

## THE BIOGEOGRAPHY OF THE ARAUCARIAN DISPERSED POLLEN *CYCLUSPHAERA*

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The pollen genus *Cyclusphaera* was first described from the Campanian of Peru. The distinctive pollen is spherical to ovoid and disc shaped, with two large openings, resembling pores, opposite each other on the pollen grain. We emend the description of *Cyclusphaera scabrata* from the Cenozoic of northern South America, based on new data from transmission electron and scanning electron microscopy. The worldwide spatial and temporal distributions of *Cyclusphaera* are examined. This taxon originated in midlatitudes in the Southern Hemisphere (Gondwana) and subsequently expanded its distribution to higher and lower latitudes, reaching a maximum latitudinal and longitudinal distribution by the middle Cretaceous. Following the Cretaceous, *Cyclusphaera* was extirpated from middle and high latitudes during the late Cretaceous and Paleogene while increasing its frequency in the tropics during the Cenozoic in both Africa and South America. By the Oligocene, *Cyclusphaera* was a common element of palynofloras in Colombia and Venezuela. During the Neogene, the distribution in tropical South America became restricted, with the youngest record occurring in the late Miocene of western Colombia. The overall biogeographic pattern of *Cyclusphaera* is similar to that of Podocarpaceae, one of the most persistent gymnosperm families in the tropics. The extinction of *Cyclusphaera* could be related to the increase in aridity and expansion of savanna habitats in the northern tropics of South America during the Neogene.

**Keywords:** Araucariaceae, biogeography, *Cyclusphaera*, Gondwana, paleoenvironment.

**Online enhancements:** appendix PDFs.

### Introduction

The Neotropics is one of the most diverse areas of the world, with ~90,000 species of plants, a majority being angiosperms (Thomas 1999). Despite the high angiosperm diversity, this region has a small proportion of gymnosperm taxa. Tropical gymnosperms are restricted mostly to high-elevation or lowland habitats with poor soils (Richards 1996). Prior to the origin of angiosperms, the tropics were dominated by gymnosperms and ferns (Crane and Lidgard 1989); however, by the early Paleocene, the Neotropics was already dominated by many angiosperm families that are in the tropics today (Wing et al. 2009). It is in this context that the *Cyclusphaera* was abundant and widespread in the tropics.

*Cyclusphaera* Elsik (1966) is a genus of dispersed pollen characterized by having an ovoid to discoidal shape with two opposite circular apertures and an equatorial thickening. Its natural affinities are controversial (Taylor et al. 1987). Del Fueyo and Archangelsky (2005) have recently demonstrated attachment to an Araucarian-like cone from the Aptian of Patagonia, Argentina.

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The genus has been reported in the fossil record from the middle Jurassic (Richards and Hillier 2000) and extensively in southern South America (Del Fueyo and Archangelsky 2005; Del Fueyo et al. 2012). The record extends to the Neogene from northern South America (Colombia and Venezuela) and West Africa (Cameroon, Gabon, Angola, and Congo Republic; Salard-Cheboldaëff 1990; Pardo-Trujillo and Sánchez 2009; Jaramillo et al. 2011b). The purpose of this article is to emend the description of *Cyclusphaera scabrata* Jaramillo and Dilcher 2001 and to present a detailed description of the taxon's biogeographic history in the Cenozoic from the Neotropics and in the context of the worldwide distribution of the genus.

### Methods

#### *Morphological Data*

Pollen was recovered from sediment samples using a modified version of Barss and Williams (1973). Pollen was prepared from light, scanning electron, and transmission electron microscopy following the methods of Taylor et al. (1987) and Zavada (1987). Pollen was examined using a Zeiss Axiophot for light microscopy, a Hitachi S-640 scanning electron microscope, and a FEI Tecnai transmission electron microscope.

### Geographic Data

We compiled published and unpublished records of *Cyclusphaera*. The data were divided into two blocks, one with qualitative information (either presence/absence data or count rankings, e.g., “frequent,” “rare”) and one with quantitative information (raw frequency counts of the flora).

**Qualitative information.** The qualitative information was gathered from the database Palynodata (White and Jessop 2002; Palynodata 2006, 2008). In this database, *Cyclusphaera* has been reported in 78 publications from 27 localities around the world. There are 101 records, with several species of *Cyclusphaera*, including *C. crassa* Archangelsky et al. (1983), *C. doubingeri* Salard-Cheboldaeff (1978), *C. euribei* Elsik (1966), *C. intacta* Venkatachala & Sharma (1974), *C. patagonica* Archangelsky et al. (1983), *C. psilata* Volkheimer & Sepúlveda (1977), *C. radiata* Archangelsky et al. (1983), *C. scabrata* Jaramillo & Dilcher (2001), *C. sutschanica* Markevich (1995), and *Cyclusphaera* sp. A Volkheimer et al. (1977). Additional records include those referred to by Del Fueyo and Archangelsky (2005) to *C. radiata*, including *Katrolaites kutchensis* Venkatachala & Kar (1967), *Zonalaplicites aegyptiaca* Saad & Ghazaly (1976), and *Inaperturopollenites* sp. 1 Scott (2001). The analysis includes *C. sutschanica*, which Del Fueyo and Archangelsky (2012) do not recognize as a member of *Cyclusphaera*; however, until there is a more detailed morphological revision of *C. sutschanica*, we prefer to include it in the analysis. The oldest record of *Cyclusphaera* is Middle Jurassic, 174 Ma (Richards and Hillier 2000), from north Falklands in the south Atlantic. The youngest published record comes from the Miocene, ~16.5 Ma (Salard-Cheboldaeff 1990), from West Africa (Cameroon, Gabon, Angola, and Congo Republic) and from the Miocene of Colombia (Pardo-Trujillo and Sánchez 2009; Jaramillo et al. 2011b).

