29 Gran Barranca: a 23-million-year record of middle Cenozoic faunal evolution in Patagonia

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Abstract

Explosive Plinian volcanism provided a rich local source of fine-grained volcaniclastic sediments to central Patagonia in the middle Cenozoic. The chronology of the accumulation extends from the Middle Eocene Climate Optimum (MECO) to the Middle Miocene Climate Optimum (MMCO) and includes the only southern hemisphere continental record across the Eocene–Oligocene transition (EOT) and into the Oi-1 glaciation of Antarctica. The continuity of sedimentation is broken by hiatuses of different temporal magnitude that appear to correspond chronologically with changing sea level and the intensity of erosion. The Sarmiento Formation at Gran Barranca is subdivided into six members, Gran Barranca (41.6–38.7 Ma), Rosado (38.7 Ma), Lower Puesto Almendra (37 Ma), Vera (35–33.3 Ma), Upper Puesto Almendra (31.1–26.3 Ma), and Colhue-Huapi (20.4–18.7 Ma).

The sequence of fossil mammal faunas in the Sarmiento Formation at Gran Barranca is the standard sequence of South American Land Mammal Ages (SALMAs) and their subdivisions. The sequence includes the Barrancan SALM Subage, an intermediate level "El Nuevo," the Mustersan SALMA, the Tinguirirican SALMA, an early Deseadan level "La Cantera," the Deseadan SALMA, Colhuehuapian SALMA, and a Pinturan level. The taxonomic composition and most distinctive features of each of these levels at Gran Barranca is summarized, with special attention to the new and rich record of small mammals recovered by intensive wet washing.

Given the climate intimacy between narrow peninsular Patagonia, the southeast Pacific and South Atlantic oceans, and the vast Southern Ocean today, the terrestrial environments of middle Cenozoic Patagonia were probably subject to the influence of global climate change as recorded in the marine sea-floor record. Evidence that the terrestrial biota responded to the trends and events recorded in marine sediments of the southern oceans depends on an understanding of how the magnitude and rate of this climate change drives evolutionary and biotic change, and whether it leaves an imprint on terrestrial sediments and their fossil archives. We summarize the fossil mammal record at Gran Barranca in light of the chronology of climate change, but are cautious in our conclusions as appropriate to the limitations imposed by deep time.

During the MECO, phytolith assemblages include graminoid elements (pooids and chloridoids) as components of savanna and/or forest communities. Climate change subsequent to the MECO is recorded at Gran Barranca by the last occurrence of crocodilians and an episode of coincident increase in hypsodonty in several clades of mammalian herbivores. Important change in paleosols, depositional environments, and ichnofacies suggest a general aridification and cooling at the close of the Barrancan and into the Mustersan. Volcanic activity intensified at this time. Pooid and chloridoid grasses become dissociated in the presence of indicators of plant stress conditions or aridification, the oldest evidence for the adaptation of chloridoid grasses to dry environments.

The EOT is preserved in the sediments of the Vera Member at Gran Barranca and the mammals of Tinguirirican SALMA. The mammals document an increase in the overall proportion of hypsodont taxa along with the continued persistence of primitive taxa within the same clades, suggesting species richness was responding to a diversification of diets in addition to the rigors of environmental abrasives. It is tempting to attribute this to the massively bedded volcaniclastic loessites, evidence of reworking by more persistent eolian processes that may have accompanied Oi-1 and an intensification of the developing circum-Antarctic flow. The first appearance of rodents in Patagonia at about 30 Ma occurs some 3 m.y. after significant change in the small marsupial fauna at the EOT.

The MMCO coincides with the presence of primates in Patagonia between 20.2 and 15.7 Ma. The mammal fauna of the Colhuehuapian is especially rich in small marsupials and rodents. Most climate indicators accord with the view that Patagonian climates at this time were warm and humid.

The South American mammal fauna evolved in geographic isolation from other continents through most of the middle Cenozoic. This geographic isolation began with the final separation of South America from Antarctica in the late Eocene prior to the opening of Drake Passage to deep-water circulation. Within Patagonia, a reduction of

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geographic area and possibly subdivision by marine barriers, may have accompanied middle Cenozoic marine transgressions, especially prior to the EOT. The arrival of primates and rodents from Africa and their radiations must represent significant perturbations to continental isolation, but their impact has yet to be fully assessed.

