

Splendid and Seldom Isolated: The Paleobiogeography of Patagonia

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Abstract

The idea that South America was an island continent over most of the Cenozoic, during which its unusual mammalian faunas evolved in isolation, is outstandingly influential in biogeography. Although large numbers of recent fossil discoveries and related advances require that the original isolation concept be significantly modified, it is still repeated in much current literature. The persistence of the idea inspired us to present here an integrated paleobiogeographic account of mammals, reptiles, and plants from the Jurassic to the Paleogene of Patagonia, which has by far the richest fossil record on the continent. All three groups show distribution patterns that are broadly consistent with South America's long separation history, first from Laurasia by the Late Jurassic, then from Africa and India-Madagascar during the late Early Cretaceous, and finally from Antarctica and Australia during the early-middle Eocene, after which "isolation" finally commenced. We highlight areas of promising future research and provide an updated view of South American isolation.

1. SPLENDID ISOLATION AND ITS LEGACY

Mais la Patagonie va sans doute contribuer à nous en donner une idée; si elle n'est pas une portion du continent antarctique, son histoire paléontologique est incompréhensible. On peut en dire autant pour l'Australie.

—Albert Gaudry, *Fossiles de Patagonie: Étude sur une portion du monde antarctique* (1906, p. 101)

George Gaylord Simpson's *Splendid Isolation: The Curious History of South American Mammals* (1980) was his final statement of one of the most influential of all biogeographic ideas: that South America was an island continent for nearly all the Cenozoic, until the Pliocene emergence of the Isthmus of Panama, and that this isolation fostered the evolution of its “peculiar” Cenozoic mammal faunas. Simpson developed this concept through most of his career (Simpson 1940, 1950, 1978), after his prolific field work in Patagonia during the early 1930s (Simpson 1934) and through many decades spent studying Patagonian fossils (see Whittington 1986) and the history of South American paleontology (Simpson 1984).

Among many antecedents to his work, Simpson (1978, 1980) particularly noted Albert Gaudry's studies of the large collection of Patagonian fossil mammals made for the Paris Museum by André Tournouër, in cooperation with the pioneers of Argentine paleontology, Florentino and Carlos Ameghino. Gaudry (1906) pointed out the dramatically different composition and evolutionary pattern of Cenozoic faunas in Patagonia compared with those of the Northern Hemisphere and that these differences lasted until the emergent Isthmus allowed unlimited faunal interchange. This observation of a closed northern connection was the foundation of Simpson's Splendid Isolation concept. However, Gaudry (1906; see epigraph) presented an additional conclusion that differed strikingly and presciently from Splendid Isolation, namely that the faunal histories of Patagonia and Australia are so similar in character—yet fundamentally different from northern faunal history—that they are “incomprehensible” unless both had once been part of a much larger Antarctica. Through the use of fossil evidence, this idea echoed Hooker's (1853) pioneering inferences based on circum-Antarctic plant distributions. However, Simpson (1940) early rejected any southern connection being relevant to mammalian evolution in South America, and he only cautiously began to acknowledge its plausibility much later (Simpson 1978, 1980).

For many nonspecialists, Splendid Isolation has retained seminal importance in biogeography to the present day, underpinning a vast literature whose scope can be quickly sensed, for example, via literature database searches for phrase combinations such as “South America” and “island continent.” However, knowledge of South American terrestrial paleobiogeography has dramatically expanded since Simpson's time (e.g., Pascual 2006), and many critical developments are not well known to the general scientific audience. Major improvements have been made in diverse areas, including geochronology and correlation, paleogeographic reconstructions, and collecting and analytical methodologies (e.g., cladistic biogeography), as well as our focus area here, knowledge of Mesozoic and Cenozoic biotas. These advances apply both to South America and to the other Gondwanan landmasses, and, importantly, to many organismal groups other than mammals, which constitute the historical basis of nearly all South American paleontology. As has always been the case in South America (Ameghino 1906, von Huene 1929, Simpson 1984, Ottone 2011), and despite many notable exceptions, most of the finds have come from Argentina, especially from the Patagonian region covered here (particularly the provinces of Neuquén, Río Negro, Chubut, and Santa Cruz).

As the knowledge has become vast, it has also become specialized, even as reliable, accessible data are increasingly needed for assessing the impact of climate change and extinction on organismal distributions and for calibrating and testing paleogeographic, biogeographic, and

Table 1 Separation times for South America

North America, direct	By Oxfordian, ~155 Ma
North America, via Africa	By earliest Cretaceous, ~145 Ma
Africa, via Antarctica	Before late Aptian, ~120 Ma
India-Madagascar, via Antarctica	Before end of Aptian, ~114 Ma
Africa, direct	Early-middle Albian, 112–106 Ma
Antarctica, and on to Australia	Eocene, increasing distance from ~50 Ma

Data from Lawver et al. 2011, 2013; L. Lawver, personal communication, 2012.

Abbreviation: Ma, million years ago.

evolutionary hypotheses (those described in, e.g., Krause et al. 2006, Ezcurra & Agnolin 2012, Mao et al. 2012). Despite numerous syntheses (e.g., Bonaparte 1996; Pascual 2006; de la Fuente et al. 2007; Gasparini et al. 2007a,b; Prámparo et al. 2007; Vucetich et al. 2007; Iglesias et al. 2011), there has been no previous attempt to integrate the records of more than one major group of Mesozoic and Cenozoic Patagonian organisms, especially in the context of Gondwanan biogeography and for a general audience.

Our goal is to provide an updated entry point and outlook for the terrestrial paleobiogeography of Patagonia, whose phenomenally rich fossil biotas have more importance than ever for understanding the history of the Southern Hemisphere and solving classic problems regarding the distributions of its extant organisms (see, e.g., Wittmann 1934, Brundin 1965, Darlington 1965, Raven & Axelrod 1974, Crisci et al. 1991). From an enormous literature, we select some of the best-understood lineages of Patagonian fossil reptiles (primarily lepidosauromorphs, crocodyli-forms, and nonavian dinosaurs), mammals, and vascular plants that have comparable records on other continents and thus hold outstanding potential for studies of interchange and biogeographic history. We cover the time period from the initial rifting of Pangea, during the Jurassic, to South America's final separation from Gondwana during the Paleogene. We highlight productive research areas and questions emerging from this first-of-its-kind comparative exercise, and we conclude with a reappraisal of Splendid Isolation in the context of the broad and enduring scientific value of Patagonian fossils and paleobiogeography.

2. SETTING

Patagonia has long been a biological crossroads—as the southwest margin of Gondwana, as the link from South America to Antarctica and beyond until the Eocene, and as a far southern range point for biota of northern origin. Historically, the Africa–South America split was postulated early (Snider 1858), and South America was part of Suess's (1897–1918) *continent de Gondwana* because it has the Permian *Glossopteris* flora. Modern paleogeographic research is diverse, but to maintain focus on the fossil record itself, we here use the paleogeographic framework of Lawver et al. (2013), who specifically investigated the settings for South American mammalian interchange in an updated geophysical context.

Table 1 summarizes South American separation dates, highlighting the Jurassic/Cretaceous separation from North America; the closely spaced series of separations from Africa and India-Madagascar during the late Early Cretaceous (**Figure 1**); and the much later separation from Antarctica, and thus Australia, from the late early Eocene (**Figure 2**). Later contact with Central and thus North America occurred during the Maastrichtian and probably during part of the Late Miocene, both via island chains (Lawver et al. 2013). The permanent establishment of the

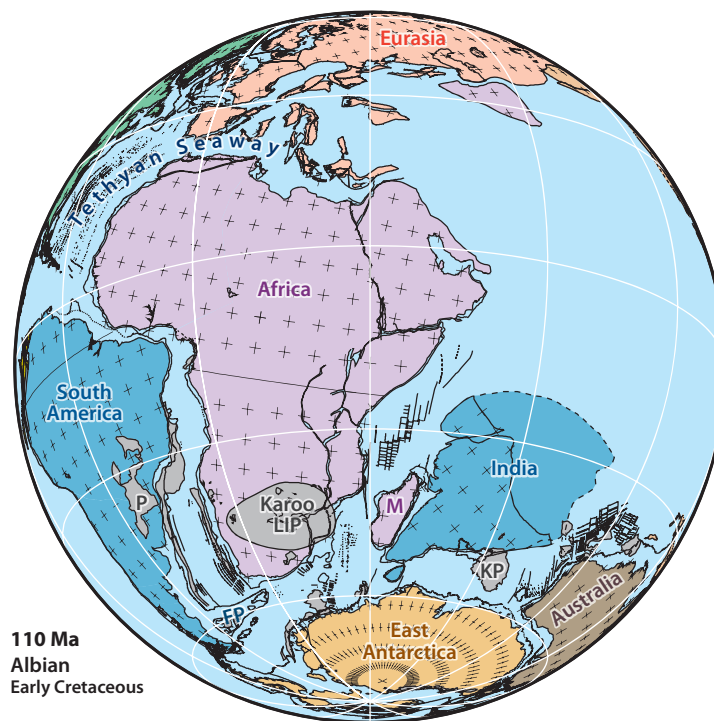


Figure 1

Reconstruction for 110 million years ago (Ma), emphasizing separations between South America and Africa and between Antarctica and India with Madagascar (India-M). New seaways are present between the Falkland Plateau (FP) and southern Africa and between India-M and East Antarctica. Other abbreviations: Karoo LIP, Karoo Large Igneous Province; KP, Kerguelen Plateau LIP; P, Paraná LIP. Reconstruction based on the plate model presented in Lawver et al. (2013), provided by the PLATES Project, Institute for Geophysics, Jackson School of Geosciences, University of Texas at Austin.

Panamanian Isthmus by the Pliocene or earlier (Iturralde-Vinent 2006, Lawver et al. 2011, Montes et al. 2012) initiated the Great American Biotic Interchange, which has been much reviewed elsewhere (Burnham & Graham 1999, Webb 2006, Woodburne 2010). Thus, since the formation of Pangea, South America has been continuously surrounded by oceans (“isolated”) only from the early-middle Eocene to the Pliocene. This time interval is shorter than Simpson thought, and it constitutes only a fraction of South America’s mammalian history as now known.

Regional paleogeographic summaries below are highly selective toward the fossiliferous units under discussion. Geologic time units follow current standards (Gradstein et al. 2012).

3. JURASSIC

South America remained connected to Pangea through the Jurassic (**Table 1**). However, Pangean rainfall zonation was pronounced, and large desert areas in the subtropical latitudes north of Patagonia would have posed significant barriers to dispersal (Rees et al. 2000, Ziegler et al. 2003). Principal Mesozoic tectonic events in Patagonia included convergence of the Pacific margin, deformation and strike-slip faulting of continental crust, and participation in the breakup of Gondwana via rifting (Spalletti & Franzese 2007). Extensional tectonics produced the Chon Aike

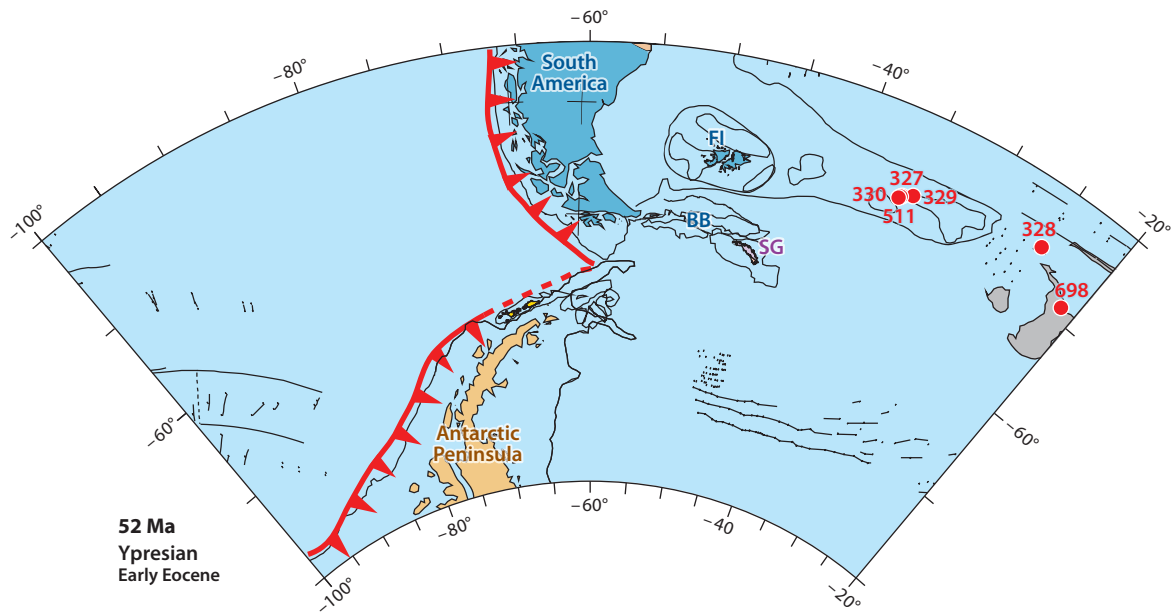


Figure 2

Polar stereographic plot of the reconstructed Drake Passage between South America and the Antarctic Peninsula at 52 Ma, early Eocene, the time of the Laguna del Hunco flora. From this time on, marine barriers to biotic interchange progressively increased, starting with an eastward shift in the tip of the Antarctic Peninsula by the middle Eocene (Lawver et al. 2011). Deep Sea Drilling Project and Ocean Drilling Project holes are labeled. The subduction zone (red) is shown with the teeth pointing in the direction of the downgoing slab. Abbreviations: BB, Burdwood Bank; FI, Falkland Islands; SG, South Georgia Island. Graphic and caption modified from Lawver et al. (2011), courtesy of L.A. Lawver.