Palynodata does not provide geographical coordinates for each locality reported in the database; rather, it provides a general locality name (e.g., “Brazil”). We used the latitude and longitude coordinates of the center of either political divisions (country or state) or a broad geographic location (e.g., Atlantic Ocean) given in Palynodata (White and Jessop 2002). Therefore, several records from different parts of a country or region are condensed in a single geographic coordinate. However, in a global-scale analysis, this lack of geographical precision probably would not affect the main geographical patterns. A few records without age, an illustration of *Cyclusphaera*, or geographic information were discarded, including a locality in China, Eocene-Oligocene (Kedves 1986), and a locality in Colombia, Bata Formation, Valanginian-Hauterivian (Etayo-Serna et al. 2003).

The last version of Palynodata was published in 2006; this required us to add 19 localities and 24 records of *Cyclusphaera* to the analysis, including records that were overlooked prior to 2006 or have been published since then (Baldoni and Medina 1989; Prámparo and Volkheimer 1999, 2002; Papú 2002; Prámparo and Papú 2003; Archangelsky and Archangelsky 2004; Del Fueyo and Archangelsky 2005; Medina et al. 2008; Archangelsky and Llorens 2009; Pardo-Trujillo and Sánchez 2009). All presence/absence data, geographic location, and age of each locality are given in appendix A, available as

a PDF in the online edition of the *International Journal of Plant Sciences*.

**Quantitative information.** Counts from 2664 samples and 55 sites were used to produce maps of the geographical abundance distribution of *Cyclusphaera* through time. This procedure was performed only with counts, including samples that had a count of at least 50 grains per sample, and where the entire palynoflora was taken into account. Data came from palynological quantitative data published in a number of articles from northern South America (Jaramillo 1999, 2002, 2005; Jaramillo and Dilcher 2000, 2001; Jaramillo et al. 2005, 2006, 2007, 2009, 2010a, 2010b, 2011a, 2011b) and include the species *C. scabrata*, *Cyclusphaera* sp. 1, *Cyclusphaera* sp. 2, *Cyclusphaera* sp., and *C. doubingeri*. Unpublished counts were also added to the analysis and include recent studies by Universidad de Caldas at five localities in western Colombia (Cauca, Choco, Valle del Cauca, Ladrilleros), Antioquia, and Nariño (Tumaco), where *C. scabrata* sp. 2 and *Cyclusphaera* sp. were found. These data include the youngest record of *Cyclusphaera* dated at 5 Ma. Age constraints for these localities include nannoplankton, foraminifera, and palynology, using the zonation of Jaramillo et al. (2011b). All counts, geographic location, and age of each sample are given in appendix B, available as a PDF in the online edition of the *International Journal of Plant Sciences*.

### Paleogeographic Analysis

**Qualitative data.** *Cyclusphaera* has a long temporal range, from Jurassic to Miocene; therefore, any paleogeographic analysis needs to be based on paleogeographic coordinates rather than modern geographic locations, as continents have moved considerably since the middle Jurassic. We calculate paleolatitude and paleolongitude of each locality using the software GPlates (Boyden et al. 2011), which is based mostly on the plate tectonic model of Muller et al. (2008). The GPlates model provides plate boundaries and rotation poles for each tectonic plate on earth that can be used to produce plate tectonic reconstructions for the past 140 Ma. Each locality with a *Cyclusphaera* record was assigned to a given tectonic plate in modern-day tectonic configuration. The plate was then translated back in time using the rotation poles until the youngest and oldest ages reported for each locality were reached. Then, the paleolatitude and paleolongitude for the locality were recorded. For reports older than 140 Ma (three records at 145, 160, and 174 Ma from Argentina and Falkland Trough), paleolatitude and paleolongitude of 140 Ma were assumed, as the GPlates model does not extend back from 140 Ma. However, there are no significant movements in southern South America during the middle and upper Jurassic that could alter the general pattern seen in this analysis.

Comparisons of paleolatitude versus time and paleolongitude versus time were produced, using only presence/absence data and the enhanced Palynodata information (app. A). The entire analysis was performed using R for Statistical Computing (R Development Core Team 2012) and GPlates, version 1.1.1 (Boyden et al. 2011). The entire code for reproducing this analysis is presented in appendix C, available as a PDF in the online edition of the *International Journal of Plant*

*Sciences*. Each step in the code sequence is fully explained, allowing any user to repeat it or use it for a unique biogeographic analysis.

