

The evolutionary impact of an epeiric seaway on Late Cretaceous and Paleocene palynofloras of South America

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Abstract. Paleogeographic reconstructions hypothesize that during the Cretaceous, South America was split into northern and southern portions by an epeiric seaway. Although the location, extent, and duration of this ancient seaway is debated, some propose that the resulting separation produced a northern South American biota that more closely resembled other equatorial biotas, distinct from a southern South American biota that more closely resembled other austral biotas. Palynological data from nine South American countries, five equatorial representatives (including the southeastern U.S. and northwestern Africa), and three austral representatives (Antarctica, Australia, and New Zealand) were assembled into a database that includes more than 450 genera from more than 150 localities spanning the Late Cretaceous and Paleocene epochs. Principal components and cluster analyses of the palynological data separate northern South America from southern South America during the Maastrichtian and Paleocene. During these epochs, northern South America clusters with the equatorial representatives; whereas southern South America clusters with austral representatives. These results suggest that biogeographic barriers, such as epeiric seaways, may have played a significant role in the evolution of distinct terrestrial biotas in South America during the Late Cretaceous and Paleocene.

Keywords. South America. Cretaceous. Paleocene. Biogeography. Palynology. Epeiric seaway.

Introduction

Although the historical patterns of terrestrial biogeography generally followed that of large-scale continental movements, the distribution of organisms has also been sensitive to transient, less easily detectable geographic features, such as climatic zones, mountain ranges, and epeiric seaways. For example, recently discovered vertebrate faunas from Gondwana suggest a Mesozoic biogeography more complex than plate reconstructions alone would predict (Serenó *et al.*, 1998; Goodwin *et al.*, 1999). Here, we investigate the effect of one such geographic barrier -an hypothesized seaway bisecting South America during the Late Cretaceous and Paleocene.

Sedimentological data indicate that during the Late Cretaceous and Paleocene, South America experienced a marine transgression that produced an epeiric seaway isolating Argentina and Chile from the remainder of South America (Malumián *et al.*, 1983; Smith *et al.*, 1994; Scotese, 1997). Based on the distribution of sedimentary facies, Uliana and Biddle (1988) suggest maximum epeiric flooding during the Maastrichtian. During this interval, they concluded

that southern South America was characterized by a western peninsula and southeastern archipelago. Malumián and Caramés (1995) used similar data to show that despite a series of eastern embayments, southern South America was a largely continuous peninsula by the Paleocene. Some propose that such marine incursions produced a northern South American biota that more closely resembled other equatorial biotas (*e.g.*, northern Africa and southeastern North America), distinct from a southern South American biota that more closely resembled other austral biotas (*e.g.*, Antarctica and Australia; Zinsmeister, 1987; Pascual *et al.*, 1992). We test this hypothesis through a quantitative comparison of Late Cretaceous and Paleocene palynofloras from South American, austral, and equatorial representatives. We chose pollen and spore, rather than macrofloral or faunal, data to evaluate this hypothesis because palynological data offered denser and more complete sampling in both space and time.

Methods and materials

We assembled a data set from the published literature that included more than 450 pollen and spore genera from more than 150 localities spanning the Late Cretaceous and Paleocene epochs. Our data covered nine of the thirteen South American coun-