Magmatic Province starting in the Early Jurassic, ~180 Ma (million years ago), in northern Patagonia and then culminating ~165 Ma in central and southern Patagonia, covering this area in lavas (Pankhurst et al. 1998) (**Figure 3a**) and tuffaceous sediments (La Matilde Formation, Santa Cruz, ~172–162 Ma; see Escapa et al. 2012). Also during the Early Jurassic (Cúneo et al. 2013b), the continental, extensional Cañadón Asfalto Basin formed in northern Patagonia; this basin included the predominantly lacustrine, highly fossiliferous, Early and Middle Jurassic Cañadón Asfalto Formation of Chubut (Cabaleri et al. 2010a,b) (**Figure 3a**). By ~150 Ma, Patagonia had three large sedimentary basins (**Figure 3b**): the waning, but still fossiliferous, Cañadón Asfalto Basin (Late Jurassic Cañadón Calcáreo Formation); the San Jorge Basin (Chubut and Santa Cruz), which produced a rich fossiliferous sequence to the late Cenozoic; and the predominantly marine Austral Basin.

3.1. Jurassic Floras

The Jurassic floral signature is heterogeneous but overall markedly Pangean; that is, most elements are known from the same or adjacent time intervals elsewhere in the Northern and Southern hemispheres, although Antarctica has the most comparable floras. Characteristic higher taxa include ferns, equisetaleans (“horsetails”), conifers, cycads, ginkgophytes (ancient relatives of the sole living species, *Ginkgo biloba*), and the extinct gymnosperm orders Bennettitales (“cycadeoids”) and Caytoniales. Notable Early Jurassic paleobotanical localities are Taquetrén–Cañadón de Zaino

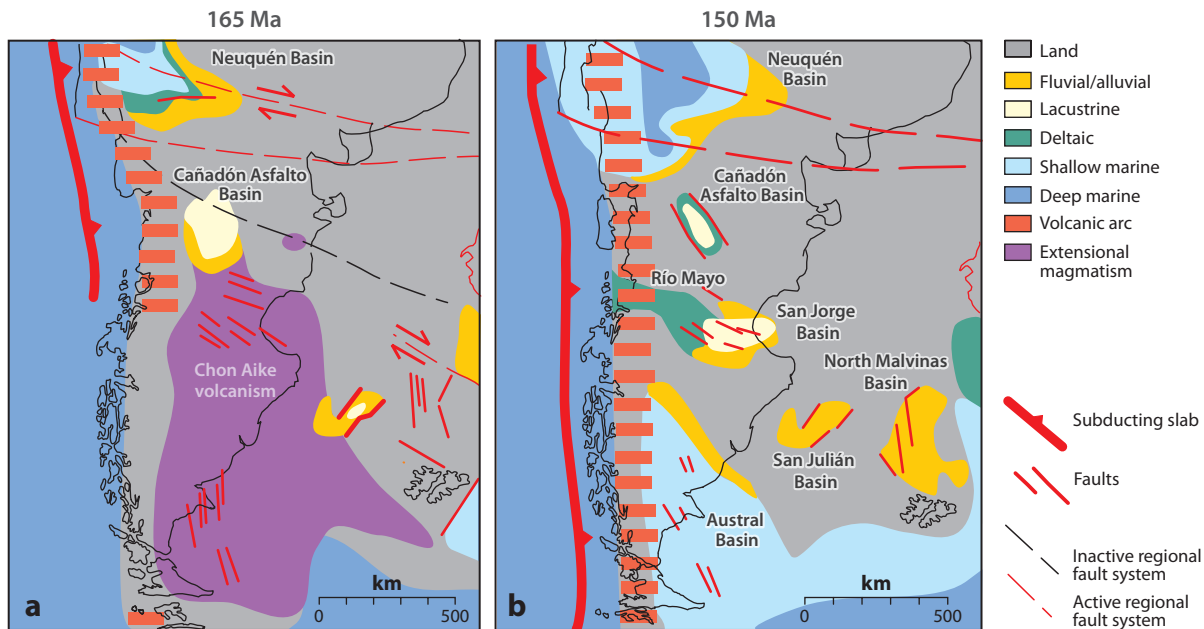


Figure 3

Reconstructions of Patagonia at (a) 165 Ma, Bathonian-Callovian, Middle Jurassic and (b) 150 Ma, Kimmeridgian-Tithonian, Late Jurassic. Key similar to that in **Figure 6**. Slightly modified from Spalletti & Franzese (2007), color plates 11B and 12A, ©2007, with permission of Indiana University Press and the authors.

and Cerro Bayo in Chubut, Piedra Pintada in Neuquén, and Roca Blanca in Santa Cruz (Bonetti 1964, Herbst 1965, Escapa et al. 2008b, Escapa & Cúneo 2012), all of which share many elements with the Middle Jurassic Hope Bay flora of Antarctica (Halle 1913b, Gee 1989, Rees & Cleal 2004, Hunter et al. 2005). The remaining Jurassic record comes mostly from the late Early–early Middle Jurassic Cañadón Asfalto (Frenguelli 1949, Escapa et al. 2008c, Cúneo et al. 2013b) and Middle Jurassic La Matilde formations (Feruglio 1937, Feraud et al. 1999, Falaschi et al. 2011, Escapa et al. 2012), and the small Late Jurassic record from the Cañadón Calcáreo Formation (Escapa et al. 2013).

3.1.1. Ferns. Early Jurassic ferns from Patagonia include Osmundaceae (the ostrich fern family), extant worldwide, and Dipteridaceae (the umbrella fern family), extant from China to Australasia. Early Jurassic Osmundaceae include *Osmundopsis* and *Todites* (Escapa & Cúneo 2012). *Osmundopsis* designates fertile foliage similar to living *Osmundastrum* and *Osmunda*, the latter of which is present in essentially modern form in the Triassic of Antarctica (Phipps et al. 1998). *Todites* belongs to a clade (*Todea* and *Leptopteris*) with a Gondwanan distribution today. *Todites* appeared in Gondwana during the Late Triassic (Herbst et al. 1998), but it was present in both hemispheres during the Jurassic. An example from Hope Bay is *T. williamsonii*. Early Jurassic Dipteridaceae include *Goepfertella* (Arrondo & Petriella 1982, Herbst 1992) and *Dictyophyllum* (*Clathropteris*; Herbst 1992). *Goepfertella* was abundant during the Late Triassic of the Northern Hemisphere and the Early and Middle Jurassic of the Southern Hemisphere (Rees 1993). *Goepfertella neuqueniana* from Patagonia is similar to *G. jeffersonii* from Hope Bay (Rees 1993). *Dictyophyllum* was diverse and widespread globally, especially during the Early Jurassic, and appears to have biostratigraphic

importance. Notable occurrences include the Triassic of Antarctica and the Jurassic of China (Guignard et al. 2009, Escapa et al. 2011). A Middle Jurassic Dipteridaceae is *Hausmannia deferrariisi* (Feruglio 1937, Herbst 1992). *Hausmannia* was a common component of Gondwanan floras from the Jurassic, and even the Late Triassic; for example, *H. papilio* is reported from Hope Bay (Rees 1993).

3.1.2. Seed plants. Patagonia has an extraordinarily rich record of fossil conifers, and during the Jurassic, the Cupressaceae (the cypress family), the Araucariaceae (the monkey-puzzle tree family), and the extinct family Cheirolepidiaceae (Triassic-Paleocene) were clearly represented. Cupressaceae are globally distributed today, although with distinct Southern and Northern Hemisphere clades that diverged early, apparently congruently with the breakup of Pangea (Mao et al. 2012). The Araucariaceae are almost entirely southern today, but *Araucaria* and extinct relatives were well represented in both hemispheres during the Mesozoic (Stockey 1982, Kunzmann 2007). The Cheirolepidiaceae were distributed globally, especially during the Jurassic and Cretaceous, and are recognized by their distinctive and widespread *Classopollis* pollen as well as occasional macrofossils (Escapa et al. 2012).

Early Jurassic *Austrohamia minuta* (Escapa et al. 2008a) (**Figure 4**) currently is the oldest reliable record of Cupressaceae in the world (Rothwell et al. 2012). A similar form reported from the Middle-Late Jurassic of China (Zhang et al. 2012) supports a broad, Pangean distribution for this group of basal Cupressaceae, which has two living representatives endemic to southeast Asia (*Taiwania* and *Cunninghamia*). *Araucaria* is represented by numerous reports in both Patagonia and Antarctica, nearly continuously from Early Jurassic to Oligocene, as recently reviewed (Panti et al. 2011). Notable Jurassic examples include the conspicuous cone scale *Araucarites cutchensis* (Frenguelli 1949), a name for a comparable Indian form (Bose & Maheshwari 1973), and the spectacular, anatomically preserved seed cones of *Araucaria mirabilis* (Spegazzini 1924, Stockey 1975). The Middle Jurassic *Pararaucaria patagonica*, also with anatomically preserved seed cones, shows diagnostic features of Cheirolepidiaceae and thus is the oldest macrofossil record of the family for the Southern Hemisphere (Wieland 1929, Stockey 1977, Escapa et al. 2012). From the Late Jurassic, *Pararaucaria delfueyii* is a new permineralized representative of the Cheirolepidiaceae from the Cañadón Calcáreo Formation (Escapa et al. 2013), where it co-occurs with *Araucaria* as part of the northern extension of the Middle-Late Jurassic conifer-dominated forests in Patagonia (Escapa & Cúneo 2006).

Jurassic ginkgoaleans in Patagonia are so far known only from fossil woods (Gnaedinger 2012). Bennettitales are represented mostly by leaf fossils that cannot be placed in specific lineages (Cúneo et al. 2010a), with the exception of Early Jurassic seed cones of *Williamsonia* of the globally distributed family Williamsonsiaeeae (Bonetti 1964, Herbst & Anzotegui 1968). A similar form occurs at Hope Bay (Gee 1989). In Caytoniales, *Sagenopteris* leaves, which are widespread and common through the Early Cretaceous in the Northern Hemisphere, are known from the Early Jurassic of Chubut (Bonetti 1964, Herbst & Anzotegui 1968, Escapa et al. 2008b) and the Middle Jurassic of Antarctica (Rees & Cleal 2004).

3.2. Jurassic Faunas

Patagonian Jurassic faunas provide a fascinating contrast between globally distributed taxa, as first reported (Bonaparte 1979a), and recent discoveries that indicate southern distributions even while the Gondwanan landmasses were still integrated with Pangea. In the absence of oceanic barriers, this contrast strongly suggests that climatic zonations or geographic features restricted some distributions (Rees et al. 2000, Remes et al. 2009, Pol & Rauhut 2012), and broadening of the subtropical evaporite zones through the Jurassic is consistent with this idea (Ziegler et al.



Figure 4

Austrohamia minuta, mature seed cones on leafy twigs, Early Jurassic, ~180 Ma (see Escapa et al. 2008a). This is the oldest known fossil of the living conifer family Cupressaceae (the cypress family), which is distributed globally today but with distinct Southern and Northern hemisphere clades. *Austrohamia* belongs to a basal lineage of Cupressaceae that had a Pangean distribution during the Jurassic and has two extant genera endemic to southeast Asia.

2003). It is of great interest that these southern distributions presumably led, in many cases, to persistent Gondwanan distributions following the breakup of Pangea.

3.2.1. Reptiles. Outside the Cañadón Asfalto Formation, Early Jurassic faunas in Patagonia and elsewhere in Argentina are represented by “prosauropod” (basal sauropodomorph) dinosaurs such as *Leyesaurus* (Apaldetti et al. 2011, Pol et al. 2011a) and poorly preserved remains of other vertebrates (Gasparini et al. 2007b). These recently discovered Early Jurassic dinosaurs are closely related to the Early Jurassic sauropodomorphs recorded from South Africa (e.g., *Massospondylus carinatus*), and they include some of the closest relatives of Sauropoda (e.g., *Leoneosaurus*). They form part of the basal radiation of Sauropodomorpha that produced successive sister taxa of the gigantic sauropods.