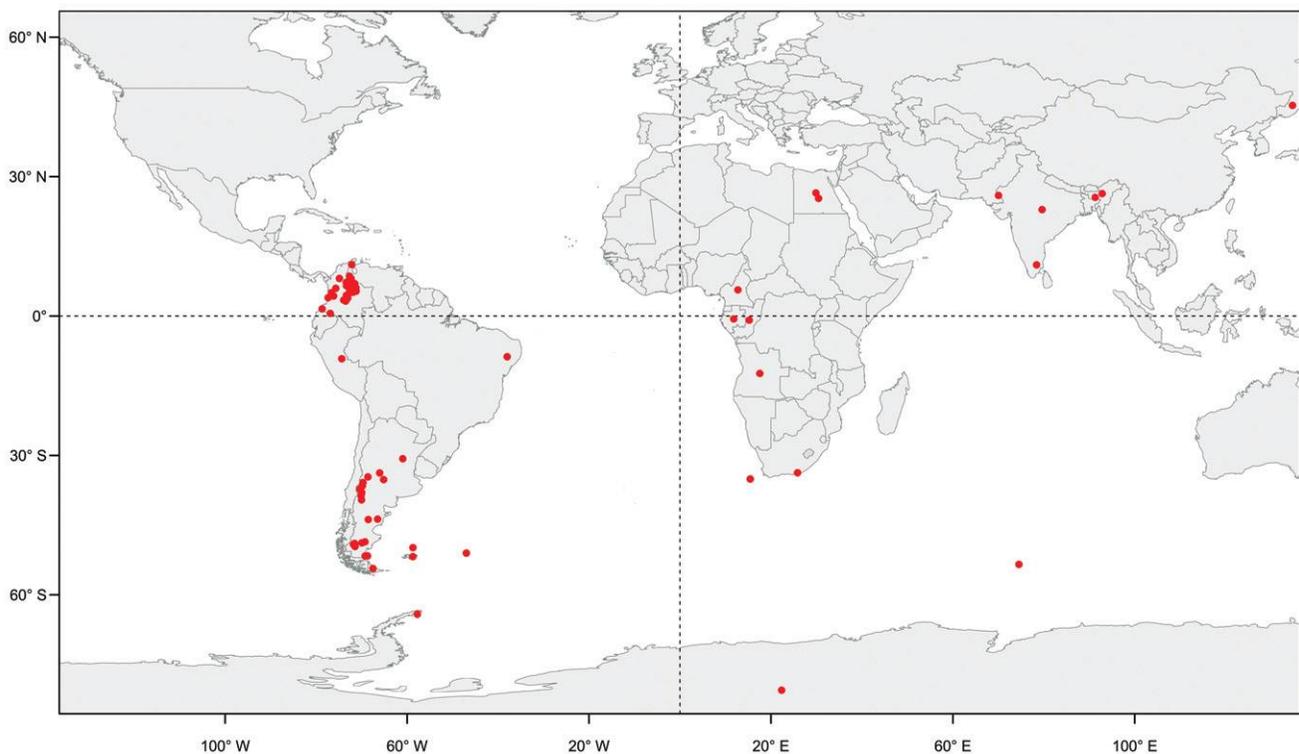
**Quantitative data.** Count data were used to analyze the temporal and spatial variation of *Cyclusphaera*. The only quantitative data available come from the northern tropics of South America; therefore, we restricted the analysis to this region. All samples with counts less than 50 grains were eliminated from the analysis, as a low count does not adequately represent the abundance distribution of a population. Counting levels per sample are not always the same; thus, we standardized the data using a Wisconsin double standardization (Bray and Curtis 1957; Cottam et al. 1973) as follows: first, species counts are standardized by dividing the empirical value versus the maximum counting value across all samples for each species; then, sample counts are standardized by finding the proportion of each species versus the total sum for each sample. A double standardization is useful because it allows comparing both samples and species with large discrepancies in raw abundance counts (Bray and Curtis 1957; Cottam et al. 1973). The double-standardized count matrix was used to construct abundance maps for the Cenozoic at 5 Ma bins, from 0 to 60 Ma range (there are no records of *Cyclusphaera* in the Neotropics older than 56.3 Ma; Jaramillo et al. 2010b). Maps were constructed as follows: each sample was assigned to a given bin based on the sample's age, and then all samples from the same locality for a given bin were summed to produce a single sample per bin per locality. The abundance of *Cyclusphaera* in a given bin could

be controlled by the total abundance per bin, thus biasing our analysis. We performed a linear correlation of the logarithm of total number of grains per bin versus the logarithm of number of *Cyclusphaera* per bin. The correlation was very poor ( $r^2 = 0.08$ ,  $P < 0.001$ ), indicating that total count per bin does not control the abundance of *Cyclusphaera* and does not represent a bias in our analysis. Analysis also was conducted by calculating the mean abundance values per sample per bin (opposite the sum as described above). Results were very similar to the maps produced by summing samples; therefore, only the summing approach is presented here. In order to produce each map, we used the logarithm of the standardized data and a bivariate linear interpolation using the Akima algorithm, which is useful for data that are unevenly spaced (Akima 1978). Analysis was performed using the package Akima 0.5-4 (Gebhardt et al. 2009) in R (R Development Core Team 2012); the code needed to reproduce the analysis is fully described in appendix C.

### Results—Systematic Palynology

#### *Cyclusphaera scabrata* Jaramillo and Dilcher 2001 (Fig. 5)

**Expanded description.** Pollen a monad, radial, isopolar, amb-elliptic. Apertures two, large, symmetrical, width of the aperture one-third of grain diameter, bordered by a thickening of the pollen grain wall, from 0.5 to 1  $\mu\text{m}$  wide; wall 0.5–2  $\mu\text{m}$  thick, thicker at the equator and adjacent to the apertures;



**Fig. 1** Geographical location of all localities reporting *Cyclusphaera*. Base map from [http://thematicmapping.org/downloads/world\\_borders.php](http://thematicmapping.org/downloads/world_borders.php).

