Perspectives in Plant Ecology, Evolution and Systematics 15 (2013) 269–280

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Forum

Trans-oceanic dispersal and evolution of early composites (Asteraceae)

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ARTICLE INFO

Article history:
Received 9 April 2013
Received in revised form 23 July 2013
Accepted 24 July 2013
Available online 22 August 2013

Keywords:
Africa
Compositae
Rafting
South America
Stepping-stones
Sweepstakes

ABSTRACT

How did Asteraceae (the daisy family) expand from its area of origin and become so widespread? This question has challenged generations of evolutionary botanists. Molecular phylogenetic and biogeographic analyses indicate a South American origin of Asteraceae, a view supported by the recent discovery of the earliest fossils of the family in Middle Eocene (ca. 50 Ma) deposits in southern South America. The early-branching lineages in the phylogenetic tree of Asteraceae are South American and African, suggesting that the earliest successful colonization of areas outside South America may have involved long-distance dispersal to Africa. However, one particularly challenging unanswered question is how early members of Asteraceae reached Africa at a time when the Atlantic Ocean constituted a barrier between the two continents. Morphological, phylogenetic, geographic, paleogeographic, and paleontologic data have been combined to propose scenarios on possible geographical and dispersal routes and vectors of dispersion of early-branching lineages of Asteraceae from South America to Africa. Of the different scenarios proposed here, two concern alternative geographical routes: (1) via the Rio Grande Rise-Walvis Ridge axis in the South Atlantic; or (2) via Antarctica, possibly including the Subantarctic islands. Three scenarios consider different dispersal routes: (1) stepping-stones; (2) single-step; and (3) sweepstakes. Finally, three vectors of dispersion are considered: (1) birds; (2) wind; and (3) floating islands. Evaluation of these scenarios suggests that early-branching lineages of Asteraceae probably dispersed from South America to Africa along an island chain formed by the Rio Grande Rise and the Walvis Ridge, transported by birds, possibly combined with rafting and/or sweepstakes. Morphological changes typically associated with evolution on islands characterize many African carduoid descendants, providing indirect evidence for step-wise dispersal along the island chain.

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Introduction

Daisies and sunflowers belong to the plant family Asteraceae characterized by: (1) flowers closely aggregated into indeterminate heads (capitula); (2) five laterally fused anthers that form a tube through which the style pushes upward, forcing the pollen out of the tube; and (3) the pappus, which is a modified calyx above the inferior ovary. Asteraceae is the most species-rich family, comprising 1600 genera and 23,000–25,000 species found worldwide, but especially concentrated in grassland, wooded grassland and montane vegetation, and comparatively few in humid tropical lowland forests (Jeffrey, 2007).

The question of how Asteraceae expanded from its area of origin and became so widespread has been and still is the subject of a long debate. Turner (1977), for example, invoked plate tectonics as an explanation for the initial distribution of the family. Other authors such as Raven and Axelrod (1974) argued that while the distribution of older flowering plant families may be the result of plate tectonics, the distribution of more advanced and presumably younger families such as Asteraceae did not result from the breakup of Gondwana (Bremer, 1993). Some angiosperm elements (e.g., Casuarinaceae, Winteraceae) had probably evolved before the separation of at least some Gondwanan landmasses, and to a significant extent the distribution of extant representatives of these groups probably reflects vicariance events. However, in families such as Asteraceae, the available geological and paleontological evidence suggests that continental breakup occurred before

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http://dx.doi.org/10.1016/j.ppees.2013.07.003

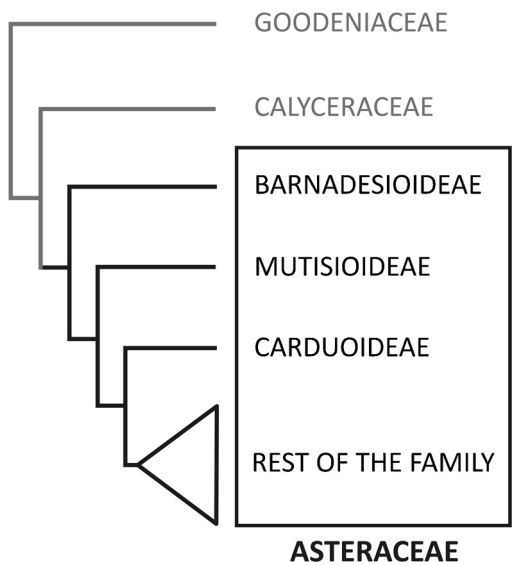

Fig. 1. Reduced molecular cladogram of Asteraceae and related families, showing the basal groups of the family. Mutisioideae is considered sensu lato (Katinas et al., 2008).

the differentiation of plant groups that are traditionally cited as having a Gondwanan heritage based on their wide distribution in the Southern Hemisphere (McLoughlin, 2001). The oldest fossil yet found in Asteraceae is a capitulum with pollen grains dated at ca. 50 million years (Ma) (Barreda et al., 2010a), which established a minimum age for the family.

For more than a century, workers have also speculated on the place of origin of Asteraceae. For example, Bentham (1873) concluded that Africa, "West America", and possibly Australia were the homes of ancestral members of the family. Small (1919) estimated that the Asteraceae originated in the Amazon and northern Andes of South America. With the advance of molecular phylogenetic and biogeographic techniques and approaches, testable hypotheses about the origin of the family have been developed. The basalmost branches (i.e., topologically close to the root node of a phylogenetic tree) in the tree of Asteraceae (Funk et al., 2009a) are represented by two subfamilies, Barnadesioideae and Mutisioideae sensu lato (Katinas et al., 2008), which are respectively distributed exclusively and mainly in South America. The next basalmost branch is subfamily Carduoideae, which is centered in Africa and the Mediterranean (Fig. 1; Appendix 1). When the progression rule (Hennig, 1966), which establishes that the primitive members of a taxon are found closer to its center of origin than more derived ones in the context of phylogenetic biogeography (Crisci et al., 2003), is applied to the Asteraceae phylogenetic tree, it supports a South American origin of the family. Funk et al. (2005) applied other historical biogeographic methods to this tree to find the ancestral area of Asteraceae, including the Ancestral Areas approach (Bremer, 1992) in its several versions, and the "Parsimony Optimization" option of MacClade (Maddison and Maddison, 1992). These analyses provided the same answer: southern South America is the most likely ancestral area of Asteraceae.

In addition, several fossils of early-branching lineages of Asteraceae have been found from the Paleogene in southern South America (e.g., Katinas et al., 2007; Palazzesi et al., 2009), the earliest from the Middle Eocene (ca. 50 Ma) (Barreda et al., 2010a, 2012) together with Eocene fossil pollen of Asteraceae found on the east coast of Antarctica (55–46 Ma.) (Pross et al., 2012). Surveys indicate that Paleocene-Miocene deposits in southwestern Africa contain pollen of Asteraceae (Partridge, 1978; Zavada and De Villiers, 2000; Zavada and Lowrey, 2010), some of which are similar to extant *Dicoma* (Carduoideae) pollen with its characteristic echinate sculpture. The temporal assignment requires further confirmation by new research and absolute dating methods (Scott et al., 2006) (Appendix 1). The age of the South American and Antarctic fossils more or less coincides with the estimates of an origin of the family in the Middle Eocene (42–49 Ma) using a molecular clock applied to the phylogenetic tree of Asteraceae and seven related families (Kim et al., 2005). This tree was calibrated with Poaceae, which resulted in an underestimate of the actual times of divergence for the Asteraceae, and Olacaceae, which resulted in an overestimate of the actual divergence times, since no unequivocal fossils for Asteraceae were available at that time; therefore new calibrations are needed. A temporal gap of unknown magnitude exists between the divergence of Asteraceae and its sister family Calyceraceae from their common ancestor, the origin of the capitulum (most important synapomorphy), and the occurrence of the oldest fossil of Asteraceae bearing a capitulum (Middle Eocene). Molecular dating methods have provided evidence of the first event, whereas the fossil record provides evidence of the third (Magallón, 2004). The age of origin of the Asteraceae is a question that still lacks a non-speculative answer. Methods that assess the uncertainty of times of origin are based on the idea that the difference between the origin of a clade and its first fossil appearance is inversely correlated with the quality of its fossil record (Magallón, 2004). Therefore, due to the richness of the South American fossil record, it is possible that the family may have originated close to the Eocene or in the Late Paleocene. On the other hand, the discovery of fossils in Antarctica added an interesting new component to the past distribution of Asteraceae, broadening the possible area of origin of the family. Hence, it is possible that the ancestor of the Asteraceae and first members of the family were distributed either in southern South America, in Antarctica, or in an area involving both continents.

If the basalmost branches in the phylogenetic tree of Asteraceae (Funk et al., 2009a) are South American and the next basalmost branches are African, an obvious question is how ancient members of the family reached Africa from South America. Bremer (1994) suggested the possibility of a Pacific-Asian dispersal route of Asteraceae from their ancestral area in South America via Hawaii, with further migration to other continents including Africa. Recent molecular phylogenetic evidence (Panero and Funk, 2008) suggests that several early successful colonization of areas outside South America may have resulted from two long-distance dispersal events, or possibly from stepping-stone migration across oceanic barriers from South America to North America and to Africa. Therefore, compared to alternative and more complex biogeographical scenarios, and taking into account the age of the fossil records, the most plausible explanation for the presence of carduoid members of the family in Africa involves a trans-oceanic dispersal. Even by the Eocene (ca. 50 Ma), when South America and Africa were about 1000 km apart at their closest geographic points (Bandoni de Oliveira et al., 2009), a strong floristic affinity prevailed.

Despite the abundance of research regarding the place and time of origin of the family, a fundamental question has not yet been answered: How did members of Asteraceae reach Africa at a time when the Atlantic Ocean constituted a barrier between South America and Africa? Modern workers have invoked rapid dispersal mainly by birds or wind (Stuessy et al., 1996) or stepping-stone migration across oceanic barriers (Raven and Axelrod, 1974; Panero and Funk, 2008) to explain the presence of Asteraceae outside South America, but specifically where and how the earliest representatives of the family accomplished this are questions that have yet to be answered with some confidence. While long-distance dispersal is a well-established fact, it is very difficult to provide clear evidence for it and so it is largely recorded on a narrative basis. However, the

Table 1
Possible scenarios' alternatives for the early lineages of Asteraceae during the Paleocene-Eocene in their past migration from South America to Africa, with the strongest evidence supporting some of these alternatives. See explanations against alternatives in the text.