The evolution of high-crowned teeth was a major feature of mammal evolution in South America throughout the Cenozoic, as a general faunal trend of increasing proportions of taxa with high-crowned teeth, as successive independent radiations of high-crowned taxa within clades, and as events of coincident increase involving diverse clades. The environmental context of these trends and events are explored.

Resumen

Un vulcanismo explosivo Pliniano fue la fuente de los finos sedimentos volcaniclásticos en la Patagonia central durante el Cenozoico medio. Cronológicamente, la acumulación de sedimentos se extiende desde el Óptimo Climático del Eoceno Medio (OCEM), hasta el Optimo Climático del Mioceno Medio (OCMM), e incluye el único registro continental del hemisferio austral de la Transición Eoceno-Oligoceno (TEO), y el inicio de glaciación antártica (Oi-1). La continuidad de la sedimentación se interrumpe por hiatos de diferente magnitud temporal, que parecen corresponder cronológicamente con cambios en el nivel de mar y en la intensidad de la erosión. La Formación Sarmiento se divide en seis miembros: Gran Barranca (41.6–38.7 Ma), Rosado (38.7 Ma), Puesto Almendra Inferior (37 Ma), Vera (35–33.3 Ma), Puesto Almendra Superior (31.1–26.3 Ma), y Colhue-Huapi (20.4–18.7 Ma).

La sucesión de faunas de mamíferos fósiles en Gran Barranca es la secuencia estandar de Edades Mamífero Sudamericanas y sus subdivisiones. La secuencia incluye: la Subedad Barranquense, un nivel intermedio "El Nuevo", la Mustersense, la Tinguiririquense, un nivel temprano del Deseadense "La Cantera", la Deseadense, la Colhuehuapense, y un nivel "Pinturense". Se resume la composición taxonómica y las características más sobresalientes de cada uno de estos niveles en Gran Barranca, con especial atención al novedoso registro de mamíferos pequeños colectados por un intensivo lavado y sarandeo de sedimentos en agua.

Dada la intimidad climática entre la angosta Patagonia peninsular y los mares y océanos australes circundantes, los ambientes terrestres del Cenozoico medio probablemente estuvieron sujetos a la influencia de cambio climático global, tal como es reconocido en los fondos oceánicos. La evidencia de que las biotas respondieron a los cambios y eventos preservados en el registro marino austral, depende de la comprensión de cómo la magnitud y la tasa de ese cambio climático influenció la biota y su evolución, y cuándo deja su impronta sobre los sedimentos y su registro fosilífero. Resumimos e interpretamos el registro fosilífero de Gran Barranca, de acuerdo a la cronología del cambio climático, con precaución dadas las limitaciones impuestas por el largo tiempo transcurrido.

Durante el OCEM, los conjuntos de fitolitos incluyen elementos graminoides (pooides y cloridoides) como componentes de comunidades de sabana y/o bosque. El cambio climático posterior al OCEM está marcado en Gran Barranca por el último registro de caimanes, y un evento coincidente de aumento en la altura de las coronas en varios clados de mamíferos herbívoros. Un importante cambio en los paleosuelos (ambientes de deposición) y en icnofácies, sugieren una aridificación y enfriamiento general al finalizar el Barranquense y en el Mustersense. La actividad volcánica se intensificó en este lapso. Gramíneas pooides y cloridoides se desasocían en la presencia de indicadores de condiciones de mayor estrés o aridificación, la evidencia más antigua de la adaptación de pastos cloridoides a ambientes secos. La TEO está preservada en los sedimentos del Miembro Vera en Gran Barranca y los mamíferos de la edad Tinguiririquense. Los mamíferos documentan un aumento en la proporción total de taxones hipsodontes, junto con la persistencia de taxones primitivos dentro de los mismos clados, sugeriendo que la diversidad de especies respondió a una diversificación de dietas y a una adaptación al estrés de la abrasividad ambiental creciente. Probablemente, se pueda atribuir el desarrollo de la hipsodoncia a la depositación de las loessitas masivas volcaniclásticas, retrabajadas por procesos eólicos más persistentes (que pudieron haber acompañado al Oi-1 y la intensificación de la circulación circum-antártica). El primer registro de roedores en la Patagonia, alrededor de 30 Ma, ocurre tres milliones de años después del cambio significativo en la fauna de marsupiales en la TEO. El OCEM coincide con la presencia de primates en Patagonia entre 20.2 y 15.7 Ma. La fauna de mamíferos del Colhuehuapense es especialmente rica en pequeños marsupiales y roedores. La mayor parte de los indicadores climáticos son acordes con condiciones de climas cálidos y húmedos en la Patagonia.