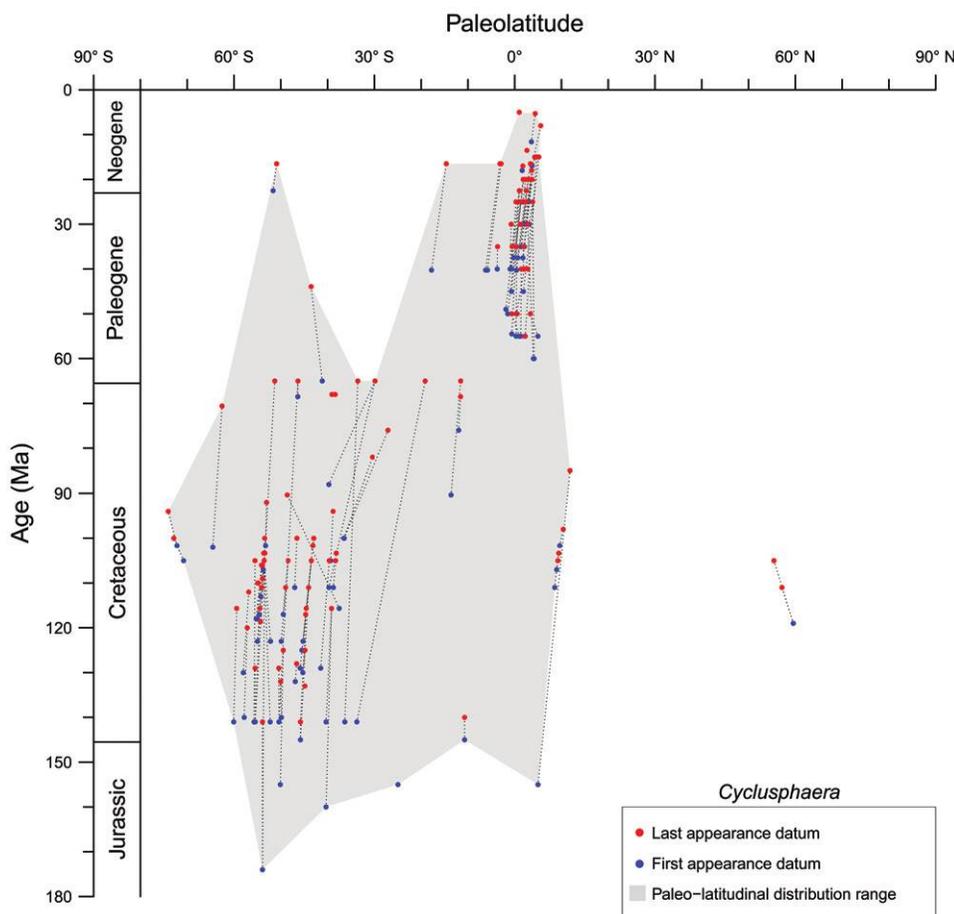
sculpture scabrate-verrucate, scabrae  $<0.5 \mu\text{m}$  wide, verrucae  $1 \mu\text{m}$  wide, very few; sculpture restricted to area between the equator and the apertures. Nonapertural areas of the pollen wall are composed of a thick sexine that ranges from  $2.6$  to  $0.5 \mu\text{m}$  adjacent to the aperture. The outermost portion of the sexine is homogeneous, ranges in thickness from  $0.2$  to  $0.5 \mu\text{m}$ . This outermost layer transitions into a middle layer that ranges between  $0.2$  and  $1.2 \mu\text{m}$  thick with numerous lacunae. The lacunae appear to be a remnant of the spaces between thick anastomosing rodlike structures. This may be due to postdepositional compression of the pollen grain, which gives a more homogeneous appearance to this layer, except for the largest spaces (i.e., the lacunae). This middle portion grades into an inner layer composed of large granules. The granules range in size between  $0.1$  and  $0.9 \mu\text{m}$ . The granulate layer is occasionally underlain by a differentially staining inner layer that occupies the position of a nexine or may be the remnants of an intine. In all the specimens studied, the aperture membrane is absent.

*Comments.* The unique feature of the pollen wall structure of *C. scabrata* is the thickness of the exine ( $2.6 \mu\text{m}$  in some areas; see table 1 in Del Fueyo et al. 2012) and the ro-

bust infrastructural elements and the large granules in the innermost portion of the sexine. This is in contrast to the more gracile anastomosing elements of the Cretaceous-occurring taxa *C. psilata* (Taylor et al. 1987) and *C. radiata* (Del Fueyo et al. 2012). The pollen wall of *C. scabrata* increases in thickness and the wall elements become more robust as their frequency in the tropics increases through time. The sporopollenin wall is known to protect the gamete from damage by ultraviolet (UV) light (Tevini and Teramura 1989), and the increase in wall thickness and robustness of the infrastructural elements may be due to the higher incidence of UV light in the tropics. In the study area, pollen grains have a tendency to increase in size up the stratigraphic section; concomitantly, there is a trend in a reduction of size of sculpturing elements and the width of the thickening adjacent to the aperture.