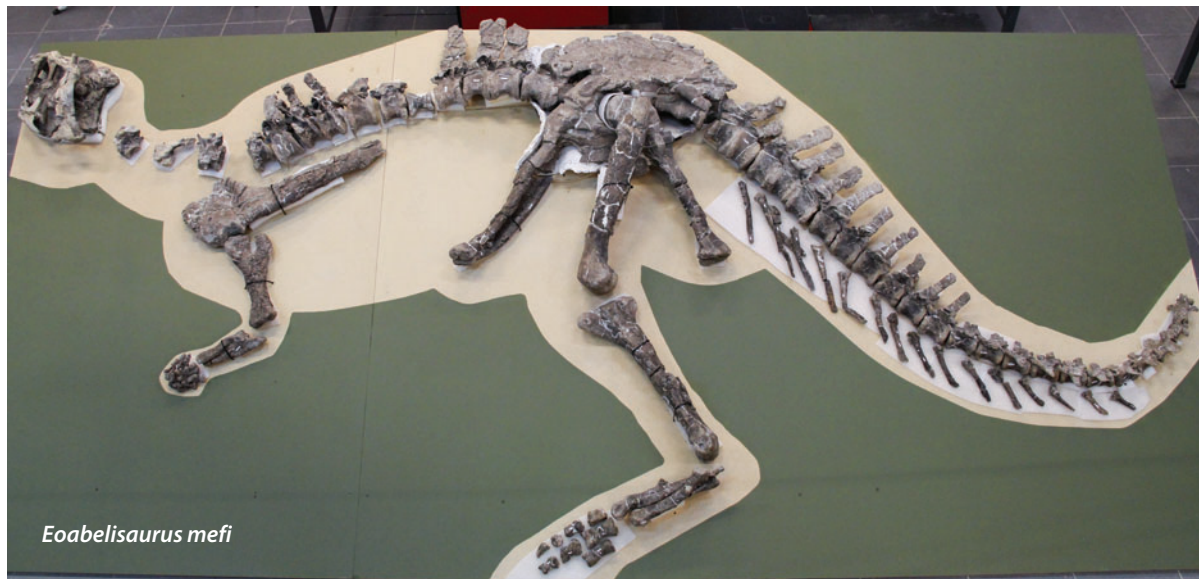


Figure 5

Eoabelisaurus mefi, the first Jurassic abelisaurid (see Pol & Rauhut 2012), being prepared for exhibit at its namesake museum [Museo Paleontológico Egidio Feruglio (MEF), Trelew, Argentina]. Reconstructed total body length is 6–6.5 m. Abelisaurids were diverse, dominant carnivores that were widespread in Gondwana, previously known only from the Cretaceous. This Early-Middle Jurassic specimen indicates a southern distribution for abelisaurids prior to the breakup of Pangea.

The Jurassic faunal record in Patagonia is otherwise overwhelmingly dominated by discoveries from the late Early and early Middle Jurassic Cañadón Asfalto Formation (Bonaparte 1979a, Escapa et al. 2008c, Cúneo et al. 2013b). This unit produces basal members of all major tetrapod clades—as well as plants (see Section 3.1)—typical of the Jurassic worldwide, as summarized by Pol et al. (2011b). The dominant dinosaurs are basal eusauropods, *Volkheimeria* and *Patagosaurus*, and basal theropods representing some of the earliest records of Tetanurae (*Condorraptor* and *Piatnitzkysaurus*; Bonaparte 1979a, Rauhut 2005) and Ceratosauria (*Eoabelisaurus*; Pol & Rauhut 2012). Basal eusauropods were widespread at this time in the Northern Hemisphere, although recent studies tentatively suggest that *Patagosaurus* belongs to a clade restricted to Gondwana (Remes et al. 2009). Similarly, *Piatnitzkysaurus* and *Condorraptor* have been interpreted as basal forms of a rapid global radiation of tetanurans during the Middle Jurassic (Benson 2010, Carrano et al. 2012), but some studies maintain that they form a basal clade restricted to South America (Smith et al. 2007).

Manidens condorensis, the first Jurassic ornithischian dinosaur from South America, provides stronger evidence for a prebreakup Gondwanan signal. This taxon belongs to a basal, widespread lineage (Heterodontosauridae), but it allies with the diverse assemblage of South African heterodontosaurids from the Early Jurassic (Pol et al. 2011b). Even more striking is *Eoabelisaurus mefi* (Figure 5), which is the oldest fossil abelisaurid by ~40 million years (Pol & Rauhut 2012). Abelisaurids were a derived, widespread, and diverse lineage of ceratosaurids that dominated the carnivorous fauna during the Late Cretaceous of Gondwana. In addition to dinosaurs, a basal sphenodontian (greater tuatara group; see Section 4.2.1) is allied with a genus from the Jurassic of India (Apesteguía et al. 2012).

Late Jurassic reptile faunas are sparse and mostly restricted to the Cañadón Calcáreo Formation, which produces diverse fishes and articulated remains of the two major groups of derived

sauropod dinosaurs (neosauropods): the Diplodocoidea (low skull, square jaw, peg teeth) and Macronaria (high skull, rounded jaw, large nasal openings). Even between these two examples, the biogeographic signal is inconsistent. *Brachytrachelopan* (Rauhut et al. 2005) is a bizarre, short-necked sauropod that belongs to a group known as dicraeosaurid diplodocoids, which occurs in the Jurassic of Tanzania (Janensch 1929) and persisted until the Early Cretaceous in Patagonia (see Section 4.2.4). In contrast, the large neosauropod *Tebuelchesaurus* belongs to a major radiation of Macronaria, inferred to have occurred globally between the Middle and Late Jurassic (Carballido et al. 2011).

3.2.2. Mammals. Remarkably, the Cañadón Asfalto Formation also preserves the oldest mammals known from South America, almost three times older than any known to Simpson. Their biogeographic pattern parallels that of dinosaurs in that some forms belong to globally widespread clades and others to exclusively Gondwanan groups. *Argentoconodon* (Rougier et al. 2007a) has a specialized (triconodont) tooth pattern found in several Mesozoic lineages worldwide; the closest relationships established are to Middle Jurassic to Early Cretaceous taxa from China and Morocco, supporting *Argentoconodon* as part of a Pangean distribution of triconodont mammals (Gaetano & Rougier 2011). *Condorodon*, a second, only distantly related triconodont, also shows affinity to many Laurasian forms, although it clusters closest to a Late Jurassic taxon from Tanzania (Gaetano & Rougier 2012). In contrast, *Asfaltomylos* and *Henosferus* (Rauhut et al. 2002, Martin & Rauhut 2005, Rougier et al. 2007b) constitute a family, Henosferidae, that is basalmost within a distinctly Gondwanan mammalian group known as the australosphenids. In some recent analyses, this group was found to include monotremes, which today are composed of platypuses and echidnas (Luo et al. 2001, Rougier et al. 2007b; but see Rowe et al. 2008). Although the australosphenids have molars that appear tribosphenic, i.e., that have the three-cusped design found in all therian mammals (marsupials, placentals, and extinct relatives), the Henosferidae have provided critical evidence that shows character differences between australosphenids and their Laurasian counterparts (boreosphenids), as originally suggested (Luo et al. 2001). Thus, the tribosphenic molar appears to have evolved convergently in the two hemispheres, and the Henosferidae belong to a prebreakup Gondwanan lineage not related to therians (Martin & Rauhut 2005, Rougier et al. 2007b). Adding greatly to the Gondwanan signal for Henosferidae is *Ambondro* from the Middle Jurassic of Madagascar (Flynn et al. 1999), the only other Jurassic australosphenid. *Ambondro* was recently placed as the lineage most closely related to Henosferidae among basal australosphenids (Rougier et al. 2007b).

4. CRETACEOUS

The breakup of Pangea greatly accelerated, and South America's separation from all other landmasses but Antarctica (and on to Australia) was complete by the end of the Early Cretaceous (**Figure 1** and **Table 1**). The many biotic similarities between the separated continents during the Late Cretaceous are most likely to represent evolutionary conservatism following vicariance, although dispersal across water always remains possible. Several proposed alternative paleogeographies accommodate the viewpoint that Late Cretaceous faunal similarity indicates prolonged contact (e.g., Sampson et al. 1998, Hay et al. 1999, Sereno et al. 2004, Krause et al. 2006), but these are in conflict with a great deal of geophysical evidence, including well-developed, intervening seaways (Lawver et al. 2013) (**Figure 1**). Episodic immigration from North America occurred during the Campanian–Maastrichtian.

In Patagonia, continental sedimentation began to increase in the Neuquén Basin, whose Pacific connection terminated by ~120 Ma (Spalletti & Franzese 2007). These changes shifted

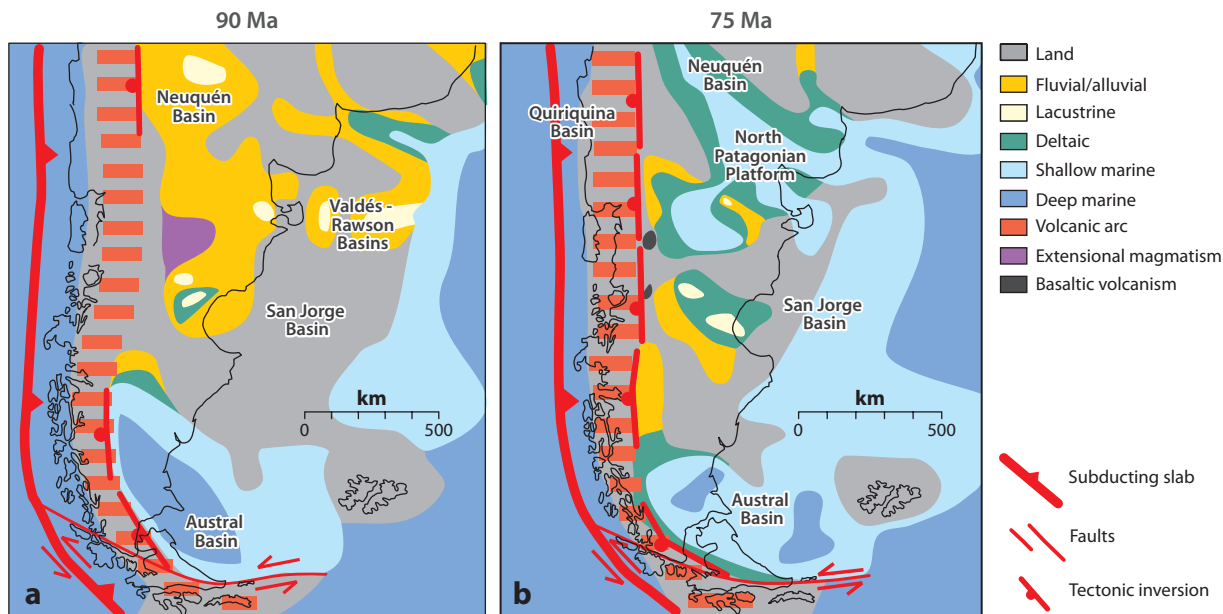


Figure 6

Reconstructions of Patagonia at (a) 90 Ma, Cenomanian-Turonian, Late Cretaceous and (b) 75 Ma, Campanian-Maastrichtian, Late Cretaceous. Slightly modified from Spalletti & Franzese (2007), color plate 14, ©2007, with permission of Indiana University Press and the authors.

the basin from a prolific source of marine reptiles to one of continental tetrapods, which are found in numerous formations and localities dating from the next ~50 million years (Bonaparte 1996, Leanza et al. 2004, de la Fuente et al. 2007, Gasparini et al. 2007b). Some of the most productive units of the Neuquén Basin are the Barremian La Amarga, Cenomanian-?Turonian Candeleros, and Campanian-Maastrichtian Allen formations. In central Santa Cruz, the volcanoclastic, paleobotanically rich Baqueró Group was deposited ~119–115 Ma, presumably accommodated by thermal subsidence following the Chon Aike magmatism (Archangelsky 1967, Cladera et al. 2002, Césari et al. 2011, Limarino et al. 2012). Near 90 Ma, intrusion of the Patagonian Batholith began to cause a major increase in continental deposition (Spalletti & Franzese 2007). The Neuquén and San Jorge basins joined and preserved extensive fluvial, predominantly red-bedded deposits that contain numerous tetrapod localities (**Figure 6a**). Marine transgressions during the very late Cretaceous (Campanian-Maastrichtian; **Figure 6b**) resulted in numerous mixed freshwater to shallow marine coastal deposits containing vertebrates. These include the La Colonia and Lepipán formations in Chubut (Scasso et al. 2012), which also contain plant fossils, and the Los Alamitos and Allen formations in Río Negro (Bonaparte et al. 1984, Leanza et al. 2004).