La fauna mamalífera sudamericana evolucionó en aislamiento geográfico de otros continentes durante la mayor parte del Cenozóico medio. Este aislamiento comenzó con la separación entre América del Sur y la Antártida antes de la apertura de Drake a una circulación de aguas profundas. En la Patagonia, una reducción de superficie y posiblemente una fragmentación por barreras marinas, pudieran haber acompañado a las transgresiones marinas del Cenozoico medio, especialmente antes de la TEO. La llegada de primates y roedores de Africa y su posterior radiación, deben haber perturbado significativamete este aislamiento, pero su impacto es todavía difícil de precisar. La evolución de coronas altas fue una característica principal en la evolución de los mamíferos en América del Sur a lo largo del Cenozoico, como una tendencia de aumentar la proporción de taxones hipsodontes, como una sucesión de radiaciones independientes de taxones dentro de clados, y como eventos de aumento coincidente involucrando a distintos clados. Se discute el contexto ambiental para estas tendencias y eventos.

Introduction

Gran Barranca is a 7-km long and 200-meter high escarpment bordering the southern margin of Lake Colhue-Huapi in Patagonian Argentina at about 45.71° South latitude (Figs. 29.1, 29.2). An outline of the stratigraphy and vertebrate faunal succession at Gran Barranca was first published in the early part of the twentieth century (Ameghino 1906; see Madden and Scarano this book). Since that time, the only English-language monographic study of mammalian faunas from the sequence at Gran Barranca was that of Simpson (1948, 1967) and Cifelli (1985) based on Simpson's field notes (Simpson 1930). As important as Simpson's legacy has proved, his contribution to our knowledge about Gran Barranca was enabled by a single collection made during a brief 1-month field season in 1930, at a time when its relevance to broader questions of biotic evolution and local and global environmental change were obscure.

This volume is the latest contribution to our knowledge of the geology and paleontology of Gran Barranca based on more than 10 years of exploration, fossil collecting, and geological study. The scope of our interest in Gran Barranca has been multifaceted. Gran Barranca exposes the most complete fossiliferous continental rock record of a ~23-million-year interval of the middle Cenozoic in South America and where the superpositional sequence of many South American mammal faunas was established. Because much of the fossil-bearing rock is composed of fine-grained volcanic ash and lava, it is possible to establish a radiometric and paleomagnetic chronology for these faunas. Through study of fossils from known stratigraphic position, we have added several new levels with distinct faunas hitherto either unknown or poorly sampled. By this means we have gained a better appreciation of how mammalian faunas changed through this temporal interval. Through study of the stable element isotope geochemistry of mammalian tooth enamel and records of paleosols, trace fossils, invertebrates, and micro-plant remains, we reconstruct the climatic and biotic conditions within which the mammalian faunas lived and evolved. Finally, as a consequence of the completeness of the rock record, we can see how regional geologic events (Andean tectonism and volcanism, opening of the ocean gateway between South America and Antarctica), and global events (changing sea-surface temperatures and sea level) may have influenced mammalian evolution in this part of the world.

The rock record

Gran Barranca exposes the most complete fossiliferous continental rock record of the middle Cenozoic in South America and the southern hemisphere. The lithology of this middle Cenozoic sequence, called the Sarmiento Formation, and a revision of its stratigraphy and sedimentology is presented by Bellosi (Chapters 2 and 19, this book). A series of magnetic polarity profiles and a number of new radiometric dates allow refinement of the age of the members and units of the formation at Gran Barranca (Ré *et al.* Chapters 3 and 4, this book). The formation was deposited at Gran Barranca between about 41.6 and 18.7 million years ago from the middle through the late Eocene, across the Eocene–Oligocene transition (EOT), and into the early Miocene (Fig. 29.3).

The oldest lithologic division of the Sarmiento Formation is the Gran Barranca Member, which intergrades with the underlying Koluel-Kaike Formation. This member spans between about 41.6 Ma and 38.7 Ma. Overlying the Gran Barranca Member is the Rosado Member, consisting of a mature paleosol radiometrically dated to about 38.7 Ma. Above the Rosado Member is the Lower Puesto Almendra Member which contains a tuff dated at 37.0 Ma. To the west, the Upper Puesto Almendra Member rests directly on the Lower Puesto Almendra Member but to the east the Vera Member is interposed between the two. The Vera Member has an estimated age between 35 and 33.3 Ma. The Upper Puesto Almendra Member is as old as 31.1 Ma and several basalt flows higher up yield a range of dates from 29.2 to 26.3 Ma. Above the Upper Puesto Almendra Member is found the Colhue-Huapi Member, dated between about 20.4 and 18.7 Ma.