Routes and vectors	Alternatives	Evidence in favour
Geographical routes	Atlantic route	Islands (now submerged) existed between South America and Africa along the Rio Grande Rise – Walvis Ridge axis.
	Antarctic route	
Dispersal routes	Stepping-stones (involving evolutionary processes)	Evolution on islands is reflected in morphological changes in descendants. Evolutionary changes in pollen of descendants.
	Single-step (not involving evolutionary processes)	
	Sweepstakes (not involving evolutionary processes)	Probably or probably not as a participant in dispersal. Hurricanes and other weather anomalies are known to have occurred in the past in the Atlantic Ocean.
Vectors	Birds	Are independent of sea currents. Are relatively dependent on favorable winds. Attachment of fruits to bird feathers or legs is known to be important for dispersal to islands. Mutisioideae and Carduoideae have fruits with sticky hairs adapted to dispersal by birds. The South American Barnadesioideae, which lacks these hairs, did not disperse to other continents. There are records of fossil birds of South America and Africa that may have migrated between continents.
	Wind	
	Floating islands	

methodological inadequacy of long-distance dispersal as a general explanation should not be taken to imply its unreality as a process (Weston and Hill, 2013).

This paper aims to bring together morphological, phylogenetic, geographic, paleogeographic, and paleontologic data (see Appendix 1) to propose and test possible scenarios regarding geographical and dispersal routes and vectors of dispersion of early-branching lineages in the phylogenetic tree of Asteraceae in their presumptive migration from South America to Africa.

Possible scenarios

Different scenarios are postulated here (Table 1) regarding possible geographical and dispersal routes, and vectors of dispersion. Geographical routes concern the paths by which early diverging South American lineages of Asteraceae dispersed to southern Africa. Two possible crossing areas are a trans-Atlantic route at a latitude corresponding to present-day 23–35° S latitude, and further south, through the Antarctic-Subantarctic region. Other emergent terrain systems at that time are either incomplete or poorly known, outside of the ancestral distribution area of the family, or are geologically too young. Dispersal routes from South America to Africa consider: (1) an island-hopping, or stepping-stone route; (2) a single-step route dispersal from South America to Africa; and (3) a sweepstakes route. It is postulated here that the first route would have involved evolutionary processes in taxa whereas the other two routes, because of the relative rapid migration, did not involve evolution. Vectors of dispersion for early-branching lineages in Asteraceae would include birds, wind currents, and floating islands linked to ocean currents.

Geographical routes

A trans-Atlantic route

Although with some critics (e.g., Mourer-Chauviré, 1999), many paleogeographic reconstructions support the existence of a series of islands and shallow terrain in the South Atlantic during the mid-Cenozoic, from the late Maastrichtian (ca. 65 Ma) at least up to the Eocene (ca. 40–50 Ma) (Detrick et al., 1977; Fodor et al., 1977; Thiede, 1977; Parrish, 1993; Bandoni de Oliveira et al., 2009; Susan Humphris, Woods Hole Oceanographic Institution, MA, pers. comm.; Luiz Gamboa, ex Columbia University, NY, pers. comm.). Multiple lines of geologic evidence (e.g., magnetic anomalies, reef limestones as records of carbonate shelves, and direct drilling data) indicate the existence of large islands in the South Atlantic between Africa and South America since the late Maastrichtian, at least, up to the Eocene (Ezcurra and Agnolín, 2012). These islands are the remnants of a wide corridor above 200 m paleodepth between South America and Africa (Sclater et al., 1977) that may have played a role in biotic interchange between the two continents, including that of Asteraceae. This shallow area was composed of what are now the landward extremities of the Walvis Ridge (southwest coast of Africa at about 35° S) and the Río Grande Rise (southeast coast of Brazil at about 23° S) (Fig. 2) and provided the latest direct connection between South America and Africa. The Rio Grande Rise and the Walvis Ridge are now separated by the Mid-Atlantic Ridge and the deep areas on either side of it, but were once part of a more or less contiguous feature across the early South Atlantic.

A trans-Antarctic route

This route would suggest that migration existed between South America and Africa via Antarctica alone, or via Antarctica and the Subantarctic islands. The plausibility of a southern dispersal route should not be precluded, in light of the discovery of fossil Asteraceae pollen in Antarctica (Pross et al., 2012; Appendix 1) and evidence of trans-Antarctic dispersal by existing species (Born et al., 2011). Born et al. (2011) demonstrated the impact of prevailing wind patterns on wind-dispersed species in the Subantarctic islands, especially those growing in windy and/or topographically heterogeneous environments such as the Marion Islands situated approximately 2200 km SE of Cape Town, South Africa.

Igneous activity and block-faulting during the early breakup of Gondwanaland produced new ridges, seas, and plateaus connecting South America to western and southern Africa to some degree through the South Atlantic Ocean-Indian Ocean. Some of these plateaus together with isolated islands could have played a role in past dispersal of southern biota. The Kerguelen Plateau comprises an area ca. 460,000 km^2 mostly submerged (to depths 1000–2000 m) in the Antarctic sector of the Indian Ocean. Before subsidence, it supported a diverse terrestrial flora during the Cretaceous, and acted as a corridor for early angiosperm dispersal

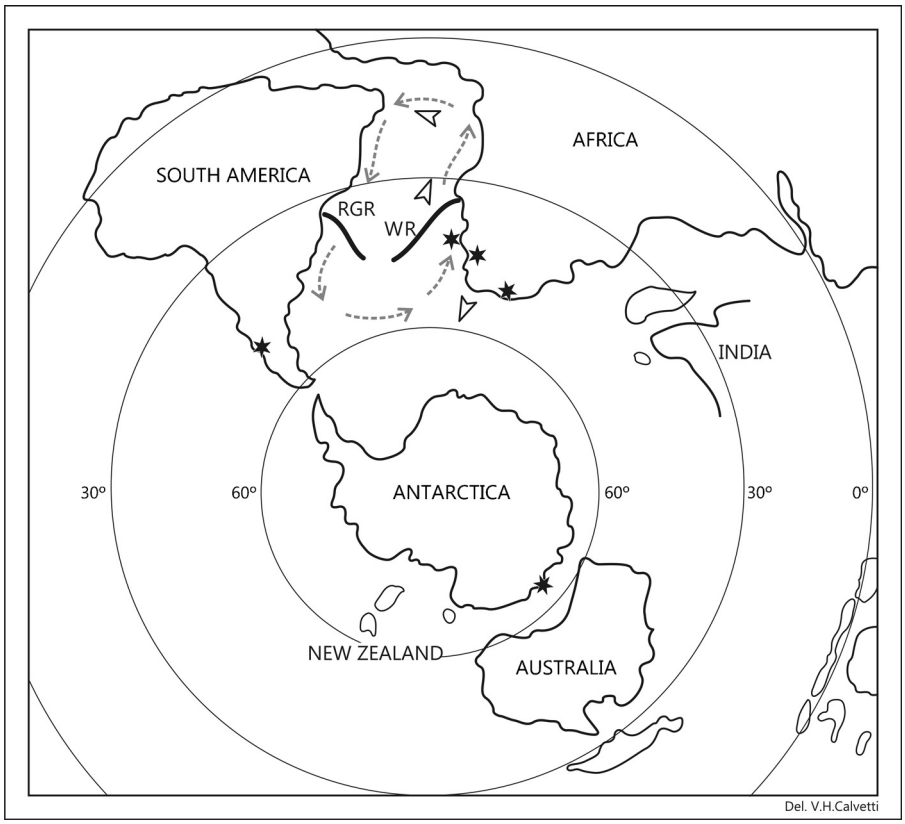

Fig. 2. Map of the southern hemisphere at the Eocene (ca. 50 Ma) with the placement of the Rio Grande Rise and Walvis Ridge, showing: pollen findings (stars), paleowinds (arrow heads) (based on Houle, 1998), and paleocurrents (dotted arrows) (based on Crame, 1999). RGR: Rio Grande Rise. WR: Walvis Ridge.

between India and Australia-Antarctica (McLoughlin, 2001). The Falkland Plateau represents a connection between South America and Africa that was severed earlier than the Walvis Ridge-Rio Grande Rise. Islands in this area with widely differing origins and geological histories that lie close to the oceanic Antarctic Polar Frontal Zone called "Subantarctic islands" include the Marion and Prince Edward islands, Kerguelen and Crozet islands, and Heard and McDonald islands in the Indian sector (Convey, 2007).

Dispersal routes

Stepping-stones route

The stepping-stone or island-hopping mode of dispersal hypothesizes that organisms migrate across large bodies of water sequentially through a series of islands. In some cases the islands do not persist during the entire migration, but adjacent islands are sufficiently connected through geological time to enable migration (Bandoni de Oliveira et al., 2009). According to this dispersal route, early-branching lineages of Asteraceae might have used islands in a trans-Atlantic or a trans-Antarctic route to disperse from South America to Africa and evolved during the process.

Single-step route

A single-step route hypothesizes that organisms cross a barrier in a direct, single event, not sequentially. Single-step routes were already postulated to explain the presence of Asteraceae in islands, such as the exemplar case of adaptive radiation of the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*) (Baldwin et al., 1991). The 28 species of this monophyletic group of genera have a diversity of life-forms derived from a single ancestral, insular taxon. The silversword alliance may have descended from a North American ancestor in a single-step route since no ancient islands bridged the oceanic barrier between North America and Hawaii, probably by migratory birds. According to this dispersal route, the ancestor of the African carduoids may have arrived from southern South America in a direct, rapid, single-step route, crossing the South Atlantic Ocean barrier.

Sweepstakes route

The paleontologist George G. Simpson (1940) coined the term "sweepstakes route" to refer to barriers that must be crossed by rare, chance interchanges, in which a small number of individuals manage to survive the journey and succeed in colonizing places far from their homeland (Hugget, 2004). Sweepstakes are here considered as random, non-permanent, with no pattern events, such as cyclones, hurricanes, floods, deviation of birds' migratory routes or temporary changes in the prevailing ocean currents or wind direction. Stochastic process involves not only the first arrival to an island from the nearest mainland, but also dispersal among islands. Stochastic dispersal patterns have been observed particularly for species with high dispersal ability such as wind-dispersed seeds (Cowie and Holland, 2006). According to this mode, seeds of Asteraceae would have been dispersed by a biological or non-biological agent by chance. If such an event took place, it represented a random, rapid migration.