4.1. Cretaceous Floras

The Cretaceous paleobotanical record of Patagonia is dominated by the Early Cretaceous (Aptian) Baqueró Group, where exceptional preservation and a sustained history of concentrated paleobotanical study have made possible a large number of strongly supported systematic assignments that allow biogeographic comparisons (e.g., Berry 1924; Feruglio 1937; Herbst

1960, 1962; Archangelsky 1963; Archangelsky et al. 2003). However, there has recently been a significant increase in paleobotanical discoveries from Late Cretaceous strata.

4.1.1. Early Cretaceous. The following discussion refers almost entirely to the Baqueró Group and a few other units of similar age and location (Del Fueyo et al. 2007). Many components of the Early Cretaceous floras show Pangean affinities, as was true for the Jurassic, but the dominant group, conifers, has a significant Gondwanan signal. Several authors (e.g., Volkheimer 1980, McLoughlin 2001, Del Fueyo & Archangelsky 2005, Archangelsky & Del Fueyo 2010) have recognized a large floral province throughout southwestern Gondwana—i.e., Patagonia to mid-South America, southern Africa, and the Antarctic Peninsula—that is primarily based on conifers and recognizably distinct from the coeval Neotropics. Major higher taxa in Early Cretaceous floras are ferns (including horsetails), ginkgophytes, cycads, Bennettitales, the conifer families mentioned above plus diverse Podocarpaceae (the yellowwood family, which is extant and diverse, primarily in Southern Hemisphere and Malesian rainforests), and the oldest angiosperms from South America (Romero & Archangelsky 1986, Archangelsky & Taylor 1993).

Early Cretaceous ferns, all from lineages with global distributions at this time, include *Hausmannia* and a close relative, *Gleichenites*, as well as the horsetail *Equisetites* (Herbst 1960, 1962; Archangelsky 1964). Ginkgophytes are represented by *Karkenina incurva*, the only member of the group with reproductive organs recognized from South America; *Karkenina* is known from several Jurassic and Early Cretaceous sites in the Northern Hemisphere (Archangelsky 1965, Del Fueyo & Archangelsky 2001). For Caytoniales, *Ktalenia circularis* ovulate organs and attached leaves are closely related to those of *Caytonia* from the Jurassic and Cretaceous of Europe (Archangelsky 1963, Taylor & Archangelsky 1985). A rich variety of cycads are preserved as leaves with cuticles (Archangelsky 1963, 1966; Menéndez 1965; Archangelsky et al. 1986; Artabe 1994), and these include several genera recently placed in a phylogenetic analysis as basal members of the living, widespread families Stangeriaceae and Zamiaceae (Hermsen et al. 2006). The cycad flora (Artabe & Stevenson 1999, Cúneo et al. 2010a) also includes three species of the pollen cone *Androstrobus*, the only examples from Gondwana of this widespread fossil genus; these fossils have possible relationships to the living families Zamiaceae or Cycadaceae (Archangelsky & Villar de Seoane 2004). For Bennettitales, as in the Jurassic, several genera of leaves with cuticles are reported, but the only remains attributable to a family are reproductive structures of *Williamsonia* (Cúneo et al. 2010a).

Early Cretaceous conifers comprise an impressive suite of remarkably preserved species bearing attached reproductive organs. A living genus of Cupressaceae was present at this time, *Athrotaxis* (Tasmanian cedar; Menéndez 1966, Del Fueyo et al. 2008). *Athrotaxis* is of great interest because its entire fossil record is from the Southern Hemisphere—including Antarctica, Tasmania, and New Zealand (Halle 1913a, Archangelsky 1963, Del Fueyo et al. 2008)—and because it survives only in Tasmania today. Thus, *Athrotaxis* is one of the oldest fossil examples of the many living plant genera that have fossil records from South America and/or Australia but that survive today only in Australasia. For convenience, we refer to this general biogeographic pattern as “eastern survival,” and to its reverse as “western survival.”

Araucariaceae were widespread and diverse in Patagonia and throughout southwestern Gondwana during the Early Cretaceous. *Araucaria grandifolia* is referred to *Araucaria* Section *Araucaria* (Del Fueyo & Archangelsky 2002, Archangelsky & Del Fueyo 2010), which is restricted today to South America but also known from the Cenozoic of Patagonia and southeastern Australia (western survival). *Notopebuen brevis* and *Araucarites baqueroensis* (Del Fueyo 1991) have features of *Araucaria* Section *Eutacta*, which has Mesozoic fossils in both hemispheres but is extant only in Australasia (eastern survival). The pollen cone *Alkastrobos peltatus* contains in situ pollen of the

Cyclospora type (Del Fueyo & Archangelsky 2005), which is of great biogeographic interest because it is widespread in Cretaceous strata of Gondwana including Africa, India, and the Antarctic Peninsula, as well as many sites in South America (Volkheimer 1980, Del Fueyo & Archangelsky 2005, Archangelsky & Del Fueyo 2010, Del Fueyo et al. 2012). Notably, Early Cretaceous strata of Patagonia bear three different pollen types associated with Araucariaceae (including *Cyclospora*) that are known in situ from fossil pollen cones and have broad Gondwanan distributions (Del Fueyo et al. 2012). Only one of these, *Araucariacites*, which is extant, has a significant record in the Northern Hemisphere.

For Early Cretaceous Cheirolepidiaceae, *Tomaxellia biforme* preserves both female and male cones, which have in situ *Classopollis* pollen and are attached to leafy twigs, thus providing strong evidence for the family (Archangelsky 1963, 1968; Archangelsky & Del Fueyo 2010). Other Cretaceous examples of Cheirolepidiaceae are *Kachaikastrobus* and *Tarphyderma* (Archangelsky & Taylor 1986, Del Fueyo et al. 2008). The distinctive *Classopollis* pollen was abundant and widespread throughout western Gondwana (Quattrocchio et al. 2011).

The Podocarpaceae have a rich record in Gondwana from the Triassic to the Recent, and they are probably the most heavily studied of “southern” conifer groups in terms of paleobotany, biogeography, and evolutionary ecology (Hill & Brodribb 1999, Archangelsky & Del Fueyo 2010, Turner & Cernusak 2011). Early Cretaceous Podocarpaceae of Patagonia make a large contribution to the record; they include four species with leafy branches that bear attached male or female cones, or both (Archangelsky 1966, Archangelsky & Del Fueyo 1989, Del Fueyo et al. 1991). In each case, the morphology of pollen cones, in situ pollen grains, and cuticles is similar to that of living podocarps, although the seed cones do not show the succulent, edible receptacles seen in many living genera that target birds for dispersal. The pollen found in *Trisacocladius tigreensis* has characteristics that are similar to those of three living podocarp genera, all of which are widespread in Australasia and two of which are exclusively Australasian to southeast Asian (*Dacrycarpus*, *Dacrydium*; Archangelsky 1966, Baldoni & Taylor 1982).

4.1.2. Angiosperms and Late Cretaceous. The advent and diversification of angiosperm pollen and leaf morphotypes through the Early and Late Cretaceous of Patagonia appears to be synchronous with general patterns observed from other continents (Romero & Archangelsky 1986, Prámparo et al. 2007, Archangelsky et al. 2009). The oldest Patagonian flora dominated by angiosperm leaves comes from the Mata Amarilla Formation in the Austral Basin, ~96 Ma (Berry 1928, Iglesias et al. 2007b, Varela et al. 2012). For Late Cretaceous cycads, there is a rich flora of petrified stems from the Allen and Bororó (possibly Paleocene) formations (Artabe et al. 2004, 2005; Cúneo et al. 2010a). Many of these forms are allied with the Zamiaceae, especially the subgroup containing extant *Lepidozamia* and *Macrozamia* (both extant in Australia) and *Encephalartos* (extant in Africa).

The Campanian-Maastrichtian La Colonia Formation, better known for reptiles and mammals, is also yielding a rich flora of freshwater aquatic plants that are of biogeographic interest. Noteworthy occurrences are the only Southern Hemisphere fossil lotuses (*Nelumbo*, extant in Asia; Australia; and North, Central, and northern South America) (Gandolfo & Cúneo 2005) and fossil water ferns of the extant genus *Regnellidium*, preserved with leaves, rhizomes, and reproductive organs (Cúneo et al. 2013a). *Regnellidium* is now a monotypic relict in the southeastern Neotropics but had a far greater distribution in the past that included much of the Northern Hemisphere (Batten et al. 2011, Cúneo et al. 2013a). In contrast, the Maastrichtian aquatic fern spore *Granelispora evansii* had a broad southern distribution that included Patagonia, the Antarctic Peninsula, Australia, and New Zealand (Palamarczuk & Gamero 1988).

4.2. Cretaceous Faunas

The prolific Cretaceous faunas of Patagonia display abundant biogeographic signals across many different groups. They comprise a classic series of broadly distributed forms and endemic radiations set against the departures of Africa, India-Madagascar, and New Zealand from the remainder of Gondwana (**Table 1** and **Figure 1**).

4.2.1. Sphenodontians. The New Zealand tuatara (*Sphenodon punctatus*) is the sole living representative of the rhychocephalians, a major clade of amniotes that has a rich global fossil record, especially during the Triassic and Jurassic (Albino 2007, Evans & Jones 2010). Although basal members of the greater tuatara group (Sphenodontia) have recently been reported for the first time from the Early-Middle Jurassic (see Section 3.2.1), an increasing diversity of derived (eupropalinal) lineages has been recently described from the Late Cretaceous rocks of Patagonia (see, e.g., Apesteguía & Novas 2003, Martinelli & Forasiepi 2004, Apesteguía & Rougier 2007). These forms include large-bodied (ophistodont) sphenodontians and, notably, a form from the Allen Formation with dental characters that closely resemble those of the living *Sphenodon*; this form is placed in the crown lineage (sphenodontines) of the group, providing another southern link and eastern survival scenario (Apesteguía & Jones 2012). Elsewhere, Jurassic sphenodontines have been found in both hemispheres, and Cretaceous sphenodontines have been found in Africa, showing a Pangean distribution of tuatara-like animals that was restricted to Gondwana by the Cretaceous and then to New Zealand by the present day (Apesteguía & Jones 2012).

4.2.2. Snakes. Madtsoids are an extinct group of small to giant snakes, currently regarded as a basal lineage of the advanced snakes (Alethinophidia). Their monophyly has not been thoroughly tested, and their alleged diagnostic characters may represent symplesiomorphies of alethinophidian snakes (Mohabey et al. 2011). However, a diverse assemblage of madtsoid snakes is currently recorded from the Cretaceous and Paleogene of all Gondwanan landmasses except Antarctica, of southern Europe, and possibly of North America (see Mohabey et al. 2011). For convenience, the Cenozoic record is considered here as well. Simpson (1933) described *Madtsoia bai*, a gigantic Eocene snake with an estimated length of ~10 m, from the Sarmiento Formation in Chubut. This species and other Patagonian fossil snakes are comparable in size with *Titanoboa* from the Paleocene of Colombia (~13 m), at ~45° higher absolute paleolatitude (Head et al. 2009). Other species of *Madtsoia* have been described from the late Paleocene of Brazil and the Maastrichtian of India and Madagascar (Hoffstetter 1961, Rage 1998, Laduke et al. 2010, Mohabey et al. 2011); these constitute a notable example of closely related taxa found on postseparation Gondwanan continents. There are now numerous records of madtsoids from the Late Cretaceous through the Eocene of Patagonia, assigned currently to five genera (see, e.g., Albino 1986, 1994, 2011). Two of the Late Cretaceous genera, *Alamitophis* and *Patagoniophis*, as well as cf. *Madtsoia*, are reported from the putatively Eocene Tingamarra (Murgon) Fauna of Australia, suggesting an Antarctic link (Scanlon 1993, 2005), and well-preserved remains indicate survival of the lineage in Australia until the Pleistocene (Scanlon & Lee 2000).