The faunal sequence

Since 1906, when the first stratigraphic profile of the Sarmiento Formation was published, the fossil mammal faunas at Gran Barranca have been the standard reference sequence of South American Land Mammal Ages (SALMAs). Here, one can climb through a rock sequence including the Barrancan (late middle Eocene), a transitional level known as "El Nuevo," the Mustersan (late Eocene), Tinguiririan (latest Eocene), an unnamed early Oligocene faunal level ("La Cantera"), the Deseadan (late Oligocene), and two early Miocene faunas, the Colhuehuapian and "Pinturan" SALMAs. Wherever middle Cenozoic fossil mammals are collected in South America or Antarctica, comparisons are necessarily made to the fossil content of the standard sequence in Patagonia which in turn relies on the quality and resolution of the paleontology, stratigraphy, and geochronology at Gran Barranca (Marshall *et al.* 1983; Flynn and Swisher 1995; Arratia 1996).

At the highest possible resolution, new collections of fossil mammals at Gran Barranca come from 49 discrete stratigraphic levels including levels never before sampled. Assemblages of taxa from these stratigraphic levels may eventually allow us to define mammalian biostratigraphic zones and to relate assemblages from elsewhere to these zones as their fossil content and geochronology become better known. Middle Cenozoic SALMAs will eventually