Vectors of dispersion

Dispersion is defined here as a property of individuals, the process by which an organism is able to spread from one place to another place, for example by means of a pappus. It is different from dispersal which is a property of taxa, the process by which a

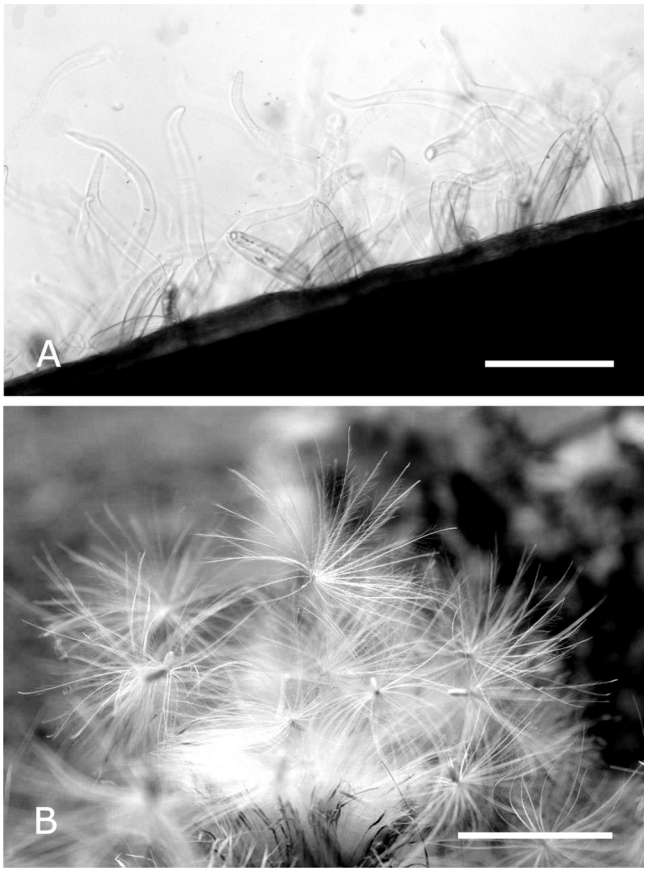

Fig. 3. (A) Cylindrical twin hairs in a fruit of *Trixis* sp. (Mutisioideae), note the filaments of mucilage emerging from the hairs. (B) Pilose pappus of *Cynara* sp. (Carduoideae) carrying fruits and ready to be transported by the wind. B, photograph by R. Steinkamp. Scale bars: A, 200 μm; B, 35 mm.

species or other group is able to spread from its previously established range to a different range (Platnick, 1976), generally crossing a biogeographic barrier.

Biological and non-biological agents or vectors may be related to the morphological mechanisms of dispersion of members of Asteraceae, or whole plants can be transported. The chief dispersion mechanisms of the one-seeded dry fruits, called achenes or cypselae in the majority of extant species of Asteraceae are the pappus – which can consist of bristles, scales or awns – and sticky hairs on the fruits that adhere to different surfaces. Among possible vectors of dispersion of early-branching lineages of Asteraceae are birds, wind, and floating islands.

Birds

Birds as dispersers of Asteraceae in islands have been postulated for example by Carlquist (1967, 1974). The fruits of most members of Asteraceae are covered by glandular hairs and specialized "twin hairs", which release mucilage and become sticky when wet (Fig. 3A). With the notable exception of Barnadesioideae, members of the other early-branching lineages Mutisioideae and Carduoideae, have these sticky hairs on their fruits and occasionally in flowers (Freire and Katinas, 1995; Sancho and Katinas, 2002). These hairs may have facilitated attachment of fruits to bird feathers or legs and being transported from South America to Africa. All species of Barnadesioideae share a unique "barnadesioid hair" type, which lacks mucilage and does not become sticky.

Wind

Early-branching lineages of Asteraceae have fruits crowned by an umbrella-like pilose or barbed pappus, which acts as a parachute and is a very efficient means of dispersal (Fig. 3B). The individual fruits can become airborne with the slightest gust of wind and disperse variable distances. Barreda et al. (2012) found pappus-like projections among flowers of the fossil capitula *Raiguenrayun cura* similar to that of extant taxa of Asteraceae, suggesting that a pilose pappus was already part of the morphology of the family in the Eocene. According to this scenario, early members of the family may have used the pappus as a device of transportation depending on the direction of paleowinds on their way to Africa.

Floating islands

In the floating island rafting model, organisms are passively transported on ephemeral islands across oceans or other bodies of water. These islands are typically formed as buoyant rafts of vegetation and debris, sometimes including soil, that detach from the margins of large rivers (Bandoni de Oliveira et al., 2009) or shorelines. Floating islands are common and found in many parts of the world. In southern South America, the Paraná River of northeastern Argentina merges with the wide Río de La Plata and flows into the Atlantic Ocean. Among the floating macrophytes of the Paraná River, the water hyacinth (*Eichhornia crassipes*) forms cohesive floating rafts of variable sizes (called "camalotales") that may detach and float free from the shore. These rafts often host a diverse flora and fauna and their diaspores. The river is subject to annual seasonal flooding, sometimes catastrophic, which can carry these rafts hundreds of kilometers to the Río de La Plata and then to the ocean. Insects, spiders, frogs, snakes, egg birds, small mammals, and even pampas deer (*Ozotoceros bezoarticus*) and white-lipped peccaries (*Tayassu pecari*) have been observed and documented on these floating islands (JVC and LK, pers. obs.; Achaval et al., 1979; Guerrero, 2011). Also, floating trees (*Phytolacca dioica*) up to 8 m long have been observed along the Uruguayan coast coming from the Paraná River (Achaval et al., 1979). Plants or diaspores of early members of Asteraceae could settle in such rafts and reach the Atlantic Ocean. Atlantic rafting depends upon prevailing ocean currents and wind direction and thus is not considered here a chance event when transported in the direction of the prevalent currents.

Evidence for alternative scenarios

Geographical routes: trans-Atlantic vs. trans-Antarctic route

The Rio Grande Rise and the Walvis Ridge in the South Atlantic were formed by an unusual extrusion of volcanic material originating from a "hot-spot" on the Mid-Atlantic Ridge. Sediment drilling along both the Walvis Ridge and the Rio Grande Rise found Middle and Late Eocene shallow water fossils and ash flow tufts indicating extrusion above sea level (Parrish, 1993). Several islands of considerable size (more than 200 km in length) persisted along the present-day submerged Río Grande Rise and Walvis Ridge. At 50 Ma, a long series of islands extended west from Africa between 20° and 30° lat. S, and at least one large island (around 500 km in length) was formed by the emergent top of the Rio Grande Rise. Sediment and stratigraphic data obtained from drilling indicate that Rio Grande Rise was a large island, 2–3 km above sea level during Santonian to Campanian times (85–75 Ma). This positive paleogeographic relief, which is now largely sediment-covered and having peaks as shallow as 600–700 m water depth, would have considerably reduced the migration distance between South America and Africa. It is estimated that the Rio Grande Rise subsided below the

surface of the Atlantic in late Oligocene (ca. 25 Ma) (Thiede, 1977). Middle Eocene volcanics were probably extruded above sea level on the western end of Walvis Ridge, but this was completely submerged by the end of the Eocene (ca. 35 Ma). These rocks now lie 1765 m below sea level (Parrish, 1993). Island chains such as the Rio Grande Rise-Walvis Ridge would suggest a way of dispersal from South America to Africa.

On the other hand, a migration route from South America to Africa via Antarctica or the Subantarctic islands, or directly from Antarctica to Africa, is less likely. There are several lines of evidence that argue against this area as a possible migratory route for early members of Asteraceae.

(a) As early as the late Cretaceous the physical separation between Africa and Antarctica was already appreciably large (Scotese et al., 1988; Smith et al., 1994), approximately 2750 km (data extrapolated from Fisher and Sclater, 1983). Transform faulting between southernmost Africa and the easterly extension of the Falklands Plateau may have maintained continental connections or close proximity of southern Africa and South America until the Early Cretaceous, ca. 105 Ma (Barron, 1987), which was too old for the presumed age of the family Asteraceae. The Kerguelen Plateau, in the Atlantic sector of the Indian Ocean, experienced subaerial erosion (Parrish, 1993) producing a substantial deep-water gap between eastern Antarctica and the southern Kerguelen Plateau since the Late Cretaceous (Ali and Aitchison, 2009).
(b) Volcanism has been involved in the formation of many of the Subantarctic islands. Kerguelen, Heard and McDonald islands are part of the Kerguelen Plateau, itself of Gondwanan age, although the islands are much younger. Marion, Prince Edward, and Crozet islands are shield volcanoes, which erupted between 9 and 0.22 Ma (Ali and Aitchison, 2009). Thus, these islands are substantially younger than the separated southern continents, and could not have been involved in dispersal of early-branching lineages of Asteraceae during the Paleocene-Eocene. Even on the older (ca. 39 Ma) Kerguelen Islands, terrestrial fossil evidence is sparse and nothing can be concluded about their potential role in past dispersal of taxa.
(c) Palaeobiogeographic reconstructions (e.g., Reguero and Gasparini, 2007; Gheerbrant and Rage, 2006; Upchurch, 2008) and historical biogeographic methods (for discussion of these methods see Crisci et al., 2003) such as tree reconciliation analysis (Ezcurra and Agnolín, 2012) and parsimony-based tree fitting in conjunction with permutation tests (Sanmartín and Ronquist, 2004) do not support biogeographical connections between Antarctica and Africa since the Aptian-Albian (ca. 120–99.6 Ma). Global palaeobiogeographic reconstructions (Ezcurra and Agnolín, 2012) show that biotic interchange was possible between Antarctica and South America through Africa only until the Barrenian-early Aptian (130-ca. 120 Ma).
(d) Regarding the possibility of dispersal by air, water, or third-party vectors (e.g., other organisms, debris) in the Antarctic area, wind is known to play a major role in the colonization of isolated environments, at least in the cases of bryophytes, lichens, many microbes, and certain invertebrates (e.g., rotifers, tardigrades) (Convey, 2007). The prevailing westerlies that sweep around the southern hemisphere following the ocean currents gyre, particularly at about latitudes 35–45° S, have apparently carried seeds from New Zealand to South America (Raven and Raven, 1976), although there are no reports of dispersal to Africa. There is no information regarding biotic dispersal in this area during the Paleocene or Eocene, when the climatic conditions in Antarctica were not so harsh. There is ample evidence to suggest that a dispersal corridor existed between South America, Antarctica, and Australia but ocean and wind currents and geology did not favor migration from Antarctica to Africa.
(e) The Eocene Circum-Antarctic current system (Crame, 1999) did not favor biotic dispersal from Antarctica to Africa, since at least 30–35 Ma, when the Drake Passage and the Tasmanian Gateway opened (Appendix 1). This current is of great oceanographic and climatic importance because it probably represents the largest volume transport of any ocean current, and is the only current that mixes the waters of all oceans. It flows completely around Antarctica (Kennett et al., 1975), essentially cutting across the route to Africa, and therefore the current gyre would not have favored biotic migration to Africa, at least for example in the case of a rafting dispersal. However, it was suggested that shallower-water connections existed in the Eocene between the South Atlantic and Pacific Oceans and that the potential for some form of proto-Circum-Antarctic current should not be overlooked (Crame, 1999).