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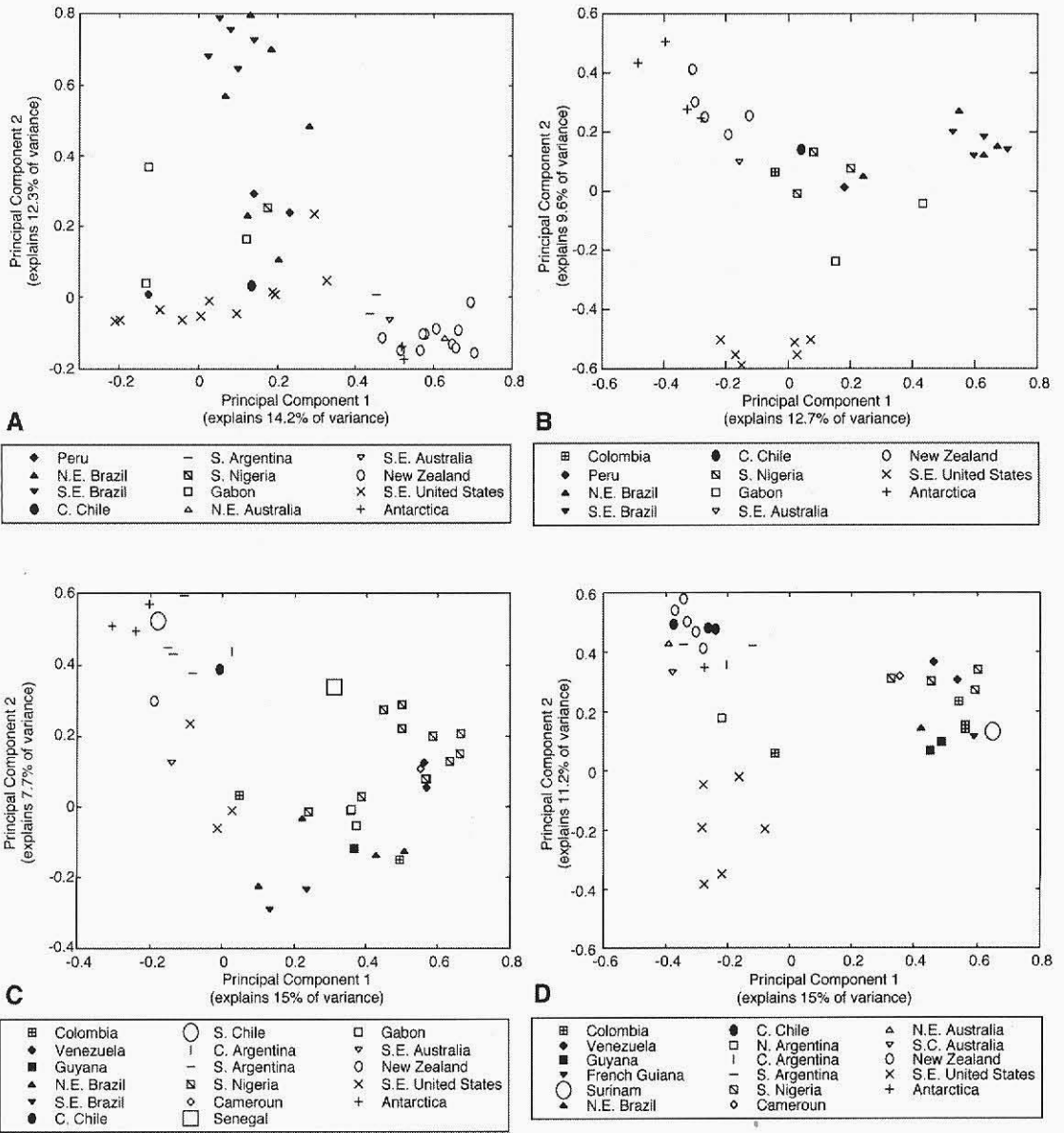


Figure 1. Principal component analysis performed in SPSS 8.0. The data set was analyzed according to the following time intervals: **A**, Albian-Coniacian; **B**, Santonian-Campanian; **C**, Maastrichtian; and **D**, Paleocene.

tries, five northern African countries, the southeastern United States, Antarctica, New Zealand, and Australia. We chose to record genera, rather than palynospecies, to minimize taxonomic variation between workers in different regions. Unique appearance data were removed from the study to reduce outlier bias in principal components analysis (PCA). A full data set with references is available from the senior author upon request. Data were assembled into a presence-absence matrix that was analyzed by time interval. We chose broad time intervals to accommodate uncertainty in age-dating of some localities. PCA and the cluster analyses were performed in SPSS 8.0 and SYSTAT 6.0 respectively. PCA solutions were not rotated. For cluster analyses, Pearson product moment correlation coefficients for binary data

were used as distance metrics, with single linkage amalgamation.

Results

PCA and cluster analysis graphically illustrate the degree of compositional similarity among geographic samples. In the absence of the proposed seaway, the paleolatitudinal and climatic effects would likely have produced a gradual compositional transition between northern and southern biotas within South America. A more discrete barrier, such as the proposed seaway, might permit evolutionary divergence between biotas, which would emerge in these analyses as more discrete biotic provinces.