4.2.3. Crocodyliforms. Cretaceous crocodyliforms were very diverse and abundant, and they occupied a greater ecological range than do the living taxa. South America has the greatest diversity of Cretaceous crocodyliforms, and it shares several lineages with Madagascar and Africa as part of a Gondwanan assemblage that was quite distinct from coeval Laurasian faunas (Gasparini et al. 1991, Buckley et al. 2000, Pol & Gasparini 2007). Among these, notosuchians were the most diverse group, characterized by a broad variety of body sizes and dietary habits (Turner & Sertich

2010). Most notosuchians had relatively small body sizes, heterodont dentitions, and apparently terrestrial lifestyles, and overall they departed from the standard crocodyliform body plan. Notosuchians, some of which survived in Patagonia to the Eocene (Pol et al. 2012), have been regarded as part of the distinctive vertebrate faunal assemblage recorded from the Cretaceous of Gondwana (Bonaparte 1986a, Pol & Gasparini 2007). Significant Patagonian genera included the small-bodied *Araripesuchus* and *Notosuchus* (Woodward 1896, Ortega et al. 2000, Pol & Apesteguía 2005, Pol & Gasparini 2007); the members of the carnivorous baurusuchid lineage, *Cynodontosuchus* and *Wargosuchus* (Woodward 1896, Martinelli & Pais 2008); and the more plesiomorphic peirosaurids *Lomasuchus* and *Gasparinisuchus* (Gasparini et al. 1991, Martinelli et al. 2012). These Patagonian taxa are most closely related to other South American Cretaceous crocodyliforms, especially those from the Late Cretaceous of Brazil (Ortega et al. 2000, Pol & Gasparini 2007, Martinelli & Pais 2008).

In general terms, the biogeography of notosuchians from Gondwana has been debated, and both (a) vicariant events during the Cretaceous breakup of Gondwana (Turner 2004) and (b) climatic controls (Carvalho et al. 2010) have been cited as explanations. Nonetheless, an undisputed biogeographic pattern is that South American taxa belong to several notosuchian clades that are also recorded on other Gondwanan landmasses. Examples include the peirosaurid/trematochampsid lineage and the genus *Araripesuchus*, both also recorded from northern Africa and Madagascar (Buffetaut 1974, Turner 2006, Rasmusson Simons & Buckley 2009, Sereno & Larsson 2009); advanced notosuchians with heterodont dentition also present in central Africa (Gomani 1997, O'Connor et al. 2010); and the large baurusuchids, currently known also from Pakistan (Wilson et al. 2001).

4.2.4. Dinosaurs. Cretaceous ornithischian dinosaurs included stegosaurians, basal ornithopods, hadrosaurs, and ankylosaurs (Coria & Cambiaso 2007, de la Fuente et al. 2007). A jaw bone famously attributed to ceratopsians (“*Notoceratops*”), and now lost, is not diagnostic of the group (von Huene 1929, Coria & Cambiaso 2007). Stegosaurians are known from fragmentary remains of a small species from the La Amarga Formation (Bonaparte 1996). Basal ornithopods appeared as a diverse series from the early Late to latest Cretaceous in Patagonia, interpreted either as members of a basal clade (*Notobypsilophodon*, *Gasparinisaura*) or as basal dryomorphs (e.g., *Loncosaurus*, *Talenkauen*). The recent discovery of the basal ornithopod *Trinisaura* (Coria et al. 2013) from the Campanian of Antarctica further supports the Patagonian assemblage of basal ornithopods as lineages that survived late into the Cretaceous of Gondwana from a widespread Pangean stock (Coria & Salgado 1996, Coria & Cambiaso 2007). Hadrosaurs and ankylosaurs appeared very late, during the Campanian and Maastrichtian (Casamiquela 1964, Bonaparte et al. 1984, Salgado & Coria 1996). The hadrosaurs are considered to be North American immigrants, and they also penetrated Antarctica (Case et al. 2000). An Antarctic, Campanian ankylosaur is not clearly related to Patagonian forms (Salgado & Gasparini 2006).

Cretaceous sauropods show a great deal of turnover corresponding to increasing dominance by titanosaurs (Titanosauria) at the expense of diplodocoids (Salgado & Bonaparte 2007). Basal titanosaurs and allies radiated near the end of the Early Cretaceous (e.g., *Chubutisaurus*, *Ligabuesaurus*), whereas diplodocoids, including the rebbachisaurids (paddle-shaped scapulas), had their last appearances during the Turonian. The Barremian *Amargasaurus*, a short-necked sauropod with strikingly elongated and bifurcated neural spines, was the last occurrence of the Gondwanan, dicraeosaurid diplodocoids (Salgado & Bonaparte 1991).

The rebbachisaurid diplodocoids were an important component of the Early Cretaceous and early Late Cretaceous sauropod faunas of Patagonia. This group was originally known from poorly preserved remains found in Africa (Lavocat 1954) and Patagonia (see, e.g., Calvo & Salgado

1995), but in recent years, well-preserved remains of a large diversity of rebbachisaurids have been discovered in different regions of South America, Africa, and Europe (see Carballido et al. 2012). Although the geographic origin of rebbachisaurids is debated (Mannion 2009; Carballido et al. 2010, 2012), it is clear that the group diversified during the Early Cretaceous in western Gondwana and Europe, showing a close faunal connection between these landmasses. Only one group seems to have diversified exclusively in Patagonia (early Late Cretaceous limaysaurine rebbachisaurids; Carballido et al. 2012).

Titanosaurs were a derived sauropod group of Gondwanan origin that became widespread globally (Salgado & Bonaparte 2007, Cerda et al. 2012). Some titanosaurs attained the largest sizes known for any land animal (*Argentinosaurus*, *Puertasaurus*; Bonaparte & Coria 1993, Novas et al. 2005b). Nearly all of ~40 titanosaur species from South America have been named only in the past decade (Mannion & Otero 2012). Through the Late Cretaceous, derived titanosaurs became the dominant sauropod group worldwide and reached significant taxonomic and morphological diversity in Patagonia (e.g., *Argentinosaurus*, *Rinconsaurus*; Bonaparte 1979b, de la Fuente et al. 2007, Salgado & Bonaparte 2007). Saltasaurids were derived titanosaurs originally recognized in Patagonia (e.g., *Saltasaurus*, *Neuquensaurus*) and closely related to Laurasian forms such as *Alamosaurus* and *Opisthocoeleicaudia*, as well as *Diamantinasaurus* from Australia. These affinities demonstrate widespread distribution (Wilson 2002, Hocknull et al. 2009, Zaher et al. 2011).

Ceratosaurian theropods underwent a significant radiation of characteristically Gondwanan forms during the Cretaceous. This included a proliferation of abelisaurids and their smaller relatives, noasaurids (Bonaparte & Novas 1985; Bonaparte 1991, 1996). Until the Campanian-Maastrichtian, abelisaurids remained as dominant carnivores (Bonaparte & Novas 1985), exemplified by *Carnotaurus* from the La Colonia Formation (Bonaparte 1985, Bonaparte et al. 1990). Abelisaurids and noasaurids also occur in Madagascar, India, Africa, Brazil, and France (Sampson et al. 2001; Sereno et al. 2004; Krause et al. 2006, 2007; Sereno & Brusatte 2008; Lindoso et al. 2012). Despite the fascinating faunal similarities among continents for these groups, a recent phylogenetic treatment of Ceratosauria could neither confirm nor reject the biogeographic signal within abelisaurids or noasaurids, owing to insufficient data and the consequent lack of well-supported clades endemic to South America or other Gondwanan landmasses (Carrano & Sampson 2008).

Tetanuran theropods included diverse maniraptorans, which had a global distribution, and carcharodontosaurids, which included the enormous predators *Giganotosaurus*, *Tyrannotitan*, and *Mapusaurus* (Coria & Salgado 1995, Novas et al. 2005a, Coria & Currie 2006, Coria 2007). Typical Laurasian theropod groups, such as tyrannosaurids, are completely absent from the Gondwanan assemblages (Krause et al. 2006). Carcharodontosaurids, along with the diplodocoid sauropods, went extinct by the end of the Turonian. Carcharodontosaurids also occur in the Cretaceous of Africa, as well as Laurasia (Krause et al. 2006, Sereno & Brusatte 2008). *Giganotosaurus* and its close relatives in Patagonia appear to form a group distinct from the African carcharodontosaurids (Coria 2007).

The Patagonian maniraptorans included alvarezsaurids (*Alvarezsaurus*, *Patagonykus*), which were basal forms of a diverse and globally distributed clade and probably represent survivor lineages of an ancient Pangean stock (Novas 1996, Novas & Pol 2002, Choiniere et al. 2010). The second group of maniraptorans (unenlagiine dromaeosaurids) was an enigmatic clade of small to medium-sized paravian theropods that have been interpreted either as basal dromaeosaurids (Makovicky et al. 2005, Novas et al. 2009) or as basal avialans (Agnolin & Novas 2011). Unenlagiines, including *Unenlagia*, *Neuquenraptor*, *Buitreraptor*, and *Austroraptor*, were first recognized in Patagonia (Novas & Puerta 1997, Makovicky et al. 2005, Novas & Pol 2005, Novas et al. 2009) but are also recorded from the Late Cretaceous of Madagascar (*Rabonavis*; Forster et al. 1998). This Gondwanan lineage was probably derived from a relatively ancient vicariance event that separated unenlagiines from Laurasian paravian theropods (Makovicky et al. 2005, Novas & Pol 2005).

4.2.5. Australia and New Zealand reptile relationships. Although Cretaceous reptilian faunas from most of Gondwana show a consistent and coherent composition and sharp differences from Laurasian faunas, as noted by Bonaparte (1986a, 1996), the relatively fragmentary faunas from Australia and New Zealand have often been interpreted differently: as a mixture of endemics, Pangean relicts, and Laurasian elements, and possibly as the source of many Laurasian lineages (see, e.g., Rich et al. 1988 and summary by Agnolin et al. 2010). The acceleration of recent discoveries throughout Gondwana has provided a much broader foundation for comparison, and several recent analyses (e.g., Molnar 1992, Upchurch et al. 2002, Hocknull et al. 2009, Agnolin et al. 2010) show the Cretaceous reptile faunas of Australia and New Zealand to be Gondwanan, with closest affinity to South America. These interpretations support the idea of interchange via Antarctica. For example, the presence of chelid turtles, an apparent abelisaurid (still disputed as an allosauroid), carcharodontosaurids, and basal ornithomimids in both Australia and Patagonia (Agnolin et al. 2010, de la Fuente et al. 2011) increases the previously overlooked faunal similarities of these two landmasses during the Cretaceous. Nevertheless, the affinities of many critical fossils, and thus their biogeographic significance, are far from settled (Benson et al. 2012, Fitzgerald et al. 2012). Importantly, the improving record of dinosaurs from the Late Cretaceous of West Antarctica shows an increasing Gondwanan signal (Coria et al. 2013, Reguero et al. 2013).

4.2.6. Mammals. Cretaceous mammals from Patagonia are represented by a variety of nontherian forms (i.e., no marsupials or placentals) that record a radiation known as the Gondwanan Episode for South America (Pascual 2006, Pascual & Ortiz-Jaureguizar 2007) (see also Section 7). There are only two significant records prior to the Campanian-Maastrichtian interval. First, *Vincelestes* is a much-debated form from the Barremian La Amarga Formation, most recently considered allied to the Gondwanan australosphenids (Bonaparte 1986b, 2008). Second, Rougier et al. (2011) reported spectacular skulls of the dryolestoid *Cronopio* (Figure 7) from the Cenomanian Candeleros Formation. Dryolestoids are well known from the Jurassic and Early Cretaceous of Laurasia, thus indicating a Pangean origin, but in South America they had a major endemic radiation during the Late Cretaceous, probably as dominants within the mammalian fauna. Dryolestoids, recorded from the early Paleocene (Gelfo & Pascual 2001) and Miocene (Rougier et al. 2012), survived into the Cenozoic in Patagonia.

Otherwise, nearly all Cretaceous mammal occurrences are from much younger strata, especially the Los Alamitos, La Colonia, and Allen formations (Bonaparte & Soria 1985; Bonaparte 1990; Pascual et al. 2000; Rougier et al. 2009a,b). These faunas collectively comprise ~17 genera, all belonging to nontherian groups and including 10 dryolestoids, a triconodont, a symmetrodont, and at least 2 gondwanatheres (de la Fuente et al. 2007, Pascual & Ortiz-Jaureguizar 2007, Rougier et al. 2009a). The gondwanatheres, best known as the earliest mammals with high-crowned (hypsodont) molariforms, had a widespread Gondwanan distribution during the Late Cretaceous that also included Africa, Madagascar, and India; they persisted in South America and Antarctica until the Eocene (Krause et al. 1997, Wilson et al. 2007; summarized by Goin et al. 2012b). There is much evidence that the gondwanatheres had multituberculate affinities, which would tie their Cretaceous, Gondwanic radiation directly to a well-known Pangean stock, as for the dryolestoids (Krause & Bonaparte 1993, Pascual et al. 1993, Gurovich & Beck 2009).