Dispersal routes: stepping-stones vs. single-step route, and a possible role of sweepstakes

Asteraceae might have dispersed between South America and Africa after continental separation via the emergent islands of Rio Grande Rise and Walvis Ridge. Volcanic islands could have acted as stepping-stones for biotic interchange between South America and Africa. According to this scenario, the most probable vectors could be birds that, inadvertently carrying sticky fruits of Asteraceae, would have flown from one continent to the other, using the islands as stepping-stones to reduce the distance to be flown without landing. Examples of modern presence of Asteraceae on oceanic, volcanic islands in the middle of the South Atlantic Ocean are *Achillea*, *Artemisia* and Quaternary *Tubulifloridites* on Gough Island (Bennet et al., 1989) at 40° 19′ S, 9° 55′ W, and *Osteospermum* on St. Helena (Cronk, 1987) at 15° 56′ S, 5° 42′ W. The Quaternary fossils and the presence of endemic plants assumed to be relict, such as the St. Helena tree fern *Dicksonia arborescens* and two extant and one extinct species of *Trochetiopsis* (Malvaceae) (Cronk, 1997) preclude the possibility of human transport of diaspores. Long-distance dispersal is the only logical explanation, since these islands never had land connections to the continents.

Another possibility is that these early-branching lineages reached Africa in a single-step route, also probably by birds, and that the oceanic islands did not participate in the process. One way to differentiate between these two dispersal routes is taking into consideration evolutionary processes in taxa. Evolution may have acted during the dispersal among islands in contrast with a single-step, relatively rapid dispersion where taxa had not time to evolve.

The geological evidence shows that not all island areas along the Rio Grande Rise-Walvis Ridge were emergent at the same geological time, suggesting that their respective biota developed in isolation as propagules arrived on some islands and evolved in situ. If so, it should be possible to detect some evolutionary signal in the African descendants (Carduoideae). We compared fossil pollen grains of early diverging members of Asteraceae found in South America and in Africa, and interpreted unusual features in the morphology of African Carduoideae in the context of a hypothesis of ancestral evolution on islands. Eocene to Miocene fossil pollen from off- and on-shore deposits of southwestern Africa were assigned to *Mutisiapollis viteauensis* by Zavada and De Villiers (2000), and were considered similar to Dicomeae (Carduoideae) by Scott et al. (2006). This fossil shares some features with *Mutisiapollis telleriae*, based on pollen of Middle Eocene to Late Oligocene found in southern South America (Fig. 4). However, the African morphotype is

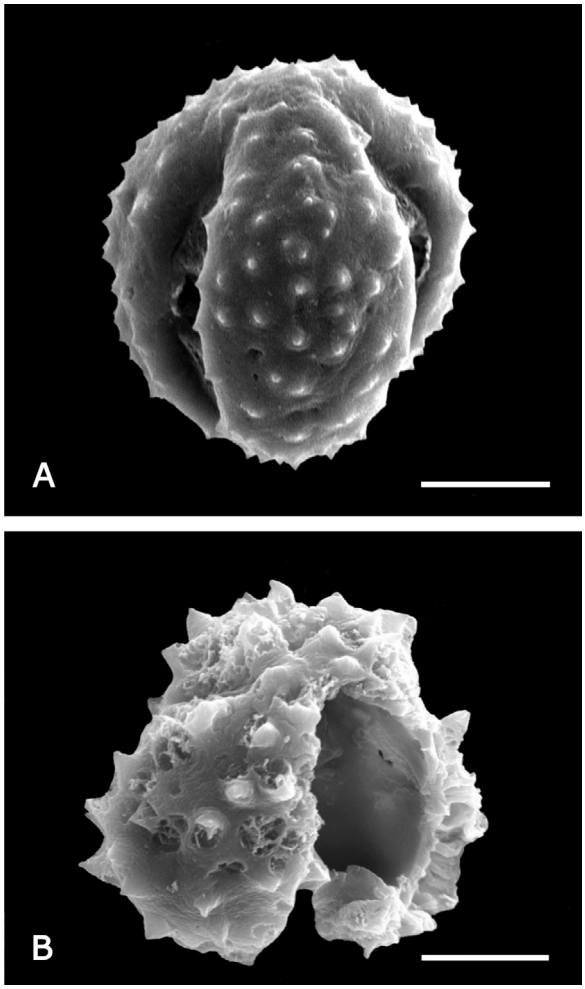

Fig. 4. Scanning electron micrographs of Eocene fossil pollen grains found in Africa and in South America. (A) *Mutisiapollis viteauensis*. (B) *Mutisiapollis telleriae*: note the uneven arrangement of the spines and the longer spines. Scale bar: 10 μm.

microechinate whereas the South American one is conspicuously echinate (Tellería et al., 2010), establishing that they may belong to two different but closely related taxa. This suggests that the process of migration between continents may have occurred over a sufficiently long time span to allow speciation in the process, which is compatible with stepping-stone migration in stable and suitable habitats of an island chain. It should be remarked that one of the fossil pollen findings in Africa came from offshore locality, approximately 50 km west of the coast of South Africa.

In addition, in his discussion of dispersal and evolution of plants on islands, Carlquist (1974) proposed several common morphological changes that plants develop over time as adaptations to island habitats. Therefore, if evolution took place on islands during the dispersal of Asteraceae from South America to Africa, it might be possible to find some imprints of this process in the African carduoid descendants. The reconstruction of a hypothetical ancestral Asteraceae based on the morphological features of the fossil *Raiguenrayun cura* and closest extant tribes performed by Barreda et al. (2010b) shows a shrubby or sub-shrubby plant with alternate leaves and fruits with a pappus. Using some of Carlquist's principles, the comparison of this fossil reconstruction and the morphology of current species yields some interesting results. According to Carlquist (1974) (a) new growth forms commonly evolve from shrubs to trees or rosette shrubs. Members of tribe Oldenburgieae (Carduoideae), which are considered paleoendemics of

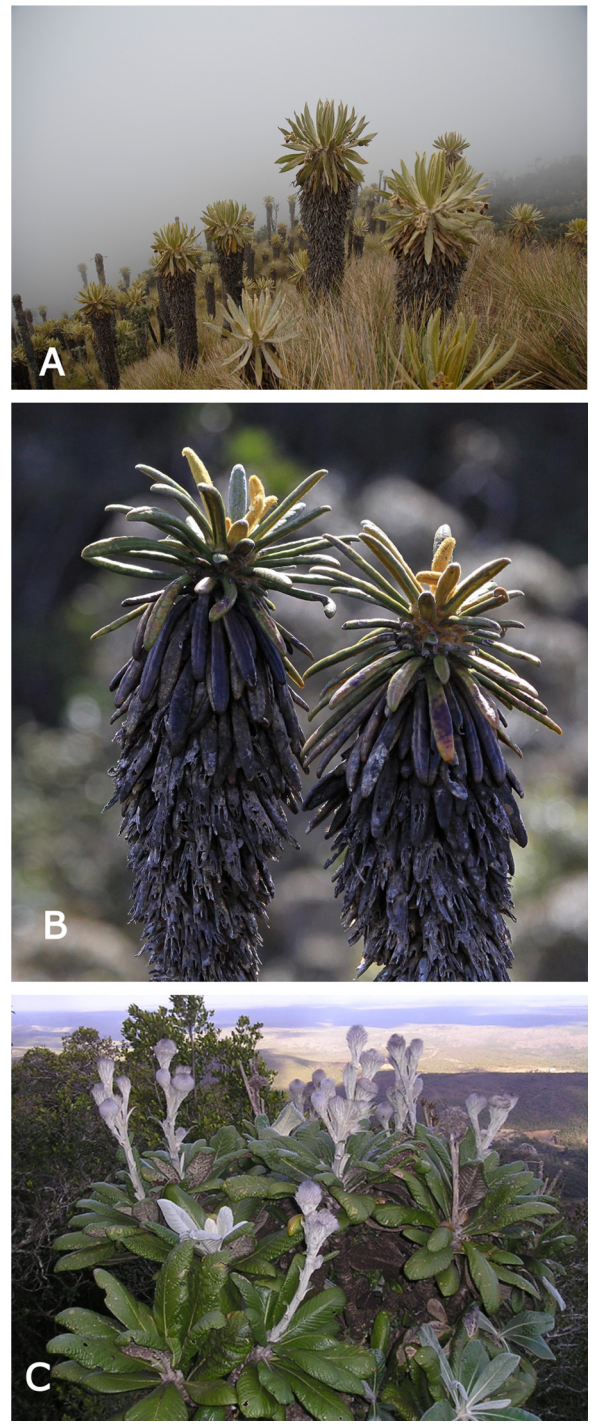

Fig. 5. Photographs comparing the habit of genera of Asteraceae with leaves clustered at the end of the branches, characteristic of island environment. (A) *Espeletia* (subfamily Asteroideae). (B) *Chimantaea* (subfamily Mutisioideae). (C) *Oldenburgia* (subfamily Carduoideae) with capitula on ramified peduncles. A, photograph by M. Bonifacino. B, photograph by J. Stankovič. C, photograph by Ş. Procheş.

the Cape Region of Africa (Goldblatt and Manning, 2002), live in non-island habitats as dwarf cushion-forming rosette shrubs to small trees that typically have a giant-rosette growth from with a massive terminal leaf rosette borne atop a thick wood stem. This morphology bears a notable parallel resemblance with members of the Asteraceae of Hawaii (silversword alliance), the Juan Fernandez Islands (*Dendroseris*), and island-like continental areas such as

the South American páramos (*Espeletia*), the East African rift valley (*Dendrosenecio*), and in the Guayana Highlands (e.g., *Chimantaea* of Mutisioideae) (Fig. 5). (b) Dispersal mechanisms may be lost during the evolution of plants on oceanic islands. It should be remarked that whereas a complete loss of pappus is common in some derived lineages of Asteraceae (e.g., Heliantheae), this loss is lacking (Barnadesioideae) or it is highly unusual (Carduoideae, Mutisioideae) in early-branching lineages. The lack of a pappus found in the African-Arabian genus *Tarchonanthus* (Carduoideae) may reflect such a loss. The potential loss of the pappus in the Eocene island habitants would enhance the value of the fruit twin hairs as the main dispersal mechanism. (c) Means of outcrossing tend to be highly developed. According to Carlquist (1974), self-sterility and heterostyly are rare on islands, but dioecism is exceptionally common in certain insular floras. *Tarchonanthus* and *Brachylaena*, which constitute tribe Tarchonantheae (Carduoideae), are dioecious trees or shrubs. Thus, some unusual morphological features of these carduoid groups provide indirect support for the hypothesis that they are derived from island-inhabiting ancestors.