### Biogeography

Geographically, *Cyclusphaera* (fig. 1) shows a distinct Gondwana distribution. Records are from the Jurassic and



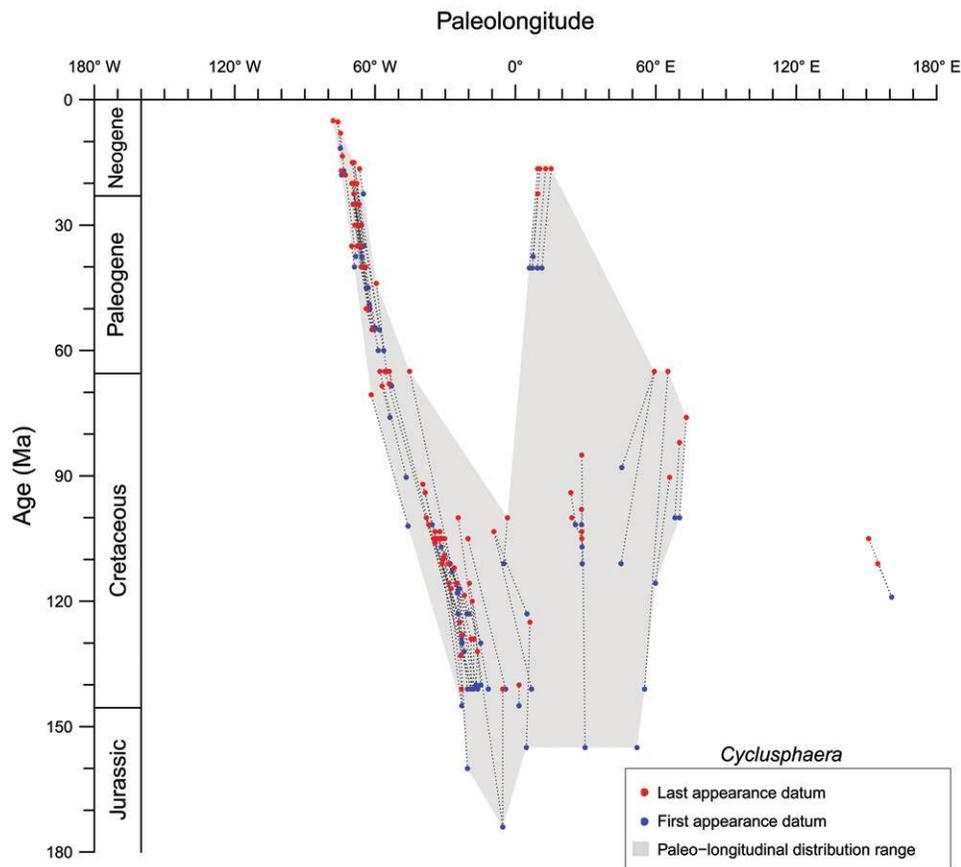
**Fig. 2** Paleolatitudinal distribution of *Cyclusphaera* through time. Dotted lines represent time range of *Cyclusphaera* reported in each locality. Geographical location of each locality mapped according to paleolatitude calculated for first- and last-appearance datums. Presence/absence data from Palynodata and additional articles (see app. A, available as a PDF in the online edition of the *International Journal of Plant Sciences*, and text for references).

younger, including South America, Antarctica, Africa, and India. No records from Australia were found. The only Laurasian records, outliers of this distribution, are lower Cretaceous localities, at 119–105 Ma, from southeast Siberia (*C. sutschanica*; Markevich 1995; Kirillova and Kiriyanova 2003). Del Fuego and Archangelsky (2012), however, have questioned the inclusion of *C. sutschanica* in *Cyclusphaera* (figs. 1, 2).

The paleolatitudinal distribution of *Cyclusphaera* shows an origin in midlatitudes of Gondwana ( $\sim 50^{\circ}\text{S}$ ) during the Jurassic followed by dispersal to both higher and lower latitudes during the mid-Cretaceous (fig. 2). Although most of the dispersal occurs throughout Gondwana, there is an isolated occurrence in Laurasia as well (records from southeastern Siberia). By the middle Cretaceous, *Cyclusphaera* reaches its maximum latitudinal range. During the late Cretaceous and Cenozoic, geographical distribution started to contract and shifted from high latitudes to lower latitudes and to tropical latitudes both in Africa and South America (fig. 2), with only scarce occurrences in the midlatitudes in South America (figs. 2, 3). By the middle Neogene, *Cyclusphaera* is restricted to the Neotropics ( $\sim 10^{\circ}\text{N}$  and S of equator), disappearing from Africa, India, and midlatitudes.

The paleolongitudinal distribution shows an origin in western Gondwana during the middle Jurassic, with an expansion toward eastern Gondwana during the early Cretaceous (fig. 3). There is isolated occurrence in Laurasia ( $\sim 150^{\circ}\text{--}170^{\circ}\text{E}$ ) during the mid-Cretaceous. By the middle Cretaceous, *Cyclusphaera* reached the maximum longitudinal extension, including eastern and western Gondwana, as well as eastern Laurasia. During the late Cretaceous and Paleogene, the distribution is gradually reduced to western South America and western Africa (fig. 3). By the middle of the Neogene, most of its distribution ended—with no evidence in eastern Gondwana (western Africa)—and *Cyclusphaera* became restricted to western South America, where it was maintained until its extinction in the late Miocene. Overall, the Cretaceous distribution of *Cyclusphaera* is more widespread, both latitudinally and longitudinally, than observed in the Cenozoic.