5. PALEOGENE

Just before and after the Cretaceous-Paleogene (K-Pg) boundary (66 Ma), nearly all of Patagonia—except the remnant highland areas—was flooded up to the proto-Andean range by an Atlantic transgression (Spalletti & Franzese 2007, Scasso et al. 2012). The Lefipán Formation in northern



Figure 7

Reconstruction of *Cronopio dentiacutus*, early Late Cretaceous, ~94 Ma. This small, insectivorous mammal shows a long muzzle, extremely long canines, and a host of peculiar dental features with no parallel among extant or extinct mammals (Rougier et al. 2011). *Cronopio* represents a Cretaceous endemic radiation in Gondwana of an originally Pangean group (dryolestoids). Artist: Jorge González. Image and part of caption copyright Guillermo W. Rougier; used with permission.

Chubut crosses the K-Pg boundary and records a variety of shoreline facies that preserve rare mammals, a palynoflora, and unpublished plant macrofossils, as well as a rich marine invertebrate fauna (Goin et al. 2006, Cúneo et al. 2007, Barreda et al. 2012a, Scasso et al. 2012). In the Danian of the San Jorge Basin, the upper, regressive strata of the Salamanca Formation produce diverse and well-preserved plant fossils (Iglesias et al. 2007a). From this point, the vertebrate fossil record shifts almost entirely to the San Jorge Basin. Near the end of the early Paleocene, the regressing Salamanca sea left behind an extensive coastal swamp deposit, known as Banco Negro Inferior, that contains the famous Peligran fauna (Bonaparte et al. 1993). Fully freshwater, fluvial, and volcanoclastic deposition then resumed in the overlying, still poorly dated Río Chico Group, namely the Paleocene Peñas Coloradas and ?Paleocene-Eocene Las Flores and Koluel Kaike formations, all of which produce vertebrate faunas (Simpson 1935a,b; Gelfo et al. 2008, 2009; Woodburne et al. 2013); the basal Peñas Coloradas Formation also has an unpublished macroflora (Iglesias 2007).

Lying unconformably above the Koluel Kaike Formation is the vertebrate-rich, regionally extensive, pyroclastic, loessic, and fluvial Sarmiento Formation (Bellosi 2010a,b). This unit is best

exposed on the long escarpment known as Gran Barranca, on the south shore of Lago Colhué Huapi. It was studied extensively by F. Ameghino, Simpson, and many others since its discovery by C. Ameghino and Tournouër in the 1890s (Simpson 1984, Madden et al. 2010, Madden & Scarano 2010). Gran Barranca holds the most complete and continuous exposure of Southern Hemisphere Cenozoic mammals in the world, and, accordingly, it is the backbone of South American paleontology and the Splendid Isolation idea. Gran Barranca is now recognized as having six major lithologic units and seven mammalian faunal zones, extending, with several gaps, from middle Eocene to early Miocene, ~42–18 Ma (Kay et al. 1999; Bellosi 2010b; Ré et al. 2010a,b; Dunn et al. 2013).

In northwestern Patagonia, during the warm early and middle Eocene, a massive volcanic province formed, broadly referred to the Huitrera Formation (Aragón & Mazzoni 1997, Cazau et al. 2005). Several caldera-lake systems of possibly montane elevations were preserved with outstandingly diverse biotas of plants as well as insects, fish, and other vertebrates from a long-lasting, volcanic rainforest biome. The most notable of these sites are Laguna del Hunco in Chubut (~52.2 Ma) and Río Pichileufú in Río Negro (~47.7 Ma) (Berry 1925, 1938; Wilf et al. 2005). Near Laguna del Hunco and the town of Paso del Sapo are local mammalian faunas dating to the early-middle Eocene (~49–47 Ma), filling the temporal gap between the faunas of the Río Chico Group and those of the Sarmiento Formation and providing a record of probable rainforest vertebrates (Gosses 2006, Tejedor et al. 2009).

5.1. Paleogene Floras

Well-preserved, diverse early Paleocene floras from coastal paleoenvironments of Patagonia provide uniquely detailed information about Gondwanan vegetation shortly after the end-Cretaceous extinction. Outstandingly diverse floras from volcanic lake paleoenvironments of the globally warm early and middle Eocene show robust, trans-Antarctic connections to Paleogene floras of southern Australia and to modern-day Australasian rainforests.

5.1.1. Paleocene coastal floras. By far the most significant Paleocene floras come from the early Paleocene Salamanca Formation in the western San Jorge Basin (Berry 1937, Iglesias 2007, Iglesias et al. 2007a). Although renewed investigations are still preliminary, several occurrences are notable. Leaves of Menispermaceae (the moonseed vine family) are especially interesting in light of Paleocene fruit and seed occurrences of this group in Colombia; these fossils, in turn, show close resemblance to fossil and living forms from a wide variety of locations (Herrera et al. 2011). The evidence collectively indicates that the Menispermaceae had a complex, mostly unknown biogeographic history that resulted in a large range in both hemispheres by the Paleocene (see also Wang et al. 2012). Several types of legume (Fabaceae) foliage and wood are present (Brea et al. 2008), comprising the oldest reliable records of one of the most diverse of all plant families worldwide (~20,000 species). The flora also contains abundant serrate leaves that can probably be assigned to *Nothofagus* (southern beeches) and would thus represent the oldest South American macrofossils of this iconic southern genus, which still has an unclear evolutionary and biogeographic history despite a rich fossil record (Cook & Crisp 2005, Sauquet et al. 2012). The flora from the basal Peñas Coloradas Formation in the same area is similar to the underlying Salamanca floras (Iglesias 2007, Iglesias et al. 2007a).

5.1.2. Eocene volcanic rainforest floras. Early Eocene floras are abundantly preserved in the 52-Ma, fossil rainforest caldera-lake deposit at Laguna del Hunco (Berry 1925, Wilf et al. 2003). These assemblages include an outstanding and growing list of extant genera that have clear

southern biogeographic connections, both living and fossil. Many of the same lineages are present in the early middle Eocene Río Pichileufú flora (Berry 1938, Wilf et al. 2005, Wilf 2012), indicating regional persistence of the rainforest biome. The Australasian signal in the Laguna del Hunco and Río Pichileufú floras was first recognized reliably in the fossil conifers (Berry 1938; Florin 1940a,b; Hill & Brodribb 1999) and now also includes angiosperms as well as ferns (Carvalho et al. 2013). For several genera, these two sites provide the only records in South America, past or present. They record the western reaches of a vast, trans-Antarctic paleorainforest flora from the warm early and early middle Eocene (Pross et al. 2012); the flora's elements, for the most part, survive in the tropical West Pacific and often still form associations with each other (eastern survival in that all currently inhabit or passed through Australia). The Australasian components of the Río Pichileufú flora could also indicate in situ survival within the biome, after separation from Antarctica was already under way by the middle Eocene. This idea is supported by the fact that so far, all Australasian-type taxa that are recognized at Río Pichileufú are also known from the older Laguna del Hunco assemblage, whereas the reverse is not true. For example, in South America, *Eucalyptus* and *Gymnostoma* (see below) are reliably known only from Laguna del Hunco.

In the conifers, several living genera of bird-dispersed Podocarpaceae are represented at Laguna del Hunco, Río Pichileufú, or both, including *Dacrycarpus*, which has other Paleogene fossils in Australia and Chile and is extant in Australasia and southeast Asia; *Acmopyle*, Paleogene fossils in Australia and ?Antarctica, extant in Fiji and New Caledonia; and *Retrophyllum*, Paleogene fossils in Australia and Chile, extant in Australasia and the Neotropics (Florin 1940a,b; Wilf 2012). Cupressaceae are represented by *Papuacedrus*, Paleogene fossils in Australia and Antarctica, extant in New Guinea and Moluccas (Wilf et al. 2009). The Araucariaceae are *Araucaria* Section *Eutacta*, Paleogene fossils in Australia, living range in Australasia (Berry 1938), and an unpublished species of *Agathis*, Paleogene fossils in Australia, extant from New Zealand to Sumatra (Wilf et al. 2012). This conifer assemblage is most characteristic, today, of subtropical and tropical montane rainforests with tall canopies (Wilf 2012).

Fossil angiosperms in one or both floras include the Australian icon, *Eucalyptus* (**Figure 8**), probable Paleogene fossils in Australia, extant nearly entirely in Australia (Gandolfo et al. 2011, Hermsen et al. 2012); *Akania*, extant in eastern Australia (Romero & Hickey 1976, Gandolfo et al. 1988); *Gymnostoma*, Paleogene fossils in Australia, extant in Australasia and to the north (Zamaloa et al. 2006); and diverse Proteaceae including *Orites*, Paleogene fossils in Australia, extant in temperate Australia and southern South America (González et al. 2007). Another outstanding occurrence involves the only known fossil flowers of Asteraceae (the sunflower family), with ~24,000 species today; *Raiguenrayun cura* represents a basal, probably bird-pollinated lineage with affinities to a set of African and South American clades of the family (Barreda et al. 2010, 2012b).

Río Pichileufú is the last macrofloral record of the hyperdiverse, volcanic rainforest province with numerous, extant Australasian genera. However, pollen data (Barreda 1996, Palazzesi & Barreda 2012) show abundant Podocarpaceae and other austral rainforest elements in Patagonia until the Miocene, when the current pulse of Andean orogeny, and its rain shadow, began. This evidence shows that widespread rainforest persisted under cooling temperatures, becoming species poor and eventually geographically restricted to the present-day, cold-temperate humid biome on the west slope of the Southern Andes. Although a large number of macrofloras are known from the later Eocene and Oligocene of Patagonia (Romero 1986), few well-identified taxa hold sufficient biogeographic interest for this discussion. From the middle Eocene to the present, *Nothofagus* leaves and pollen are abundant, and *Araucaria* stays prominently in the record as well (Romero 1986, Panti 2011, Panti et al. 2011).

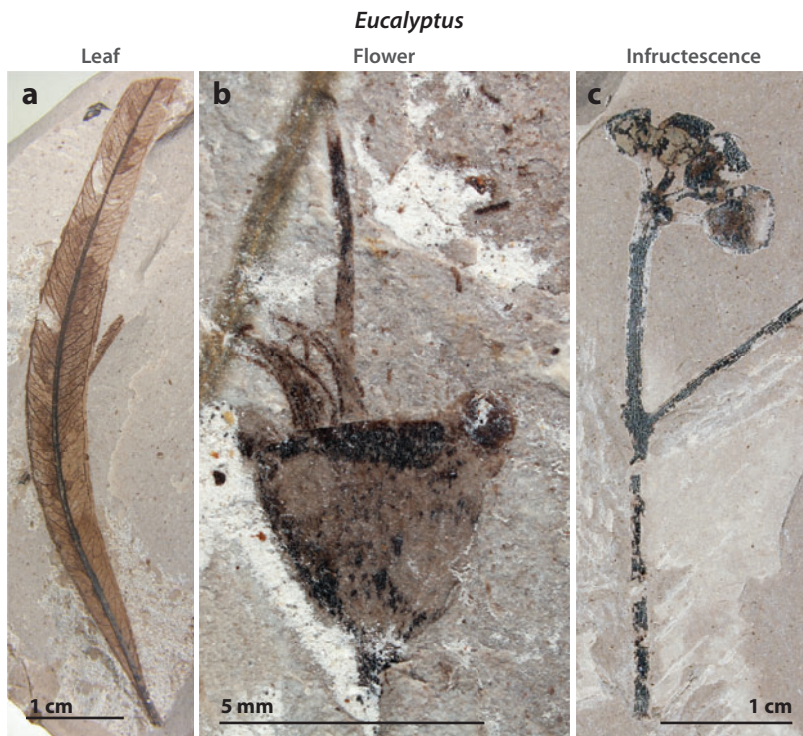


Figure 8

Eucalyptus (gum tree) fossils from Laguna del Hunco, early Eocene, ~52 Ma: (a) leaf, (b) flower, (c) infructescence. *Eucalyptus* is the iconic Australian tree genus; it has more than 600 species, nearly all of which are confined to Australia. These fossils exemplify the trans-Antarctic connection from South America to Australia during the globally warm early Eocene. Panels a and b reprinted from Gandolfo et al. (2011). Images courtesy E. Hermsen and M. Gandolfo.

5.2. Paleogene Faunas

The Paleogene faunal sequence of Patagonia was traditionally based on the Sarmiento Formation at Gran Barranca and correlative strata, although there were some reports from older units as well. Major developments in Patagonia since Simpson's time include discoveries of early Paleocene mammals; expanded and novel collections from other older strata, especially the Río Chico Group, the Las Flores Formation, and the Paso del Sapo exposures; and several decades of new geological and paleontological data from the Sarmiento Formation itself. In addition, a large suite of discoveries from the Antarctic Peninsula and from elsewhere in South America has greatly enriched understanding of faunal interchange.