One argument against the hypothesis of southern oceanic islands acting as sites for evolution of these groups could be made in view of widely known cases in Asteraceae of single-step dispersion, such as the North America-Hawaiian Islands silversword alliance, already mentioned, with morphological adaptation of some members to island environments. However, our study case may be analogous if we consider the Hawaiian Islands as stepping-stones. The North America-Hawaii dispersal would represent a first stage of migration comparable to our South American-South Atlantic Ocean islands. In a second stage there is evolution of members of Asteraceae on Hawaiian Islands with morphological adaptation to island environments, similar to what we propose here to have occurred in the islands of Rio Grande Rise-Walvis Ridge. The third stage of our hypothesis, South Atlantic Ocean islands-Africa migration has no analogy in the silversword alliance but it could occur in evolutionary time if a silversword ancestor were to reach another land mass.

Another line of argument against our hypothesis could be that there are extant species of Mutisioideae in Africa which have not developed the typical evolutionary giant-rosette morphological adaptation to islands. This is the case of the morphologically very homogeneous *Gerbera*-complex, consisting of seven genera of scapose herbs distributed in the Americas, Asia, and two genera (*Gerbera*, *Perdicium*) in Africa (Katinas, 2004). However, independent calibrations of nuclear and chloroplast DNA sequence data using relaxed clock methods and either mean rate or fossil-based priors (Baird et al., 2010) unanimously support Miocene and Oligocene (12–8 Ma) divergence times for the complex, which is a very young age compared with the Eocene times mentioned here. Ancestral areas analysis (Bremer, 1992) performed in Baird et al.'s work showed a South American origin of the group. Thus, a possible explanation for the distribution of these young lineages is an overland dispersal from South America to the north, crossing the Panamanian (3 Ma; Coates and Obando, 1996) and the Beringian bridge (emerged in the glacial periods of the Quaternary in the last 2 Ma; DeChaine, 2008) to Eurasia and finally reaching Africa.

We cannot dismiss the role of sweepstakes in this scenario, as rare, chance events occurring in the past. Some authors have argued that sweepstakes dispersal rarely leads to successful colonizations because they usually involve single, or just a few, individuals (Nelson and Platnick, 1981), and the most likely post-dispersal fate of these individuals is death without reproduction. However, these risks are diminished in the case of plants since, for example, one single individual of Asteraceae with its capitula of flowers already cross-pollinated, self-pollinated, or with some type of asexual reproduction is capable of generating a new population. The Hawaiian flora has been subject to numerous studies and represents a key archipelago to understand evolutionary processes in oceanic volcanic islands (Wagner and Funk, 1995). Fosberg's (1948, 1951) studies on the colonization of the Hawaiian Islands determined that, in order to establish the Islands' flora, only one successful colonization every 25,000 years would be necessary. In this way, random events such as birds flying unusual routes, cyclones, hurricanes, or other phenomena may have played a role in the transport of fruits between South America and Africa. There are few examples for which sweepstake events have been tested. Stankiewicz et al. (2006) found that the largest distance traveled by an identifiable object in a tornado is around 300 km. Other phenomena that could be included in the sweepstakes category are pumice floating and El Niño events. Although mainly postulated for marine organisms, such as barnacles, Gastropods, Bivalves, Bryozoa, corals, sponges, and algae, pumice floating and long-distance dispersal due to volcanism was recently reported (Bryan et al., 2012). Pumice is an extremely effective rafting agent whose physical properties indicate positive buoyancy. On the other hand, there is evidence that El Niño or ENSO (El Niño Southern Oscillation), with its associated climatic changes, coastal upwelling, storms and floods, was a continual phenomenon in the Early Pliocene and very probably before that time (Federov et al., 2006). West to east wind anomalies due to systems analogous to El Niño in the tropical Atlantic Ocean were already invoked to explain some plant distributions in Africa by Givinish et al. (2004). In conclusion, past chance events are very difficult to test but cannot be disregarded as possible factors affecting dispersal of organisms.

Vectors: floating islands, birds, and wind

Houle (1998) established many physical, physiological, and behavioral objections to transoceanic migrations in floating islands, mainly focused on vertebrates. Some of them are not applicable to vegetation, and thus, such migrations can be considered potentially more successful in plants than in animals. Houle's (1998) arguments for a low probability of success that includes plants and animals are: (a) the floating island has to form and has the potential to reach the ocean; (b) the floating island has to detach from the mainland; (c) at least one genetically viable organism or population of organisms has to be on the island when it detaches; (d) local currents and winds have to transport the island to the ocean; (e) both the floating island and the organisms on it have to survive oceanic storms; (f) the vegetation on the island must resist desiccation due to salt spray; (g) the organisms have to be able to endure wind and heat stresses; (h) the floating island has to reach the targeted continent, suggesting that it was favored by paleowinds and oceanic paleocurrents; (i) the organisms have to be able to adjust to the new environment, including climate, changes in seasonality, presence of predators and diseases, absence of suitable pollinators, etc. Another factor impacting the probability of successful colonization is the type of shore at the area of arrival, since an essentially rocky shore with a narrow littoral zone may offer minimal suitable habitat. On the other hand, some factors that limit survival of animals on such rafts have no effect on plants, for example: (a) plants on the raft have no ethological impulse to escape; (b) plants may survive dehydration with minimal impact, and even a small amount of rain during the journey may meet the plant's requirements; (c) no food is needed, since plants only need water and sun for photosynthesis; (d) there usually are no barriers to reproduction comparable to the behavioral challenges experienced by animals; (e) many plants are capable of self-pollination, asexual or vegetative reproduction; and (e) very commonly, the plant is transported as seeds, which may be relatively impervious to harsh conditions, have some dormancy to allow for a sustained trip, and be present in

considerable numbers on the raft, increasing chances for successful establishment.

When considering floating islands, the paleocurrents are key for this transoceanic mode of dispersal. Evidence in rodents (Rowe et al., 2010), monkeys (Houle, 1998, 1999; Schrago and Russo, 2003), birds (Mayr et al., 2011) and some angiosperms (Renner, 2004) suggests that paleocurrents favored dispersal east to west across the Atlantic, i.e., from Africa to South America. But recent phylogenetic evidence in some groups such as sirenians (Domming, 2005), birds (Voelker et al., 2009; Mourer-Chauviré et al., 2011), and the plant families Rapateaceae and Bromeliaceae (Givinish et al., 2004) suggests dispersal in the opposite direction, from South America to Africa. In addition, dispersal-vicariance analyses indicate the presence of bi-directional (caviomorphs) and some eastwards (malpighiaceans and amphisbaenians) dispersion fluxes, contrasting with the westward model (Ezcurra and Agnolín, 2012). At present, the Brazil Current is a warm-water current that flows south along the southeastern coast of Brazil to the mouth of the Río de la Plata, Argentina, about latitude of 30–40° S, where the northward-flowing Malvinas (Falkland) Current deflects it to the east toward southern Africa, along the South Atlantic Current. There it feeds the Benguela Current, which flows north along the west coast of Africa, deflecting near the equator to the west toward northern Brazil as the South Equatorial current, thus completing the South Atlantic gyre (Joyeux et al., 2001; Stramma and Peterson, 1990) (Fig. 2). The past history of currents in the South Atlantic remains a major unknown and many factors must be considered. The Atlantic Ocean basin has been continuously altered as a result of plate tectonic forces such as spreading along the Mid-Atlantic Ridge; there have been major changes in water temperature; and two major gateways, the Drake Passage (between South America and Antarctica) and the Tasmanian Gateway (between Australia and Antarctica) have opened. These factors suggest that there may have been markedly different potential for surface-water flow in the South-Atlantic during the period when biotas crossed the ocean. Despite these uncertainties, the existence of a subtropical South Atlantic gyre can be postulated by coupling general ocean circulation model simulation in equilibrium with reconstructed early Paleogene topography, bathymetry, vegetation and pCO_2 (Huber et al., 2003). According to this model, an anticlock-wise gyre directed water flow from South America to Africa and back again, providing the mechanism for organisms on floating islands to disperse in both directions. The time involved in the Atlantic Ocean crossing is not as long as one might expect. Considering a conservative scenario, the Paleogene Atlantic Ocean could have been crossed from east to west in 8 days at 30 Ma (Houle, 1998). There are no time projections for crossing in the opposite direction, i.e., from South America to Africa. Rafting is also dependent on winds, which were more favorable for migration from Africa to South America during the Cenozoic (Bandoni de Oliveira et al., 2009). In defiance of wind directions and paleocurrents, the probabilities of successful raft dispersal are so small that even vast tracts of time cannot compensate (Stankiewicz et al., 2006), thus weakening any argument for rafting as a primary mode of dispersal from South America to Africa.

Birds as vectors of plant propagules dispersion have been thoroughly studied since Darwin's (1859) times. Carlquist (1967) in his studies of long-distance dispersal of Asteraceae established that adherence of barbed or bristly or viscid seeds or fruits to bird feathers is of maximum importance on dry volcanic islands. Shore birds and water birds may be responsible for transport of numerous plant species. His empirical studies establish that such birds account for considerable inter-island dispersion, demonstrating that they are entirely adequate as potential vectors of plant propagules dispersion. In the Galápagos Islands, for example, the flora includes a high percentage of plants whose seeds/fruits have barbs and hairs capable of such bird-mediated transport. In contrast, Carlquist (1967) suggested that the proportion of seeds and fruits digested and transported internally by birds is very low. The achenes of Barnadesioideae, Mutisioideae and Carduoideae of Asteraceae are not notably resistant to the acids of the digestive tract of birds or other animals (e.g., tortoises), unlike fruits of other groups such as Heliantheae with hard walls.