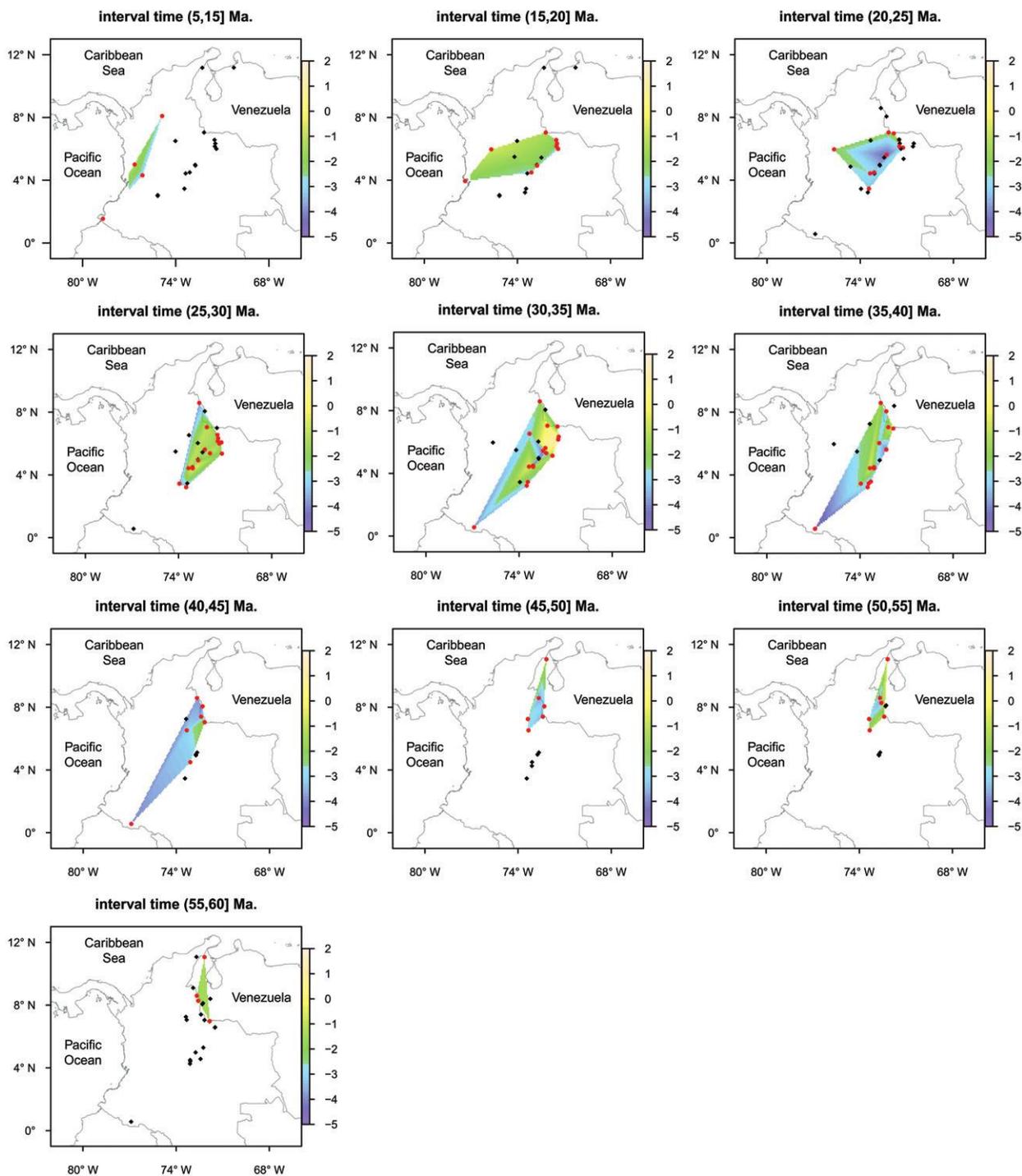
The maps of abundance distribution of *Cyclusphaera* in the Neotropics indicate that the record starts at the onset of the global warming at the Paleocene-Eocene boundary (Paleocene-Eocene thermal maximum) with the origination of *C. scabrata* (Jaramillo et al. 2010b) in northeastern Colombia—