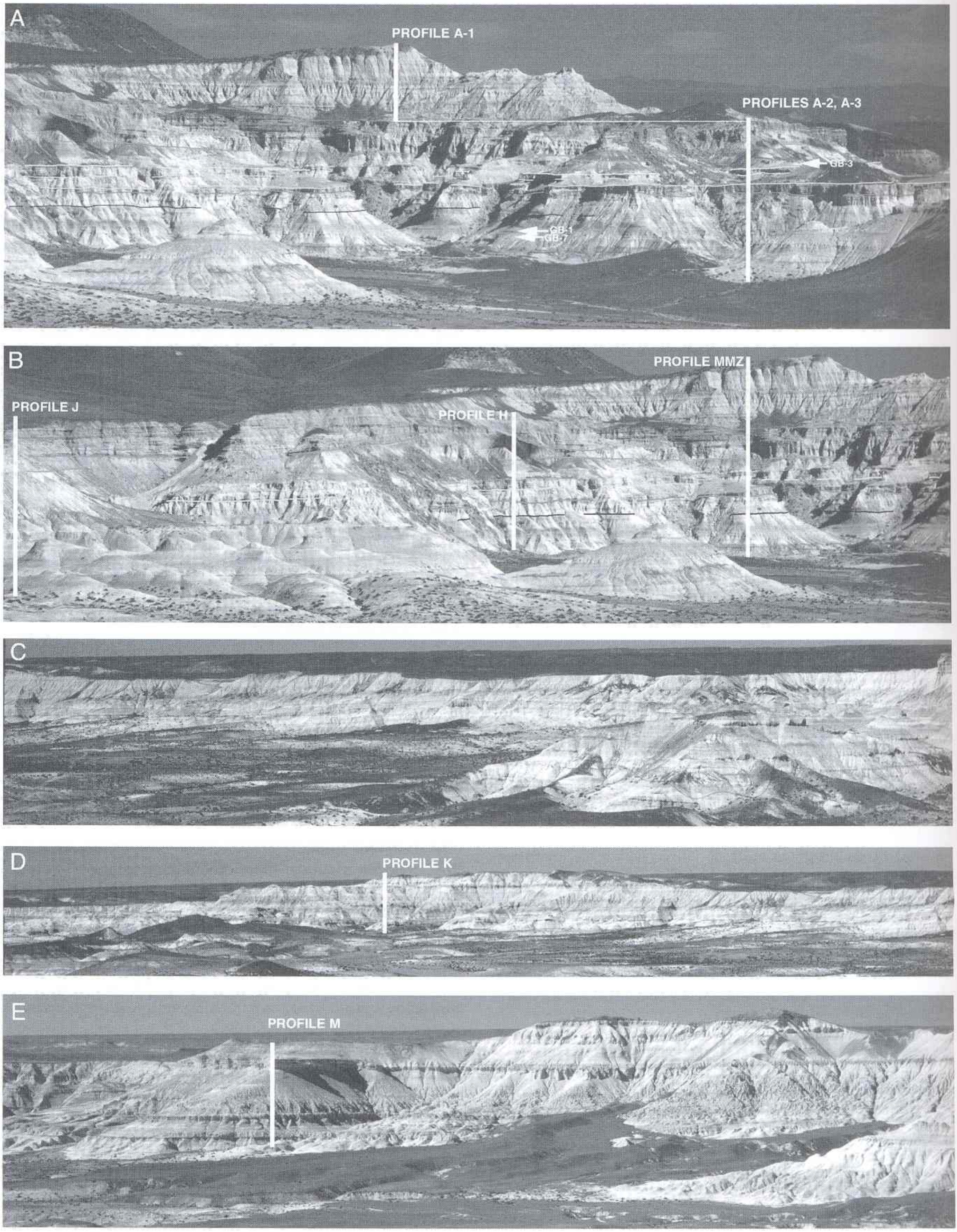

Fig. 29.1. Panorama of Gran Barranca from west (A) to east (E) showing the approximate position of the stratigraphic profiles of the Sarmiento Formation.