In the Albian through the Campanian, PCA re-

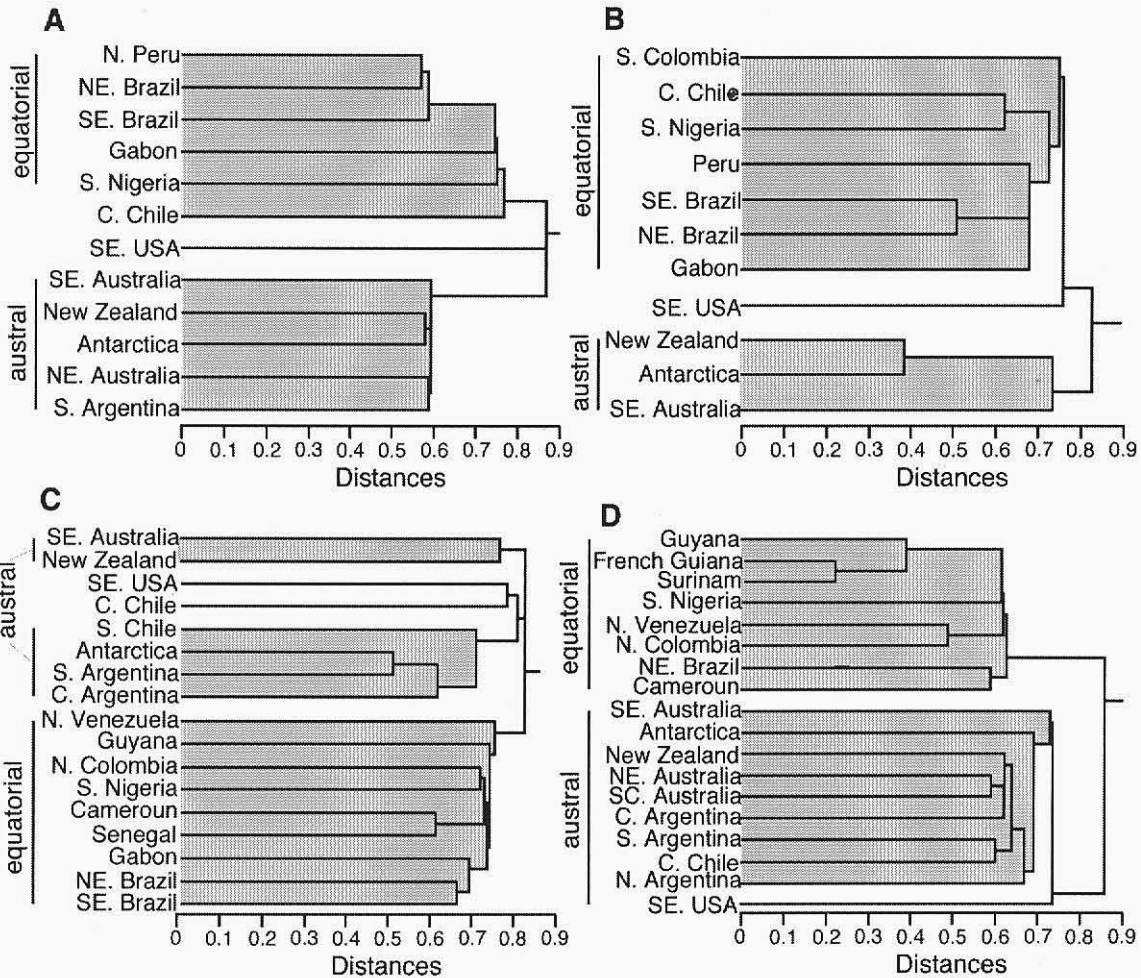


Figure 2. Cluster analyses performed in SYSTAT 6.0. The data set was analyzed according to the following time intervals: A, Albian-Coniacian; B, Santonian-Campanian; C, Maastrichtian; and D, Paleocene.

sults showed a north-to-south gradient in palynofloral similarity, without distinct provinces on both principal component axes (figures 1.A-B). The one exception was the southeastern United States, which formed a distinct province during the Santonian and Campanian (figure 1.B). Cluster analyses did show separate austral and equatorial groupings (figures 2.A-B). However, the palynofloras from central Chile are unexpectedly positioned among typical equatorial representatives (Colombia, Brazil, Perú, Nigeria, and Gabón).

In contrast, PCA results from the Maastrichtian and Paleocene show distinct separation between austral and equatorial palynofloras on the first principal component (figures 1.C-D). Likewise, cluster analyses results show distinct austral and equatorial subdivisions (figures 2.C-D). In both time intervals, palynofloras from central Chile lie among other austral localities (Argentina, Antarctica, Australia, and New Zealand). Southeastern United States remained largely isolated from Gondwanan palynofloras.