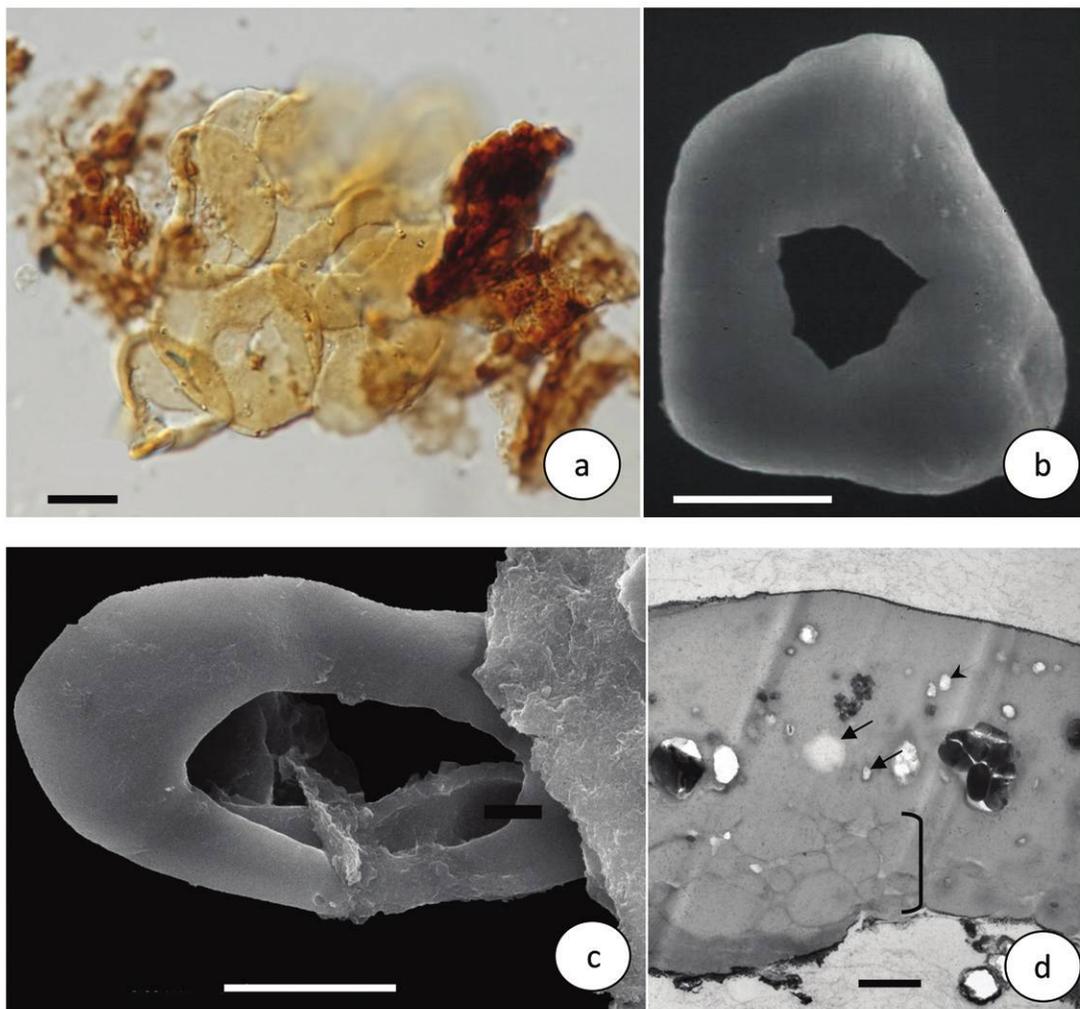
**Fig. 3** Paleolongitudinal distribution of *Cyclusphaera* through time. Dotted lines represent time range of *Cyclusphaera* reported in each locality. Geographical location of each locality mapped according to paleolatitudes calculated for first- and last-appearance datums. Presence/absence data from Palynodata and additional articles (see app. A, available as a PDF in the online edition of the *International Journal of Plant Sciences*, and text for references).

northwestern Venezuela (fig. 4). During the 55–30 Ma interval, *Cyclusphaera* spread toward the south, reaching a maximum aerial distribution by the Oligocene (30–35 Ma bin). Subsequently, during the late part of the Oligocene and the Miocene,

*Cyclusphaera* is restricted to central-western Colombia, disappearing from eastern Colombia and Venezuela, with the last occurrence at 5.3 Ma in the westernmost part of Colombia, the Chocó region (fig. 4, bin 5–15 Ma).



**Fig. 4** Geographical abundance distribution of *Cyclusphaera* through time in the northern tropics of South America. Maps at 5 Ma bins encompassing the complete age range of *Cyclusphaera* in the region. Color scale represents the variation in the logarithm of the double-standardized *Cyclusphaera* abundance: red circles correspond to localities that report *Cyclusphaera*; black diamonds represent sites where the genus was not reported. Count data presented in app. B, available as a PDF in the online edition of the *International Journal of Plant Sciences*.



**Fig. 5** Pollen of *Cyclusphaera scabrata*. *a*, Light micrograph of a cluster of pollen grains. Scale bar = 10  $\mu\text{m}$ . *b*, Scanning electron micrograph showing circular aperture and somewhat angular shape. Scale bar = 10  $\mu\text{m}$ . *c*, Scanning electron micrograph showing circular aperture and oval shape. Note that the rim of the opposing aperture is visible. Scale bar = 10  $\mu\text{m}$ . *d*, Same pollen figured in *c*. Transmission electron micrograph of the nonapertural wall showing homogeneous outer layer, large lacunae (arrows), and compressed inner layer of granules in the innermost region of the sexine (bracket). Note the discontinuous dark-staining inner layer, which may represent nexine or the remnants of an intine. Scale bar = 0.5  $\mu\text{m}$ .

### Discussion

*Cyclusphaera*, *Araucariacites*, and *Balmeiopsis* are the most common types of araucariacean pollen types in Cretaceous Gondwana forests (Del Fueyo et al. 2012). *Cyclusphaera* is an important component, in both diversity and abundance, of Mesozoic floras of Patagonia, Antarctica, India, and Africa (Archangelsky et al. 1983; Taylor et al. 1987; Zavada 1987; Del Fueyo and Archangelsky 2005; Medina et al. 2008; Del Fueyo et al. 2012). The natural affinities of *Cyclusphaera* were uncertain until pollen of *Cyclusphaera psilata* was found inside microsporangia of *Alkastrobus peltatus*, which, based on microsporophyll anatomy, suggests an araucariacean affinity (Del Fueyo and Archangelsky 2005).

The biogeographic analysis (figs. 2–4) supports previous interpretations that indicate a Gondwana distribution for the genus (Del Fueyo et al. 2012). This pollen type originated during the late Jurassic in midlatitudes of western Gondwana, with a subsequent expansion to high and low latitudes across Gondwana, both east and west, with a maximum latitudinal and longitudinal distribution during the mid-Cretaceous, possibly reaching eastern Laurasia (figs. 2, 3). During the late Cretaceous and Paleogene, the distribution gradually became restricted to lower latitudes of both South America and Africa (figs. 3, 4). There are some Paleogene records of *Cyclusphaera* of midlatitudes in southern South America, but they are restricted (figs. 2, 3). In contrast to middle and high latitudes, *Cyclusphaera* became a common element of Cenozoic tropical floras, in

both South America and Africa. The record from western South America shows that *Cyclusphaera* was widespread by the Oligocene and a common element across Colombia and western Venezuela (fig. 4). This contrasts sharply with the record of *Araucariacidites* and *Balmeiopsis*, which became extinct by the end of the Cretaceous in the tropics (Muller et al. 1987; Salard-Cheboldaef 1990; De la Parra et al. 2008; Jaramillo et al. 2011b).