Birds are highly vagile organisms, and consequently their movements cannot be easily tracked; this is especially difficult when trying to analyze bird's long-distance dispersal role in the past. Even when there are records of Palaeogene fossil birds in Patagonia (Tambussi, 2011), little is known about their possible routes of dispersal. There is some evidence that birds migrated between southern continents during the Eocene-Miocene period that support the possibility of bird-mediated dispersal of Asteraceae. Ten families of fossil avifaunas with a Paleogene record were shared between Africa and South America (Vuilleumier and Andors, 1993): Pelagornithidae (false-toothed, wide ranging, pelagic, extint birds), possibly Spheniscidae (penguins; non-volant birds), Ardeidae (herons), Ciconidae (storks), Phoenicopteriade [typo] (flamingos), Anatidae (ducks), Accipitridae (hawks, eagles), Rallidae (rails; the weakness of their flight means they are easily blown off course and thus are common vagrants, leading them to colonize isolated oceanic islands), Jacanidae (jacanas), Cuculidae (cuckoos). Some zoologists relate the hoatzin to the last family. Dispersal from Africa to South America of the hoatzin *Opisthocomus hoazin* (Opistocomiformes) by transatlantic rafting was suggested by Mayr et al. (2011) because of the weak flight capabilities of these birds. Another group was represented by the phororhacoid bird *Lavocatavis africana*. Small forms of these birds dispersed from South America to Africa by flying and later evolved large flightless forms (Mourer-Chauviré et al., 2011). Not surprisingly, a large proportion of shared bird families between Africa and South America are waterbirds with high potential for overwater dispersal (Vuilleumier and Andors, 1993).

We already have suggested that a pilose pappus is an effective means of wind dispersion in Asteraceae. Currently, the prevailing westerlies blow from west to east across the South Atlantic between 30° and 60° south latitude. Muñoz et al. (2004) analyzed the shared floristic affinities among extratropical southern hemisphere landmasses and found a stronger correlation of floristic similarities with prevailing wind patterns than with geographic proximity, suggesting that wind is an important dispersal agent for many organisms in the southern hemisphere. There is, however, some evidence that may refute the possibility of wind dispersal in ancient Asteraceae from South America to Africa. First, paleowinds during the Cenozoic may have been more favorable for migration from Africa to South America (Bandoni de Oliveira et al., 2009 and references herein) (Fig. 2). Second, there is controversy about the relatively effectiveness of the pappus for long-distance dispersal. Dandeno (1905) calculated that seeds of the pappose thistle [*Carduus arvensis* (L.) E. Robson.)], dispersed only about one fifth of a mile (=0.32 km) per hour with the wind blowing at 20 miles per hour, with all cross currents and air changes neglected. Sheldon and Burrows (1973) established that the transport of capillary pappose fruits through the air is influenced by relative humidity as well as air currents. Modeling of long-distance dispersal of plant diaspores by wind (Tackenberg, 2003), on the other hand, showed that sunny weather conditions with thermal turbulence and updrafts may result in a high proportion of long-distance dispersal, even if the horizontal wind speed is low. Studies in Cardueae (Susanna and Garcia-Jacas, 2007) suggested that the pappus does not seem to function as an effective long-distance dispersal mechanism in the tribe because it is often too small or, if large, it is deciduous.

Also, windy or stormy weather may be of much smaller importance for long-distance dispersal than is commonly assumed. Third, even if fruits reached the ocean and could float, it would be difficult for them to disperse further because of the limited ability of the fruit wall to prevent sea water from rupturing internal tissues. In addition, almost everything as small as Asteraceae fruits floating in the surface of oceans is consumed by grazing zooplankton and removed from the water column fairly close to its point of entry (Steven Hovan, IUP Geoscience Dept., IN, pers. comm.).

Where and how did early-branching lineages of Asteraceae disperse from South America to Africa?

The evaluation of the scenarios presented here suggests that early-branching lineages of Asteraceae had major opportunities to disperse from South America to Africa along an island chain formed by the Rio Grande Rise and the Walvis Ridge, which is now submerged. The slight morphological differences of African fossil pollen regarding their relatives in South America and current giant-rosette shrubby habit, dioecism, and loss of the pappus in some carduoid descendants compatible with island environments, are features congruent with ancestral evolution during the dispersal process. Since fossil pollen evidence in southern Africa indicates the existence of subtropical rain forests (Coetzee and Muller, 1984) and subtropical-austrotemperate forest vegetation (Cowling et al., 2005) in these regions during the Tertiary not compatible with continental island-like environments, only the stable and suitable environments of oceanic islands could have allowed the time span for this process to occur and produce island-inhabiting plant features. Bird feathers most likely provided the primary vector for dispersion of the sticky fruits of Asteraceae, a well-documented mode of dispersal for the family in oceanic islands. The distribution of another early-branching lineage of Asteraceae, the Barnadesioideae, provides indirect support for the importance of bird-mediated fruit dispersal. Barnadesioideae, which occur exclusively in South America, lack the sticky fruit hairs that can facilitate attachment to bird wings and thereby enable long-distance dispersal. Transport of the pappus-bearing fruit by wind, on the other hand, provides more efficient dispersal on land surfaces and/or involving short distances. If falling into the ocean, fruits of early-branching lineages of Asteraceae would not have survived floating in the sea water.

Although stepping-stone dispersal along islands involving birds is favored here as the best scenario to explain how early-branching lineages of Asteraceae reached Africa from South America, alternative hypothetical modes and vectors – floating islands and sweepstakes dispersal – cannot be discounted as participant of the process. Some examples of possible scenarios might include:

(1) A floating island with plants (or more likely fruits) of Asteraceae detaches from the South American coast and disperses to the closest oceanic island. The population establishes on the island, evolves through time, and eventually is dispersed by birds in stepping-stone fashion to Africa. Other combinations of stepping-stone dispersal by birds and rafting dispersal are possible.
(2) The seeds of Asteraceae are transported by birds from South America to Africa in a stepping-stone fashion along islands, but modified by a rare weather event causing deviation of the normal migration route of the bird species or even of solitary birds.
(3) Another scenario could combine bird-mediated stepping-stone dispersal with rafting and rare weather-related sweepstakes dispersal. A remarkable case of such combined dispersal modes was documented in the Caribbean when at least 15 iguanas appeared on the island of Anguilla several weeks after Hurricanes Luis and Marilyn swept through the region in September 1995. The iguanas washed ashore on rafts of floating vegetation blown in from Guadeloupe Island, some 320 km away after surviving at least 3 weeks at sea (Censky et al., 1998).

After their arrival in Africa those ancestral elements of Carduoideae experienced progressive drying of the African climate at the end of the Tertiary (Ortiz et al., 2009). A recent study performed for estimating ages of divergence between lineages of Cardueae (Barres et al., 2013) resulted in a Middle Eocene time of divergence among the tribes of Carduoideae, with the ancestor of Cardueae dispersing from northeastern Africa to west Asia. The prevailing tropical/subtropical vegetation in southern Africa began to change early in the Late Miocene (10 Ma), as vegetation types characteristic of drier environments appeared (Cronk, 1992; Linder, 2005). Therefore, in parallel with the South American radiation of Mutisioideae and other groups, there was a much larger African radiation. Of the 1600–1700 genera in Asteraceae today, about two-thirds are in clades that originated in Africa, many in southern Africa. In fact, with the exception of Mutisioideae, Barnadesioideae and Heliantheae, all of the major clades in the family appear to have an African origin or a major African presence near the base of their phylogenies (Funk et al., 2009b). From these South American and African radiations, Asteraceae diversified rapidly into the other continents, resulting in the current widespread distribution that the family has today.

Acknowledgements

We are strongly indebted to Viviana Barreda, Carlos Cingolani, Luiz Gamboa, Elián Guerrero, Steven Hovan, Susan Humphris, Luis Palazessi, Judith Parrish, and Enrique Schnack for discussions and their fruitful comments on the manuscript. We acknowledge the editor and reviewers for their comments, Víctor Hugo Calvetti for drawing of figures, and Mauricio Bonifacino, Karol Marhold, Şerban Procheş, Jaroslav Stankovič, and Ramona Steinkamp for providing excellent photographs of plants. The study was financially supported by PIP 0729 from CONICET (Argentina) and PICT01977 from ANPCyT (Argentina).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2013.07.003.

References

Achaval, F., González, J.G., Meneghel, M., Melgarejo, A.R., 1979. Lista comentada del material recogido en costas uruguayas, transportado por camalotes desde el Río Paraná. Acta Zool. Lilloana 35, 195–200.
Ali, J.R., Aitchison, J.C., 2009. Kerguelen plateau and the late Cretaceous southern-continent bioconnection hypothesis: tales from a topographical ocean. J. Biogeogr. 36, 1778–1784.
Baird, K.E., Funk, V.A., Wen, J., Weeks, A., 2010. Molecular phylogenetic analysis of *Leibnitzia* Cass. (Asteraceae: Mutisieae: Gerbera-complex), an Asian-North American disjunct genus. J. Syst. Evol. 48, 161–174.
Baldwin, B.G., Kyhos, D.W., Dvorak, J., Carr, G.D., 1991. Chloroplast DNA evidence for a North American origin of the Hawaiian silversword alliance (Asteraceae). Proc. Natl. Acad. Sci. U. S. A. 88, 1840–1843.
Bandoni de Oliveira, F., Cassola Molina, E., Marroig, G., 2009. Paleogeography of the South Atlantic: a route for primates and rodents into the New World? In: Garber, P.A., Estrada, A., Bicca-Marques, C.J., Heymann, E.W., Strier, K.B. (Eds.), South American Primates, Developments in Primatology: Progress and Prospects. Springer Science, New York, pp. 55–68.