Discussion

The north-to-south gradient present from the Albian through the Campanian supports the hypothesis that biogeographic distributions were more cosmopolitan during this interval, and largely controlled by paleolatitudinal and associated climatic influences. Although cluster analyses produced austral and equatorial groupings, the position of central Chile within the equatorial group suggests that no strong physical barrier to biotic exchange existed north of central Chile. Because the clustering algorithm forces dichotomy, central Chile was likely placed among the equatorial localities because it is geographically intermediate between northern and southern sites. This pattern follows the predictions of a biogeographic distribution shaped primarily by latitudinal variation.

Conversely, more distinct groupings of palynofloras during the Maastrichtian and Paleocene support the hypothesis that distributions were shaped by a

barrier to biotic exchange. Geographically intermediate palynofloras, such as northern Argentina and southeastern Brazil, do not span the similarity gap between the geographic extremes as predicted by a latitudinal or climatic effect. Likewise, the clusters show distinct subdivisions with geographic intermediates well nested within their respective provinces. This lack of similarity, despite geographic proximity, argues for a physical division, between neighboring South American palynofloras. Additionally, our results indicate that the equatorial province did not become phytogeographically distinct from the austral province until the Maastrichtian, contrary to Srivastava (1994) who suggested an Early Cretaceous origin for these provinces, as well as the inclusion of southeastern United States in the equatorial province.

Although Haq *et al.* (1987) argued for a eustatic sea level low during the Maastrichtian, sedimentological evidence indicates that continental beds covered much of the Northwestern Argentine Basin, western Paraguay and southern Bolivia from the Cenomanian through Campanian (Malumián *et al.*, 1983). By the early Maastrichtian, a transgression had inundated most of these intracratonic basins and much of southern Argentina (Uliana and Biddle, 1988). Marine facies extended over most of northern Patagonia and, at minimum, to the borders of Argentina, Uruguay, Paraguay, and Bolivia. This marine incursion continued through the middle Paleocene.

Available vertebrate data also support Maastrichtian provincialization. Pascual *et al.* (1992) noted that faunas recovered from upper Cretaceous and Paleocene rocks of Patagonia show greater overall affinity with eastern Gondwanan biotas (Antarctica, India, Australia, and Madagascar) than with fossil assemblages from Laguna Umayo (Perú) or Tiupampa (Bolivia). For example, gondwanatheres were present in India, Madagascar, and southern South America during the Campanian and Maastrichtian (Bonaparte, 1990, 1996). However, gondwanatheres were absent in northern South America during the Paleocene (Krause *et al.*, 1997). Although this is negative evidence, it is consistent with a Maastrichtian and Paleocene barrier to northward migration. Collectively, the independent geological and biogeographic evidence point toward a significant degree of evolutionary isolation for northern and southern South America biotas during the Maastrichtian and Paleocene. Despite noted climatic differences between high and low latitudes during the Maastrichtian (Parrish, 1987; Askin and Spicer, 1995), this biogeographic pattern is best explained by a more discrete biogeographic barrier, such as an epeiric seaway. However, closely related elements

among the early Paleocene Itaboraí (Brazil), Las Flores (Patagonia, Argentina), and Tiupampa (Bolivia) faunas (Pascual *et al.*, 1996) suggest that whatever the nature of the barrier, it is best described as inhibiting, rather than completely blocking, dispersal.

Our results must be considered in light of the limitations of the data. First, pollen and spore genera are descriptive form taxa (parataxa, as specified by the International Code of Botanical Nomenclature) and do not translate directly into evolutionary groups. Morphological similarity due to plesiomorphy or convergence may misrepresent evolutionary relatedness. Second, palynological studies may be hampered by variation in taxonomic assignment by workers in different regions. Third, this study could benefit from greater temporal resolution, but we have conservatively divided our data set into large time intervals, reflecting the uncertainty in the age assignments of some palynofloras.

Conclusions

Plate tectonics has contributed much to our understanding of paleobiogeographic patterns. However, organisms are sensitive to a variety of barriers that exist within plate boundaries. Biogeographic hypotheses must incorporate knowledge of regional and sometimes transient geographic features, such as major ecotones and epeiric seaways. We bring an additional line of evidence -the palynofloral record- to the discussion of biogeographic evolution of South American biotas. These data, combined with sedimentological and faunal evidence, suggest that an epeiric seaway played an important role in the divergent evolutionary pathways of terrestrial biotas in northern and southern South America during the Maastrichtian and Paleocene.