5.2.1. Below Gran Barranca. The introduction of therian mammals during the Late Cretaceous or earliest Paleocene brought into South America the antecedents of the faunas that formed the basis for Splendid Isolation (Simpson 1980). The marsupial *Cocatherium* is the oldest therian, recovered from earliest Paleocene strata of the Lefipán Formation (Goin et al. 2006). This was a derived (polydolopimorphian) marsupial that had affinities to Late Cretaceous relatives in North America (Case et al. 2005). *Cocatherium* also appears to belong to a clade (australidelphians) that includes living and fossil South American mammals, the microbiotheres, that are considered to

be related to Australian marsupials (Goin et al. 2006, Nilsson et al. 2010). Whereas *Cocatherium* is not thought to be closely related to any living or fossil Australian marsupial, the presence of australidelphians in earliest Paleocene South America is compatible with general proposals that Australian marsupials might have been derived from South American relatives at approximately this time (Woodburne & Case 1996).

In the early Paleocene Tiupampan fauna of Bolivia, 9 of the 17 genera are marsupials, showing the robust diversity of South America's early marsupial fauna. Belonging to a group known as didelphimorphians (Gelfo et al. 2009), these genera had affinities with precursors in North America, and their endemic diversity supports an argument in favor of their yet-unknown ancestors having entered South America during the Late Cretaceous (see, e.g., Pascual & Ortiz-Jaureguizar 1990, Woodburne & Case 1996, Case et al. 2005). Also at Tiupampa, the seven new placental mammals included an endemic radiation of five new mioclaenid condylarths, which are relatively small-sized herbivores-omnivores of early Paleocene, North American ancestry (de Muizon & Cifelli 2000). The lone pantodont also was of Northern Hemisphere derivation (de Muizon & Marshall 1992). The remaining (henricosborniid) notoungulate was an early representative of the typically South American groups that dominated later Paleogene faunas.

Returning to the Patagonian sequence, the next-youngest Paleocene fauna of South America comes from Punta Peligro in the San Jorge Basin (Bonaparte et al. 1993, Gelfo et al. 2009). In contrast to the Tiupampan, the Peligran fauna retained a minor diversity of nontherian mammals considered to be survivors from the Cretaceous, such as the dryolestoid *Peligrotherium*, the hypsodont gondwanather *Sudamerica*, and the monotreme *Monotrematum* (Pascual et al. 1992a,b; Gelfo & Pascual 2001; Woodburne et al. 2013). Whereas the first two were locally derived, the monotreme reflects an early Paleocene dispersal from Antarctica, where the group is still unknown, and Australia. The six therians comprise three marsupials and three placentals (Gelfo et al. 2009). Of the marsupials, the two ameridelphians extended into later faunas and were the first therian mammal group to do so (the gondwanatheres are found later as well; see Section 4.2.6 and below). The placentals show an increased diversity in some of the ungulate-like groups that also continued later—including *Requisia*, the oldest known litoptern (Bonaparte & Morales 1997)—but none of the Peligran genera is found in younger deposits.

The next Paleocene fauna, known from the Peñas Coloradas Formation, is referred to as “Carodnian” after the basal placental xenungulate *Carodnia* that, with *Notoetaoia*, is the only occurrence of that group in South America (Simpson 1935b, Gelfo et al. 2008). Another placental, *Wainka*, was another new litoptern. A genus of the rodent-like polydolopid marsupials, *Amphidolops*, also is found in later faunas, and so the classic coherence between South American mammal faunas was increasingly being shown through the Paleocene. The Carodnian faunas are the oldest from Patagonia that were known to Simpson (1935a,b).

Land mammal faunas in South America reach their greatest early Paleogene diversity at sites often inferred to be early Eocene in Patagonia (Las Flores Formation) and Brazil (Itaboraí; Gelfo et al. 2009, Woodburne et al. 2013). Among the collective 35 genera in Brazil, the still-diverse 17 marsupials filled insectivore-carnivore niches (ameridelphians, sparassodontans), whereas others were more omnivorous-herbivorous (caroloameghiniids, microbiotheres), and the rodent-like polydolopimorphians were also present. Work on the Las Flores fauna is still preliminary, but current results suggest that the Brazilian diversity may also be found in Patagonia (Oliveira & Goin 2011). This ecological diversity continued into later faunas. Although South America's first edentate is recorded from Brazil (Bergqvist et al. 2004), the group is still absent from the Las Flores fauna and thus constitutes one example of biofacies or compositional differences from north to south. Another is the absence of Las Flores polydolopine marsupials in the north (Chornogubsky 2010).

The faunas from near Paso del Sapo in Chubut (~49–47 Ma), which are temporally and geographically close to the Laguna del Hunco and Río Pichileufú rainforest floras, show 16 marsupial genera and a comparable number of placental mammals, as well as one of the last gondwanatheres from South America (Tejedor et al. 2009, Goin et al. 2012b). The placentals show a new diversity in xenarthrans and notoungulates. The Paso del Sapo fauna also has affinity with the middle Eocene La Meseta fauna of the Antarctic Peninsula, including derorhynchid marsupials and litoptern placentals (Goin et al. 1999, 2012b; Reguero & Marenssi 2010; Reguero et al. 2013).

As summarized by Reguero & Marenssi (2010), the La Meseta fauna was dominated by marsupials and litopterns, in contrast to the typical South American Eocene faunas, which were dominated by notoungulates and basal condylarths. The La Meseta contains what may (Vizcaíno & Scillato-Yané 1995) or may not (MacPhee & Reguero 2010) be the oldest pilosan edentate in Gondwana, and it also records an Eocene gondwanathere generally similar to that from the Paso del Sapo fauna (Reguero et al. 2013). The endemism shown by some of the marsupials and litopterns suggests prior isolation; for example, the litoptern *Notiofolos* is known from deposits dating to 51.5 Ma, whereas the rest of the La Meseta fauna dates to 49–47 Ma. Reguero et al. (2013) summarized the phyletic implications of the gondwanathere, the eight marsupials, the litoptern, and the two astrapotheres of the La Meseta fauna and concluded that their presence can be best accounted for via numerous dispersals from South America during an interval that ranged from approximately Late Cretaceous to late Paleocene. We note that this scenario is compatible with an early Paleocene dispersal of monotremes to Patagonia.

5.2.2. Australian mammal connection? The mid-Paleocene monotreme dispersal from Antarctica may have had an ultimate Australian source, and molecular studies of living taxa strongly support a South American origin for Australian marsupials (Nilsson et al. 2010). Nevertheless, there remains no demonstrated close relationship between any Cretaceous or Paleogene mammals in South America and Australia. In contrast to the hypothesis presented by Sigé et al. (2009), the proposed ~55-Ma dispersal between the fauna of Chulpas, Peru, and Australia's Tingamarra fauna is not accepted here. In addition to the uncertain dating at Tingamarra (Woodburne & Case 1996), we consider the dental remains on which the two alleged species of *Chulpasia* are based to be too few in number (basically two molariform teeth for each of the two compared species) to provide conclusive synapomorphies. Whereas further study may validate the two species and support the proposal that they represent a trans-Antarctic dispersal between South America and Australia, this conclusion appears premature at present. Also, Beck et al. (2008) proposed a plesiomorphic position for the Tingamarra marsupial *Djartbia*, but this does not demonstrate an explicit link to South America. Furthermore, the Tingamarra fauna constitutes the only pre-late Oligocene record of mammals in Australia, and, although extremely important, it should be evaluated in that context. Over time, additional perspective on Paleogene mammal diversity and phyletic relations in Australia will undoubtedly emerge.

5.2.3. The Gran Barranca sequence. The Casamayoran mammal zone, the first of the classic Gran Barranca sequence, was traditionally considered to be of early Eocene age, but Kay et al. (1999) showed that it was partly late Eocene. Cifelli (1985) distinguished the Vacan and Barrancan as subages of the Casamayoran; the Vacan (not exposed on Gran Barranca itself) is older, ~45 Ma (Carlini et al. 2010), and the Barrancan is now constrained to ages ranging from 41.7 to 39.0 Ma (Dunn et al. 2013). The Vacan rodent-like polydolopids were still diverse (there were 3), and the strong placental diversity of 4 edentates, 2 litopterns, and 19 notoungulates supports the interpretation of a diverse set of cursorial herbivore niches (Gelfo et al. 2009). One of the oldest hypsodont notoungulates, *Acropithecus*, is thought to indicate the presence of, at least locally, more

open conditions that fostered a more abrasive diet for these animals (Reguero et al. 2010). Pascual & Ortiz-Jaureguizar (1990) recorded that 13% of the mammals from the Casamayoran as a whole were hypsodont and that an additional 13% were hypselodont (tall-crowned and ever-growing), and they considered these data as further indication of climatic cooling, spread of grasslands, and more open conditions. However, recent palynological data from Patagonia show that reduction of key rainforest trees (podocarps and *Nothofagus*) and dominance of the major steppe components (asters, amaranths, and *Ephedra*) did not occur until ~10 Ma and that grasses did not dominate until the Pleistocene; accordingly, humid environments persisted, and open, dry-adapted vegetation developed considerably later than did Paleogene hypsodonty, even though temperatures were cooling and thermophilic plant and animal lineages were disappearing (Barreda & Palazzesi 2010, Palazzesi & Barreda 2012).

The Barrancan interval clearly shows a turnover that heralded a major faunal change during the late Eocene to early Oligocene. Additional genera included a strong representation of carnivorous marsupials (five sparassodontans) as well as polydolopimorphs (six). Among placentals, edentates were diminished, but astropotheres maintained their presence prior to their subsequent diversification. Many elements of the previously more tropical habitats were declining or became extinct, including the ancient condylarths and a large number of notoungulates. The Splendid Isolation that was largely maintained since the Paleocene among the mammal faunas was breached, at continental scale, by the introduction of four genera of cavioid rodents into Peru ~41 Ma, apparently from Africa via an ancient rafting event (Antoine et al. 2012). Returning to our discussion of Gran Barranca, the last Eocene mammal unit (Mustersan, ~38 Ma) continues the changes seen in the Barrancan. There was a diminution of rodent-like and didelphid-like marsupials; edentates were more diverse; and camel-like and horse-like (macraucheniid and proterotheriid) litopterns were new, as were the granivorous (rosendolopid) marsupials and hypercarnivorous sparassodontans.

South American earliest Oligocene faunas were first recognized in Chile and are known as Tinguirirican (Wyss et al. 1990; Flynn et al. 2002, 2003, 2012), constrained to 33.6–31.3 Ma by Dunn et al. (2013). An early Tinguirirican fauna known as La Cancha occurs on Gran Barranca (Goin et al. 2010). The relatively cool climates of this time were reflected in some significant faunal changes, including the evolution of the first hypsodont (argyrolagoid) marsupials and the first glyptodont (armored) edentate (Shockey & Anaya 2011). A major radiation of 17 hypsodont notoungulates accounts for 71% of Tinguirirican land mammal species and records a remarkable example of convergence in this feature across several clades (Croft et al. 2008). Goin et al. (2010) noted the significant faunal turnover in marsupials exhibited by the La Cancha fauna, along with their adaptations to major open-area landscapes following cooling temperatures (but see Palazzesi & Barreda 2012). Although it has the last of the more basal (caroloameghiniid) didelphimorphians, this fauna shows a diversification of rodent-like polydolopimorphians, and *Kramadolops* is the largest of these ever known.

Deseadan (29.4–24.2 Ma; Dunn et al. 2013) faunas represent the last South American faunas of the Paleogene (Pascual & Ortiz-Jaureguizar 2007), by which time climates had rebounded somewhat from the earliest Oligocene cooling. “Archaic” elements of the South American fauna became extinct during the Deseadan, whereas more “modern” groups, including large notoungulates and other mammals with hypsodont dentitions, continued their expansion (Pascual & Ortiz-Jaureguizar 1990, Flynn et al. 2012). The interruption of Splendid Isolation traditionally began with the introduction of primates and rodents at this time (Simpson 1980). Rodents are now recorded earlier, from the Barrancan of Peru as discussed above, but the monkey *Branisella boliviana* (Bolivia) remains the oldest primate in South America, probably terrestrial to scansorial in habit (Hoffstetter 1969, Kay et al. 2002).

5.2.4. Summary. The Paleogene land mammal fauna of South America began with the introduction of therian mammals from North America during the Late Cretaceous or earliest Paleocene, coupled with the survival of certain endemic lineages from the Cretaceous. This was followed by a later Paleocene interval of endemic faunal diversification and brief monotreme input from Antarctica, which did not modify the basic Splendid Isolation of the faunas. Diversification continued into the warm Eocene. Hypsodonty was well under way by at least 45 Ma, approximately coeval with the introduction of rodents from Africa that brought the initial end of Splendid Isolation. Thereafter, climates continued to cool toward the early Oligocene Antarctic glaciations, and the mammal fauna responded with increased “modernization” of its components, extinction of “archaic” forms, and increased ecological diversity. Although there is demonstrated interchange with the Antarctic Peninsula until perhaps the late Paleocene, there remains no convincing fossil evidence—other than *Monotrematum*—of mammalian exchange between South America and Australia at any time during the Cenozoic.