Barreda, V.D., Palazzesi, L., Tellería, M.C., Katinas, L., Crisci, J.V., Bremer, K., Passalia, M.G., Corsolini, R., Rodríguez Brizuela, R., Bechis, F., 2010a. Eocene Patagonia fossils of the daisy family. Science 329, 1621.
Barreda, V.D., Palazzesi, L., Tellería, M.C., Katinas, L., Crisci, J.V., 2010b. Fossils indicate an explosive radiation of basal Asteracean lineages and allied families during Oligocene and Miocene times in the Southern Hemisphere. Rev. Palaeobot. Palynol. 160, 102–110.
Barreda, V.D., Palazzesi, L., Katinas, L., Crisci, J.V., Tellería, M.C., Bremer, K., Passalia, M.G., Bechis, F., Corsolini, R., 2012. An extinct Eocene taxon of the daisy family (Asteraceae): evolutionary, ecological, and biogeographical implications. Ann. Bot. 109, 127–134.
Barres, L., Sanmartín, I., Anderson, C.L., Susanna, A., Buerki, S., Galbany-Casals, M., Vilatersana, R., 2013. Reconstructing the evolution and biogeographic history of tribe Cardueae (Compositae). Am. J. Bot. 100, 867–882.
Barron, E.J., 1987. Cretaceous plate tectonic reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 59, 3–29.
Bennet, K.D., Gribnitz, K.-H., Kent, L.E., 1989. Pollen analysis of a Quaternary peat sequence on Gough Island, South Atlantic. New Phytol. 113, 417–422.
Bentham, G., 1873. Notes on the classification, history, and geographic distribution of Compositae. J. Linn. Soc. Bot. 13, 335–577.
Born, C., Le Roux, P.C., Spohr, C., McGeoch, M.A., van Vuuren, B.J., 2011. Plant dispersal in the sub-Antarctic inferred from anisotropic genetic structure. Mol. Ecol. 21, 184–194.
Bremer, K., 1992. Ancestral areas: a cladistic reinterpretation of the center of origin concept. Syst. Biol. 41, 436–445.
Bremer, K., 1993. Intercontinental relationships of African and South American Asteraceae: a cladistic biogeographic analysis. In: Goldblatt, P. (Ed.), Biological Relationships Between Africa and South America. Yale University Press, New Haven/London, pp. 105–135.
Bremer, K., 1994. Asteraceae: Cladistics and Classification. Timber Press, Portland.
Bryan, S.E., Cook, A.G., Evans, J.P., Hebden, K., Hurrey, L., Colls, P., Jell, J.S., Weatherley, D., Firn, J., 2012. Rapid long distance dispersal by pumice rafting. PLoS ONE 7 (7), e40583.
Carlquist, S., 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific islands. Bull. Torrey Bot. Club 94, 129–162.
Carlquist, S., 1974. Island Biology. Columbia University Press, New York.
Censky, E.J., Hodge, K., Dudley, J., 1998. Over-water dispersal of lizards due to hurricanes. Nature 395, 556.
Coates, A.G., Obando, J.A., 1996. The geologic evolution of the Central American Isthmus. In: Jackson, B.C., Budd, A.F., Coates, A.G. (Eds.), Evolution and Environment in Tropical America. University of Chicago Press, Chicago, pp. 21–56.
Coetzee, J.A., Muller, J., 1984. The phytogeographic significance of some extinct Gondwana pollen types from the Tertiary of the southwestern Cape (South Africa). Ann. Missouri Bot. Gard. 71, 1088–1099.
Convey, P., 2007. Influences on and origins of terrestrial biodiversity of the Sub-Antarctic islands. Pap. Proc. R. Soc. Tasmania 141, 83–93.
Cowie, R.H., Holland, B.S., 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. J. Biogeogr. 33, 193–198.
Cowling, R.M., Procheş, Ş., Vlok, J.H.J., 2005. On the origin of southern African subtropical thicket vegetation. S. Afr. J. Bot. 71, 1–23.
Crame, J.A., 1999. An evolutionary perspective on marine faunal connections between southernmost South America and Antarctica. Sci. Mar. 63 (Suppl. 1), 1–14.
Crisci, J.V., Katinas, L., Posadas, P., 2003. Historical Biogeography: An Introduction. Harvard University Press, Boston.
Cronk, Q.C.B., 1987. The history of endemic flora of St. Helena: a relictual series. New Phytol. 105, 509–520.
Cronk, Q.C.B., 1992. Relict floras of Atlantic islands: patterns assessed. Biol. J. Linn. Soc. 46, 91–103.
Cronk, Q.C.B., 1997. Islands: stability, diversity, conservation. Biodivers. Conserv. 6, 477–493.
Dandeno, J.B., 1905. The parachute effect of thistle-down. Science 22, 568–572.
Darwin, C., 1859. On the Origin of Species. A Facsimile of the First Edition [1976]. Harvard University Press, Cambridge.
DeChaine, E.G., 2008. A bridge or a barrier? Beringia's influence on the distribution and diversity of tundra plants. Plant Ecol. Divers. 1, 197–207.
Detrick, R.S., Sclater, J.G., Thiede, J., 1977. The subsidence of aseismic ridges. Earth Planet. Sci. Lett. 34, 185–196.
Domming, D.P., 2005. Fossil Sirenia of the West Atlantic and Caribbean region. VII. Pleistocene *Trichechus manatus* Linnaeus, 1758. J. Vertebr. Paleontol. 25, 685–701.
Ezcurra, M.D., Agnolín, F.L., 2012. A new global palaeobiogeographical model for the Late Mesozoic and Early Tertiary. Syst. Biol. 61, 553–566.
Federov, A.V., Dekens, P.S., McCarthy, M., Ravelo, A.C., de Menocal, P.B., Barreiro, M., Pacanowski, R.C., Philander, S.G., 2006. The Pliocene paradox (mechanisms of a permanent El Niño). Science 312, 1485–1489.
Fisher, R.L., Sclater, J.G., 1983. Tectonic evolution of the southwest Indian Ocean since the Mid-Cretaceous: plate motions and stability of the pole of Antarctica/Africa for at least 80 Myr. Geophys. J. R. Astr. Soc. 73, 553–576.
Fodor, R.V., Husler, J.W., Kumar, N., 1977. Petrology of volcanic rocks from an aseismic rise: implications for the origin of the Rio Grande Rise, south Atlantic Ocean. Earth Planet. Sci. Lett. 35, 225–233.
Fosberg, F.R., 1948. Derivation of the flora of the Hawaiian Islands. In: Zimmermann, E.C. (Ed.), Insects of Hawaii. University of Hawaii Press, Honolulu, pp. 107–119.
Fosberg, F.R., 1951. The American element in the Hawaiian flora. Pacific Sci. 5, 204–206.
Freire, S.E., Katinas, L., 1995. Morphology and ontogeny of the cypsela hairs of Nassauviinae (Asteraceae, Mutisieae). In: Hind, D.J.N., Jeffrey, C., Pope, G.V. (Eds.), Advances in Compositae Systematics. Royal Botanic Gardens, Kew, pp. 107–143.
Funk, V.A., Bayer, R.J., Keeley, S., Chan, R., Watson, L., Gemeinholzer, B., Schilling, E., Panero, J.L., Baldwin, B.G., Garcia-Jacas, N., Susanna, A., Jansen, R.K., 2005. Everywhere but Antarctica: using a supertree to understand the diversity and distribution of Compositae. Biol. Skr. 55, 343–374.
Funk, V.A., Susanna, A., Stuessy, T.F., Robinson, H., 2009a. Classification of Compositae. In: Funk, V.A., Susanna, A., Stuessy, T.F., Bayer, R. (Eds.), Systematics, Evolution and Biogeography of the Compositae. IAPT, Vienna, pp. 171–189.
Funk, V.A., Anderberg, A.A., Baldwin, B.G., Bayer, R.J., Bonifacino, M., Breitwieser, I., Brouillet, L., Carbajal, R., Chan, R., Coutinho, A.X.P., Crawford, D.J., Crisci, J.V., Dillon, M.O., Freire, S.E., Galbany-Casals, M., Garcia-Jacas, N., Gemeinholzer, B., Gruenstaeudl, M., Hansen, H.V., Himmelreich, S., Kadereit, J.W., Källersjö, M., Karaman-Castro, V., Karis, P.O., Katinas, L., Keeley, S., Kilian, N., Kimball, R.T., Lowrey, T.K., Lundberg, J., McKenzie, R.J., Tadesse, M., Mort, M.E., Nordenstam, B., Oberprieler, C., Ortiz, S., Pelser, P.B., Randle, C.P., Robinson, H., Roque, N., Sancho, G., Semple, J.C., Serrano, M., Stuessy, T.F., Susanna, A., Unwin, M., Urbatsch, L., Urtubey, E., Vallès, J., Vogt, R., Wagstaff, S., Ward, J., Watson, L.E., 2009b. Compositae metatrees: the next generation. In: Funk, V.A., Susanna, A., Stuessy, T.F., Bayer, R. (Eds.), Systematics, Evolution and Biogeography of the Compositae. IAPT, Vienna, pp. 747–777.
Gheerbrant, E., Rage, J.-C., 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 224–246.
Givinish, T.J., Millam, K.C., Evans, T.M., Hall, J.C., Pires, J.C., Berry, P.E., Sytsma, K.J., 2004. Ancient vicariance or recent long distance dispersal? Inferences about phylogeny and South American-African disjunctions in Rapateaceae and Bromeliaceae based on ndhF sequence data. Int. J. Plant Sci. 165 (4 Suppl.), S35–S54.
Goldblatt, P., Manning, J.C., 2002. Plant diversity of the Cape Region of southern Africa. Ann. Missouri Bot. Gard. 89, 281–302.
Guerrero, E.L., 2011. Dispersión hacia el sur en seis especies de opiliones en el sector distal del corredor fluvial Paraná-Plata: ¿reflejo de un movimiento biotico mayor? In: Libro de resúmenes. IV Jornadas de Jóvenes Investigadores y I Jornada de Jóvenes Extensionistas, Facultad de Ciencias Naturales y Museo, La Plata, Argentina, p. 17.
Hennig, W., 1966. Phylogenetic Systematics. University of Illinois Press, Urbana.
Houle, A., 1998. Floating islands: a mode of long-distance dispersal for small and medium-sized terrestrial vertebrates. Divers. Distrib. 4, 201–216.
Houle, A., 1999. The origin of Platyrrhines: an evaluation of the Antarctic scenario and the floating islands model. Am. J. Phys. Anthropol. 109, 541–559.
Huber, M., Sloan, L.C., Shellito, C., 2003. Early Paleogene oceans and climate: a fully coupled modeling approach using the NCAR CCSM. Geol. S. Am. S. 369, 25–47.
Hugget, R.J., 2004. Fundamentals of Biogeography, 2nd ed. Routledge Fundamentals of Physical Geography, New York.
Jeffrey, C., 2007. Compositae: introduction with key to tribes. In: Kubitzki, K. (Ed.), The Families and Genera of Vascular Plants, vol. 8. Springer, Berlin/Heidelberg, pp. 61–87.
Joyeux, J.-C., Floeter, S.R., Ferreira, C.E.L., Gasparini, J.L., 2001. Biogeography of tropical reef fishes: the south Atlantic puzzle. J. Biogeogr. 28, 831–841.
Katinas, L., 2004. The *Gerbera*-complex (Asteraceae, Mutisieae): to split or not to split. Sida 21, 935–940.
Katinas, L., Crisci, J.V., Tellería, M.C., Barreda, V., Palazzesi, L., 2007. Early history of Asteraceae in Patagonia: evidence from fossil pollen grains. N. Z. J. Bot. 45, 605–610.
Katinas, L., Pruski, J., Sancho, G., Tellería, M.C., 2008. The subfamily Mutisioideae (Asteraceae). Bot. Rev. 74, 469–716.
Kennett, J.P., Houtz, R.E., Andrews, P.B., Edwards, A.R., Gostin, V.A., Hajos, M., Hampton, M., Jenkins, D.G., Margolis, S.V., Ovenshine, A.T., Perch-Nielsen, K., 1975. Cenozoic paleoceanography in the southwest Pacific Ocean, Antarctic glaciation, and the development of the Circum-Antarctic Current. In: Kennett, J.P., Houtz, R.E., et al. (Eds.), Init. Repts. DSDP, 29. U. S. Govt. Printing Office, Washington, pp. 1155–1169.
Kim, K.J., Choi, K.S., Jansen, R.K., 2005. Two chloroplast DNA inversions originated simultaneously during the early evolution of the sunflower family (Asteraceae). Mol. Biol. Evol. 22, 1783–1792.
Linder, P., 2005. Evolution of diversity: the Cape flora. Trends Plant Sci. 10, 536–541.
Maddison, W.P., Maddison, D.R., 1992. MacClade: Interactive Analysis of Phylogeny and Character Evolution, Version 3.0. Sinauer Associates, Inc., Sunderland.
Magallón, S.A., 2004. Dating lineages: molecular and paleontological approaches to the temporal framework of clades. Int. J. Plant Sci. 165, S7–S21.
Mayr, G., Alvarenga, H., Mourer-Chauviré, C., 2011. Out of Africa: fossils shed light on the origin of the hoatzin, an iconic Neotropical bird. Naturwissenschaften 98, 961–966.
McLoughlin, S., 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. Aust. J. Bot. 49, 271–300.
Mourer-Chauviré, C., 1999. Les relations entre les avifaunes du Tertiaire inférieur d'Europe et d'Amerique du Sud. Bull. Soc. Géol. Fr. 170, 85–90.
Mourer-Chauviré, C., Tabuce, R., Mahboubi, M., Adaci, M., Bensalah, M., 2011. A Phororhacoid bird from the Eocene of Africa. Naturwissenschaften 98, 815–823.

Muñoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R., Martínez, I., 2004. Wind as a long-distance dispersal vehicle in the southern hemisphere. Science 304, 1144–1147.
Nelson, G., Platnick, N., 1981. Systematics and Biogeography: Cladistics and Vicariance. Columbia University Press, New York.
Ortiz, S., Bonifacino, J.M., Crisci, J.V., Funk, V.A., Hansen, H.V., Hind, D.J.N., Katinas, L., Roque, N., Sancho, G., Susanna, A., Tellería, M.C., 2009. The basal grade of the Asteraceae: the fate of Mutisieae (sensu Cabrera) and Carduoideae. In: Funk, V.A., Susanna, A., Stuessy, T.F., Bayer, R. (Eds.), Systematics, Evolution and Biogeography of the Compositae. IAPT, Vienna, pp. 193–213.
Palazzesi, L., Barreda, V., Tellería, M.C., 2009. Fossil pollen grains of Asteraceae from the Miocene of Patagonia: Barnadesioideae affinity. Rev. Palaeobot. Palynol. 155, 83–88.
Panero, J.L., Funk, V.A., 2008. The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. Mol. Phylogenet. Evol. 47, 757–782.
Parrish, J.T., 1993. The palaeogeography of the opening South Atlantic. In: George, W., Lavocat, R. (Eds.), The Africa-South America Connection. Clarendon Press, Oxford, pp. 8–27.
Partridge, A.D., 1978. Palynology of the Late Tertiary sequence at the site 365, Leg 40, Deep Sea Drilling Project. Rep. Deep. Sea Drill Proj. 40, 953–961.
Platnick, N.I., 1976. Concepts of dispersal in historical biogeography. Syst. Zool. 25, 294–295.
Pross, J., Contreras, L., Bijl, P.K., et al., 2012. Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. Nature 488, 73–77 (more than 300 coauthors).
Raven, P.H., Axelrod, D.I., 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61, 539–673.
Raven, P.H., Raven, T.E., 1976. The genus *Epilobium* (Onagraceae) in Australasia: a systematic and evolutionary study. N. Z. Dept. Sci. Industr. Res. Bull. 216, 1–321.
Reguero, M.A., Gasparini, Z., 2007. Late Cretaceous-Early Tertiary marine and terrestrial vertebrates from James Ross Basin, Antarctic Peninsula: a review. In: Rabassa, J., Borla, M.L. (Eds.), Antarctic Peninsula and Tierra del Fuego: 100 years of Swedish-Argentine Scientific Cooperation at the End of the World. Taylor Francis, London, pp. 55–76.
Renner, S., 2004. Plant dispersal across the tropical Atlantic by wind and sea currents. Int. J. Plant Sci. 165 (4 Suppl.), S24–S33.
Rowe, D.L., Dunn, K.A., Adkins, R.M., Honeycutt, R.L., 2010. Molecular clocks keep dispersal hypotheses afloat: evidence for trans-Atlantic rafting by rodents. J. Biogeogr. 37, 305–324.
Sancho, G., Katinas, L., 2002. Are the trichomes in corollas of Mutisieae really twin hairs? Bot. J. Linn. Soc. 140, 427–433.
Sanmartín, I., Ronquist, F., 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. Syst. Biol. 53, 216–243.
Schrago, C.G., Russo, C.A.M., 2003. Timing the origin of New World monkeys. Mol. Biol. Evol. 20, 1620–1625.
Sclater, J.G., Hellinger, S., Tapscott, C., 1977. The paleobathymetry of the Atlantic Ocean from the Jurassic to the present. J. Geol. 85, 509–552.
Scotese, C.R., Gahagan, L.M., Larson, R.L., 1988. Plate tectonic reconstructions of the Cretaceous and Cenozoic ocean basins. Tectonophysics 155, 27–48.
Scott, L., Cadman, A., McMillan, I., 2006. Early history of Cainozoic Asteraceae along the southern African west coast. Rev. Palaeobot. Palynol. 142, 47–52.
Sheldon, J.C., Burrows, F.M., 1973. The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. New Phytol. 72, 665–675.
Simpson, G.G., 1940. Mammals and land bridges. J. Wash. Acad. Sci. 30, 137–163.
Small, J., 1919. The origin and development of the Compositae. New Phytol. 18, 1–35.
Smith, A.G., Smith, D.G., Funnell, B.M., 1994. Atlas of Mesozoic and Cenozoic coastlines. Cambridge University Press, Cambridge.
Stankiewicz, J., Thiart, C., Masters, J.C., de Wit, M.J., 2006. Did lemurs have sweepstake tickets? An exploration of Simpson's model for the colonization of Madagascar by mammals. J. Biogeogr. 33, 221–235.
Stramma, L., Peterson, R.G., 1990. The South Atlantic Current. J. Phys. Oceanogr. 20, 846–859.
Stuessy, T.F., Sang, T., DeVore, M.L., 1996. Phylogeny and biogeography of the subfamily Barnadesioideae with implications for early evolution of Compositae. In: Hind, D.J.N., Beentje, H. (Eds.), Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994. Royal Botanical Garden, Kew, pp. 463–490.
Susanna, A., Garcia-Jacas, N., 2007. Tribe Cardueae. In: Kubitzki, K. (Ed.), The Families and Genera of Vascular Plants, vol. 8. Springer, Berlin, Heidelberg, pp. 123–146.
Tackenberg, O., 2003. Modeling long-distance dispersal of plant diaspores by wind. Ecol. Monogr. 73, 173–189.
Tambussi, C.P., 2011. Palaeoenvironmental and faunal inferences based on the avian fossil record of Patagonia and Pampa: what works and what does not. Biol. J. Linn. Soc. 103, 458–474.
Tellería, M.C., Barreda, V., Palazzesi, L., Katinas, L., 2010. Echinate fossil pollen of Asteraceae from the Late Oligocene of Patagonia: an assessment of its botanical affinity. Plant Syst. Evol. 285, 75–81.
Thiede, J., 1977. Subsidence of aseismic ridges: evidence from sediment on Rio Grande Rise (south-west Atlantic Ocean). Am. Assoc. Petr. Geol. Bull. 61, 939–940.
Turner, B.L., 1977. Fossil history and geography. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (Eds.), The Biology and Chemistry of the Compositae. London, Academic Press, pp. 21–39.
Upchurch, P., 2008. Gondwanan break-up: legacies of a lost world? Trends Ecol. Evol. 23, 229–236.
Voelker, G., Rohwer, S., Outlaw, D.C., Bowie, R.C.K., 2009. Repeated trans-Atlantic dispersal catalyzed a global songbird radiation. Glob. Ecol. Biogeogr. 18, 41–49.
Vuilleumier, F., Andors, A.V., 1993. Avian biological relationships between Africa and South America. In: Goldblatt, P. (Ed.), Biological Relationships Between Africa and South America. Yale University Press, New Haven/London, pp. 289–328.
Wagner, W.L., Funk, V.L. (Eds.), 1995. Hawaiian Biogeography: Evolution on a hot Spot Archipelago. Smithsonian Institution Press, Washington and London.
Weston, P.H., Hill, R.S., 2013. Southern (Austral) ecosystems. In: Levin, S.A. (Ed.), Encyclopedia of Biodiversity, vol. 6, second ed. Academic Press, Waltham, pp. 612–619.
Zavada, M.S., De Villiers, S.E., 2000. Pollen of Asteraceae from the Paleocene-Eocene of South Africa. Grana 39, 39–45.
Zavada, M.S., Lowrey, T.K., 2010. Comparative pollen morphology of *Brachylena*, *Tarchananthus* and two species of *Tubulifloridites* (Asteraceae) from the Eocene, Knysna lignite of South Africa. Rev. Palaeobot. Palynol. 162, 183–192.