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References

- Askin, R.A. and Spicer, R.A. 1995. The Late Cretaceous and Cenozoic history of vegetation and climate at northern and southern latitudes: A comparison. In: *Effects of Past Global Change on Life*, National Academy Press, Washington D.C., pp. 156-173.
- Bonaparte, J.F. 1990. New Late Cretaceous mammals from the Los Alamitos Formation, northern Patagonia. *National Geographic Research* 6: 63-93.

- Bonaparte, J.F. 1996. Cretaceous tetrapods of Argentina. *Munchner Geowissenschaftliche Abhandlungen, Reihe A* 30: 73-130.
- Goodwin, M.B., Clemens, W.A., Hutchison, J.H., Wood, C.B., Zavada, M.S., Kemp, A., Duffin, C.J. and Schaff, C.R. 1999. Mesozoic continental vertebrates with associated palynostratigraphic dates from the northwestern Ethiopian plateau. *Journal of Vertebrate Paleontology* 19: 728-741.
- Haq, B.U., Hardenbol, J. and Vail, P.R. 1987. Chronology of fluctuating sea levels since the Triassic. *Science* 235: 1156-1167.
- Krause, D.W., Prasad, G.V.R., von Koenigswald, W., Sahni, A. and Grine, F.E. 1997. Cosmopolitanism among Gondwanan Late Cretaceous mammals. *Nature* 390: 504-507.
- Malumián, N. and Caramés, A. 1995. El Daniano marino de Patagonia (Argentina): Paleobiogeografía de los foraminíferos bentónicos. In: *Paleogeno de America del Sur; Asociación Paleontológica Argentina, Publicación Especial* 3: 83-105.
- Malumián, N., Nullo, F.E. and Ramos, V.A. 1983. The Cretaceous of Argentina, Chile, Paraguay, and Uruguay. In: M. Moullade and A.E.M. Nairn (eds.), *The Phanerozoic Geology of the World II: The Mesozoic*, B. Elsevier, Amsterdam, pp. 265-304.
- Parrish, J.T. 1987. Global palaeogeography and palaeoclimate of the Late Cretaceous and Early Tertiary. In: E.M. Friis, W.G. Chaloner and P.R. Crane (eds.), *The Origins of Angiosperms and Their Biological Consequences*, Cambridge University Press, New York, pp. 51-73.
- Pascual, R., Archer, M., Ortiz-Jaureguizar, E., Prado, J.L., Godthelp, H. and Hand, S.J. 1992. The first non-Australian monotreme: an early Paleocene South American *Platypus* (Monotremata, Ornithorhynchidae). In: M.L. Augee (ed.), *Platypus and Echidnas*, The Royal Zoological Society of New South Wales, Sydney, pp. 2-15.
- Pascual, R., Ortiz, J.E., and Pardo, J.L. 1996. Land mammals: paradigm for Cenozoic South American geobiotic evolution. *Munchner Geowissenschaftliche Abhandlungen, Reihe A* 30: 265-319.
- Scotese, C.R. 1997. *Paleogeographic Atlas: PALEOMAP progress report 90-0497*. Department of Geology, University of Texas at Arlington, Arlington, Texas, 45 p.
- Sereno, P.C., Beck, A.L., Dutheil, D.B., Gado, B., Larsson, H.C.E., Lyon, G.H., Marcot, J.D., Rauhut, O.W.M., Sadleir, R.W., Sidor, C.A., Varricchio, D.D. and Wilson, G.P. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science* 282: 1298-1302.
- Smith, A.G., Smith, D.G. and Funnell, B.M. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*, Cambridge University Press, New York, 99 p.
- Srivastava, S.K. 1994. Evolution of Cretaceous phytogeographic provinces, continents and climates. *Review of Palaeobotany and Palynology* 82: 197-224.
- Uliana, M.A. and Biddle, K.T. 1988. Mesozoic-Cenozoic paleogeographic and geodynamic evolution of southern South America. *Revista Brasileira de Geociências* 18: 172-190.
- Zinsmeister, W.J. 1987. Cretaceous paleogeography of Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 59: 197-206.

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