable as sources of the main New World lineage, estimated to have become established during the middle Pliocene (3–4 Ma; Coleman et al., 2003).

Käss and Wink (1997) hypothesized long distance dispersal of Old World (Mediterranean and African) lupines (Fabaceae) to the eastern parts of South America ("Atlantic region") and, independently, to North America and western regions of South America during the end of the Miocene (~8 Ma for dispersal to eastern parts of South America) and Pliocene (~3–4 Ma for dispersal to North America and western regions of South America).

Hypochaeris L. (Asteraceae, Chichorieae) has about 15 species in the Old World, including Morocco, and more than 40 species in South America (Tremetsberger et al., 2004). DNA sequencing suggests a NW African origin for the South American group with long distance dispersal across the Atlantic Ocean. Based on molecular clock evidence, the trans-Atlantic dispersal from Morocco to South America can be estimated to have taken place ~3.5 Ma or less; i.e., during Pliocene or Pleistocene times (Tremetsberger et al., 2005).

Among other examples, Davis et al. (2004) suggest that in the Malpighiaceae, six amphi-Atlantic disjunctions occurred from South America to Africa between 60–31 Ma (middle Paleocene to early Oligocene) and at about 17 Ma (early Miocene). Divergence of neotropical and African *Symphonia* L.f. is placed at 17.36 ± 1.53 Ma (Dick et al., 2003). As the list increases it is worthwhile to monitor the examples for estimated times of dispersal, correspondence with warm intervals of the geologic past, and the distribution potential of the propagules, to determine if significantly increased directional winds and currents might be a factor in those patterns difficult to explain by vicariance or gradual overland migration alone.

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