Extant gymnosperms represent ~987 species compared to ~235,000 species of angiosperms worldwide (Anderson et al. 2007) and yet dominate extensive temperate ecosystems. Gymnosperms show a maximum peak of diversity and geographical distribution during the Triassic, with continuous turnover and high diversity during the Jurassic and early to middle Cretaceous (Anderson et al. 2007) and a steady decline toward the end of the Cretaceous. This strong decline continued during the Cenozoic. The general pattern of *Cyclusphaera* described here follows that similar trend of expanded Mesozoic distribution and decline during the Cenozoic but with an important distinction: while its global Cenozoic distribution was being reduced, its geographical range shifted mostly toward the tropics. This pattern is ever-more interesting, as angiosperms fully dominated the extant Neotropical forests with more than 90,000 species (Thomas 1999) while only a few hundred species are gymnosperms.

*Cyclusphaera* may have affinities with the Araucariaceae (Del Fueyo and Archangelsky 2012). The Araucariaceae is restricted in South America to temperate regions with high levels of precipitation (1000–2000 mm; Graham 2011). All living Araucariaceae are large trees with the leaf-bearing branches forming a dense crown (Taylor et al. 2009). Araucariaceae in tropical zones are present today in Australasia, mostly in the ever-wet heath forests of Borneo and the forests of northeast Australia and New Guinea. In Borneo, heath forest distribution is controlled mostly by soil types (podzolized sandy soils) characterized by coarse texture, low water-holding capacity with recurrent periods of water stress, low levels of available nutrients (N and P), and acidic soils (Richards 1996). The biogeographic history of Araucariaceae has a slightly different pattern compared to that of *Cyclusphaera*, with a widespread Cretaceous Gondwana distribution in both high and low latitudes and then a continuous Cenozoic persistence in Australasia at high and low latitudes (Morley 2000) and in temperate latitudes of South America becoming extinct in tropical latitudes of South America (Anderson et al. 1999, 2007).

A better analogue to the pattern seen in *Cyclusphaera* seems to be Podocarpaceae, which is the most successful gymnosperm family in extant tropical rainforests (Brodribb 2011). Extant Podocarpaceae have mainly a Southern Hemisphere distribution, with some populations extending as far north as China and Japan. The family originated in the Triassic-Jurassic in Gondwana (Anderson et al. 2007), expanding its distribution during the Mesozoic. Podocarpaceae did not migrate into the tropical zones of Southeast Asia until the late Eocene (Morley 2011), South America in the Paleocene (Jaramillo et al. 2011a, 2011b), or Africa in the Pliocene (Morley 2011).

Tropical podocarps are most abundant in mid- to high-elevation forests but also occur at low elevations, as in Borneo heath forests, or in white sands or nutrient-poor soils in South America (Cernusak et al. 2011). It seems that podocarps in lowland tropical rainforest reach highest abundance on low-fertility soils (Cernusak et al. 2011; Punyasena et al. 2011). The advantage of *Podocarpus* over angiosperms on poor-nutrient environments seems to come from a higher nutrient use efficiency that is the product of a longer nutrient residence time (nutrient residence time is the amount of time that a unit of nutrient spends in the plant between acquisition from the environment and loss through above- and belowground litter production; Cernusak et al. 2011). A longer leaf life and root spans, low tissue nutrient concentration, and efficient use of mycorrhizal symbioses are some of the traits that podocarps use to increase nutrient residence time (Kitayama et al. 2011). Additionally, podocarps do not tolerate drought (Brodribb 2011) or fire (Cernusak et al. 2011). In summary, Podocarpaceae can be successful in tropical lowlands and outcompete angiosperms by occupying areas with low soil fertility under regimes of intense rainfall. The *Cyclusphaera* distribution in northern South American tropics started with the onset of the Paleocene-Eocene thermal maximum, a time where temperatures in tropics increased by 3°–5°C, CO<sub>2</sub> levels doubled, and plant diversity and perhaps biomass increased significantly under high levels of rainfall (Jaramillo et al. 2010b; McInerney and Wing 2011). The plants that produced *Cyclusphaera* expanded during the warm times of the Eocene (Zachos et al. 2001) and started to decline during the early Oligocene (fig. 4), when global climate began to cool and the first significant Antarctic glaciation occurred (Oi-1 glaciation; Zachos et al. 2001). The distribution of *Cyclusphaera* is even more restricted by the late Miocene-early Pliocene (fig. 4), when there is large increase in aridity in the tropics and C<sub>4</sub> grasses and savannas expand (Zachos et al. 2001; Edwards et al. 2010). Perhaps, as with extant Podocarpaceae, *Cyclusphaera* were also living in the tropics by occupying regions with poor soil nutrients under high levels of rainfall. By not being tolerant to drought, populations became decimated as tropical dry habitats expanded (e.g., savannas). The region with the youngest record of *Cyclusphaera* (fig. 4), before it became extinct, is located in western Colombia, in the Choco region, one of the wettest regions of the world, receiving up to 12.7 m of annual rainfall (Poveda et al. 2006).

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