6. DISCUSSION

Several compelling patterns emerge from this review that we highlight for future study. First and foremost is the continuing acceleration of discovery and its impact on paleobiogeographic knowledge. Jurassic abelisauroids, Cretaceous tuataras, and Eocene gum trees are only a few of the transformative finds of just the past few years. Nevertheless, it is clear that the fossil riches of Patagonia are only beginning to be tapped, and large gaps in time and sampling remain. The explicit comparison of plant, reptile, and mammal records attempted here, set against an updated paleogeographic framework, shows some of the consistencies and discrepancies that should be productive for future research.

The prebreakup Gondwanan signal in some Jurassic vertebrates with Cretaceous descendants (*Eoabelisaurus*, *Brachytrachelopan*, and Henosferidae) shows that the biogeography of certain lineages was a legacy of their Pangean distributions, which may have been originally southern owing to marked wet-dry biome distributions on the supercontinent or other physical limitations. Although this idea makes much common sense, the fossil vertebrate evidence to support it was thin until recently. The Jurassic plant record so far presents a marked contrast, wherein all major groups are Pangean in distribution but with closest affinity to pre-Antarctica.

The Cretaceous vertebrate and plant records both show abundant, true Gondwanan signals and provide an extremely rich system for examining vicariance among South America, Africa, and India-Madagascar as well as for studying continuing interchange with Antarctica, Australia, and elsewhere. In addition, a set of originally Pangean groups radiated in Gondwana following the Jurassic-Cretaceous break with North America; this group includes cypresses, sphenodontids, dryolestoids, and gondwanatheres (if derived from multituberculates). North America also had episodic influence during the Campanian-Maastrichtian interval, exemplified by hadrosaurs and therian mammals (not seen in Patagonia until earliest Paleocene).

The K-Pg extinction deserves continuing investigation as a biogeographic filter on a hemispheric scale (Wolfe 1987), and Patagonia has great potential to provide important data (Case & Woodburne 1986, Pascual 1998, Iglesias et al. 2007a). The K-Pg interval so far shows very different dynamics for both plants and animals in Patagonia (and perhaps all of Gondwana) compared with areas much closer to the Chicxulub impact site in Mexico, including the heavily studied Western Interior of the United States. Madtsoids, notosuchids, chelid turtles, dryolestoids, gondwanatheres, monotremes (possibly as Paleocene immigrants), and ceratodontid lungfish (Cione et al. 2011) are outstanding examples of Mesozoic vertebrate lineages that “refused to die.” For plants, numerous gymnosperm groups that were previously considered to be globally restricted

to the Mesozoic now have Cenozoic fossil records in Gondwana (e.g., McLoughlin et al. 2011), and in Patagonia these records include abundant Paleocene Cheirolepidiaceae (*Classopollis* pollen) and archaic Eocene ginkgophytes (Archangelsky 1976, Cúneo et al. 2010b, Barreda et al. 2012a). *Araucaria*, extinct after the Maastrichtian in the Northern Hemisphere, is a living example of the same historical pattern. Palynological data show a relatively muted K-Pg extinction and rapid recovery (Barreda et al. 2012a) that is consistent with data from New Zealand (Vajda et al. 2001) and with hemispheric-scale patterns in calcareous nannoplankton (Jiang et al. 2010). Furthermore, the early Paleocene Salamanca Formation macrofloras are much more diverse than comparable North American samples (Iglesias et al. 2007a). However, many groups clearly did not survive; these include nonavian dinosaurs and marine reptiles, which have been found in Patagonia less than 2 m below the K-Pg boundary (Gasparini et al. 2003, Fernández et al. 2008).

During the Paleocene and especially the early and middle Eocene, there is an apparently striking contrast between the robust southern connection for the floras (particularly with respect to Paleogene Australia and modern Australasia) and the lack of such a connection for the mammals, much as in Simpson's time. However, any comparisons remain fundamentally limited by the extremely scarce Australian record of Paleogene mammals, versus the extensive paleobotanical record there. The Paso del Sapo fauna, from the early-middle Eocene interval of trans-Antarctic rainforest floras, does show abundant connections to the Antarctic Peninsula, including its derorhynchid marsupials (Tejedor et al. 2009, Goin et al. 2012b) and liptopterns (Reguero et al. 2013). However, we stress that affinities between these and other Patagonian and Antarctic faunas are considered to reflect Late Cretaceous to late Paleocene dispersals (Reguero et al. 2013). We briefly mention additional fossil vertebrates from Patagonia that show strong Australian connections, including Eocene ceratodontid lungfish (Cione et al. 2011); Campanian-Eocene helmeted (australobatrachid) frogs (Gómez et al. 2011); madtsoid snakes (see Section 4.2.2); and Cretaceous and Paleogene chelid turtles (De Broin & de la Fuente 1993, Gasparini et al. 2001, de la Fuente et al. 2011). All this evidence makes Paleogene mammalian exchange with Australia seem very likely but does not prove that it occurred. Thus, Gaudry's concept (see epigraph) of a fully trans-Antarctic mammalian fauna is not yet demonstrated, but there is abundant evidence for trans-Antarctic history in other organismal groups.

7. SPLENDID ISOLATION REVISITED

Simpson's (1978, 1980) classic faunal series of Splendid Isolation is a late chapter of a considerably longer mammalian history in South America (Goin et al. 2012a). Bonaparte and Pascual, in particular, each presented a series of syntheses in light of subsequent discoveries, especially Mesozoic, early Paleocene, and Antarctic faunas, all of which were unknown or poorly defined in Simpson's time (Bonaparte 1986a, 1996; Pascual & Ortiz-Jaureguizar 1992, 2007; Pascual 1996, 1998, 2006). One of the most salient observations from both authors was that South America participated in a much longer period of Gondwanan isolation (i.e., from Laurasia) during the Cretaceous, which Pascual later termed the Gondwanan Episode (see Section 4.2.6). Furthermore, this interval featured endemic radiations from ancient stocks (Bonaparte 1986a) that originated from what Pascual referred to as the Pangeic Stage. By the early Paleocene, as seen concretely in the Peligran fauna, the relict survivors of the Gondwanan Episode were being replaced by the rians that immigrated episodically from North America, probably just prior to the K-Pg boundary. Pascual termed the evolutionary radiation derived from these immigrants the South American Episode. As South America separated from Antarctica during the Eocene, and as climates cooled, Patagonian mammals became more distinct, endemic, and "isolated" than ever in their history.

Bonaparte's and Pascual's accounts are generally consistent with the Mesozoic reptile, mammal, and plant record from Patagonia reviewed here. In all three groups, we see evidence for a Pangeic Stage dominated by widespread lineages (in the Jurassic) and a Gondwanan Episode featuring evolution of vicariant stocks on the separated and fragmenting supercontinent (in the Cretaceous). As a broad refinement, we note the prebreakup Gondwanan Jurassic faunas, whose distributions were probably climatically determined. The South American Episode seems applicable only to mammals, as it was defined, wherein a single immigrant group (therians) became diverse and dominant. Reptile immigrants (hadrosaurs) that potentially could have become dominant went extinct early, and there is certainly no clear analog for the highly diverse plants.

Regarding this review's title, we suggest that the colorful, widely used, and historically rich terms "island continent" and "isolation" are not well suited to an enormous landmass such as South America, which dwarfs any island and was seldom truly isolated, much less to the Gondwanan supercontinent. South America is, and always has been, too large of a target for dispersing organisms to be realistically considered "isolated." The arrivals of rodents and primates during "isolation" are the most famous examples supported by fossils. However, molecular data indicate an important historical role for transoceanic dispersal into and out of southern South America for many plant and animal groups (Sanmartín & Ronquist 2004), and biome matching appears to be the strongest filter, at least for plants (Crisp et al. 2009). Likewise, as more data come from outside Patagonia, both intercontinental and intracontinental biogeographic patterns will become better understood in the context of physiographic and climatic barriers within South America (see, e.g., Volkheimer 1980, Wilson & Arens 2001, Ziegler et al. 2003, Ortiz-Jaureguizar & Cladera 2006, Pascual 2006).

Simpson's Splendid Isolation sequence began approximately 115 million years after the Cañadón Asfalto mammals lived, and it encompassed an interval of Antarctic, and at least some Australian, mammalian interchange, as broadly deduced much earlier by Gaudry (see epigraph). Only after the Antarctic connection was progressively weakened and severed through the Eocene came the interval of true oceanic separation and corresponding mammalian endemism that most closely corresponds to the ideas of Splendid Isolation and a South American "island continent." Of course, the continuing evolution of the scientific context of the iconic fossil mammals of Patagonia in no way diminishes their enduring importance or their splendor. Fantastic, "peculiar" animals such as *Notostylops*, *Pyrotherium*, *Macrauchenia*, and *Megatherium* will continue to inspire for generations to come, as will the equally splendid new mammals, dinosaurs, plants, and much else now being hewn from the rocks, as Patagonia's golden age of fossil discovery continues.

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Contents

On Escalation <i>Geerat J. Vermeij</i>	1
The Meaning of Stromatolites <i>Tanja Bosak, Andrew H. Knoll, and Alexander P. Petroff</i>	21
The Anthropocene <i>William F. Ruddiman</i>	45
Global Cooling by Grassland Soils of the Geological Past and Near Future <i>Gregory J. Retallack</i>	69
Psychrophiles <i>Khawar S. Siddiqui, Timothy J. Williams, David Wilkins, Sheree Yau, Michelle A. Allen, Mark V. Brown, Federico M. Lauro, and Ricardo Cavicchioli</i>	87
Initiation and Evolution of Plate Tectonics on Earth: Theories and Observations <i>Jun Korenaga</i>	117
Experimental Dynamos and the Dynamics of Planetary Cores <i>Peter Olson</i>	153
Extracting Earth's Elastic Wave Response from Noise Measurements <i>Roel Snieder and Eric Larose</i>	183
Miller-Urey and Beyond: What Have We Learned About Prebiotic Organic Synthesis Reactions in the Past 60 Years? <i>Thomas M. McCollom</i>	207
The Science of Geoengineering <i>Ken Caldeira, Govindasamy Bala, and Long Cao</i>	231
Shock Events in the Solar System: The Message from Minerals in Terrestrial Planets and Asteroids <i>Philippe Gillet and Ahmed El Goresy</i>	257
The Fossil Record of Plant-Insect Dynamics <i>Conrad C. Labandeira and Ellen D. Currano</i>	287

The Betic-Rif Arc and Its Orogenic Hinterland: A Review <i>John P. Platt, Whitney M. Bebr, Katherine Jobanesen, and Jason R. Williams</i>	313
Assessing the Use of Archaeal Lipids as Marine Environmental Proxies <i>Ann Pearson and Anitra E. Ingalls</i>	359
Heat Flow, Heat Generation, and the Thermal State of the Lithosphere <i>Kevin P. Furlong and David S. Chapman</i>	385
The Isotopic Anatomies of Molecules and Minerals <i>John M. Eiler</i>	411
The Behavior of the Lithosphere on Seismic to Geologic Timescales <i>A.B. Watts, S.J. Zhong, and J. Hunter</i>	443
The Formation and Dynamics of Super-Earth Planets <i>Nader Haghighipour</i>	469
Kimberlite Volcanism <i>R.S.J. Sparks</i>	497
Differentiated Planetesimals and the Parent Bodies of Chondrites <i>Benjamin P. Weiss and Linda T. Elkins-Tanton</i>	529
Splendid and Seldom Isolated: The Paleobiogeography of Patagonia <i>Peter Wilf, N. Rubén Cúneo, Ignacio H. Escapa, Diego Pol, and Michael O. Woodburne</i>	561
Electrical Conductivity of Mantle Minerals: Role of Water in Conductivity Anomalies <i>Takashi Yoshino and Tomoo Katsura</i>	605
The Late Paleozoic Ice Age: An Evolving Paradigm <i>Isabel P. Montañez and Christopher J. Poulsen</i>	629
Composition and State of the Core <i>Kei Hirose, Stéphane Labrosse, and John Hernlund</i>	657
Enceladus: An Active Ice World in the Saturn System <i>John R. Spencer and Francis Nimmo</i>	693
Earth's Background Free Oscillations <i>Kiwamu Nishida</i>	719
Global Warming and Neotropical Rainforests: A Historical Perspective <i>Carlos Jaramillo and Andrés Cárdenas</i>	741
The Scotia Arc: Genesis, Evolution, Global Significance <i>Ian W.D. Dalziel, Lawrence A. Lawver, Ian O. Norton, and Lisa M. Gabagan</i>	767