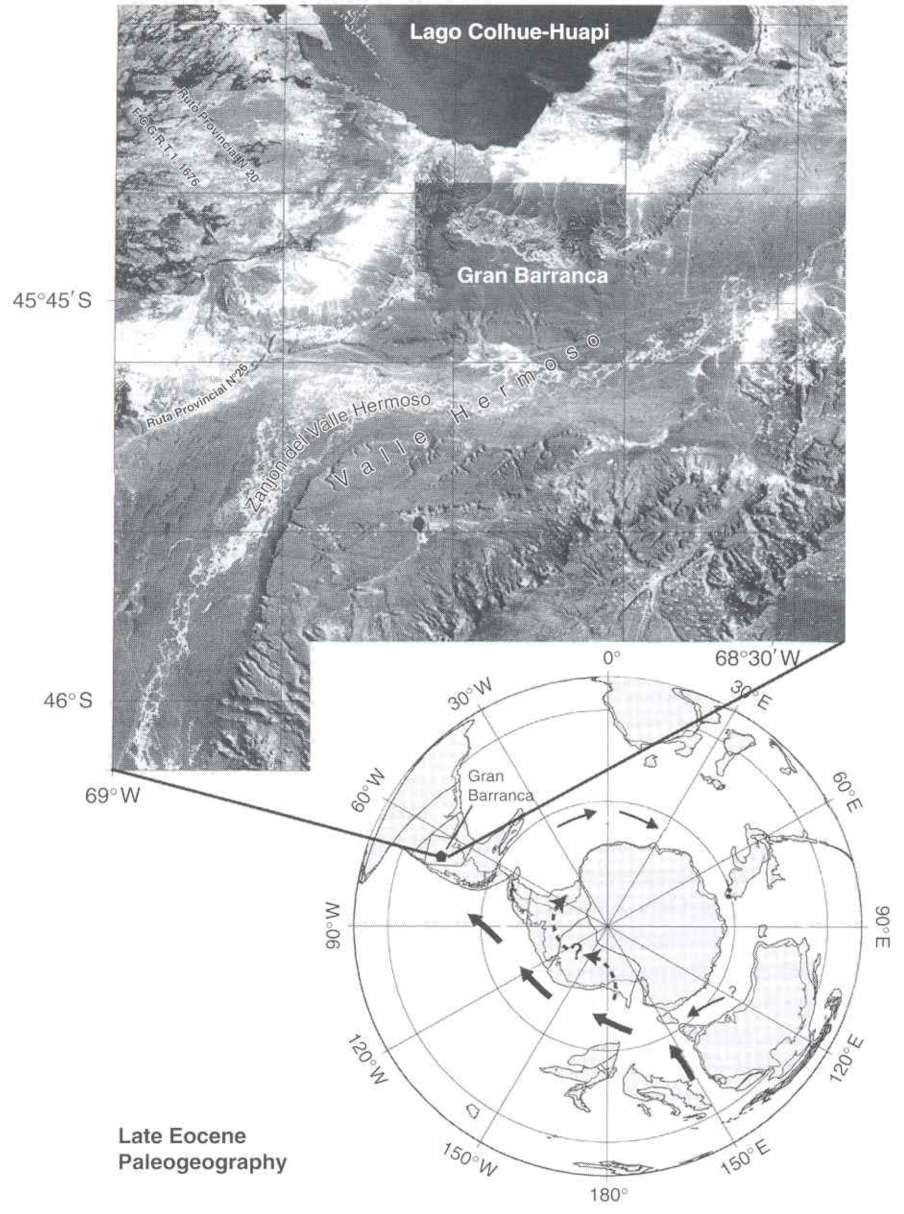

Fig. 29.2. Map of Gran Barranca. Aerial photograph of Gran Barranca superimposed on portion of a satellite map (Instituto Geográfico Militar 1998) and paleogeography of the southern oceans in the late Eocene. (After Bohaty and Zachos 2003; Lawver and Gahagan 2003.)

become substantiated as biochronological units based in large part on the age-calibrated sequence of fossil levels and zones at Gran Barranca. In some instances at Gran Barranca, SALMAs are confined to single lithostratigraphic units (members or their subdivisions) but in other instances a SALMA incorporates all or part of two rock units and in one case a member contains more than one SALMA.

Barrancan

Near the base of the Sarmiento Formation there appear faunas collectively referred to as the Barrancan SALM Subage, a subage of the Casamayoran SALMA. Duke/Museo de La Plata (MLP) Expeditions expended relatively little effort to collect in the 12 Barrancan levels at Gran Barranca. The composition of the Barrancan fauna at Gran Barranca is still best known through papers by Simpson (1948, 1967) and Cifelli (1985). Our understanding of the age of the Barrancan fauna is based on the geochronology at Gran Barranca (Ré *et al.* Chapters 3 and 4, this book). To date, only three localities or exposures of the Sarmiento Formation elsewhere in Patagonia can be correlated with the Gran Barranca Member on the basis of fossil content;

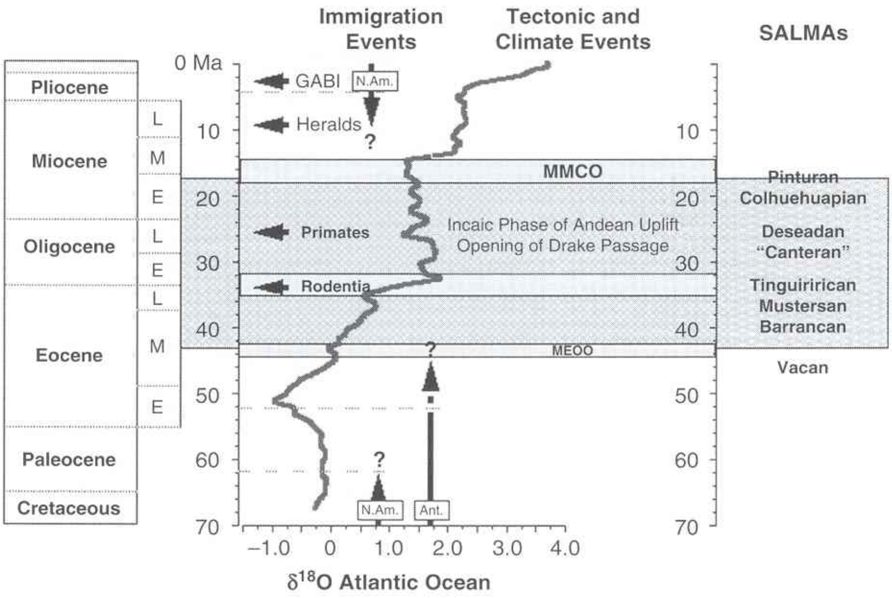

Fig. 29.3. Middle Cenozoic of South America indicating faunal immigration, faunal exchange, tectonic and climatic events, Atlantic Ocean benthic foraminiferal $\delta^{18}O$ curve (from Miller *et al.* 1987), and superposition and approximate age of South American Land Mammal Ages recorded at Gran Barranca. N. Am., North America; Ant., Antarctica; GABI, Great American Biotic Interchange; MECO, Middle Eocene Climate Optimum; MMCO, Middle Miocene Climate Optimum; EOT = Eocene–Oligocene transition.

Colhue-Huapi Norte, Cañadón Lobo (= Cañadón Tournouër at Punta Casamayor), and Tapera de López localities I, II, III, and V (Cifelli 1985). The only emendations we offer to the composition of the Barrancan fauna at Gran Barranca is to point out that the fossil mammal assemblage from GBV-60 El Nuevo is no longer included in the Barrancan.

El Nuevo

The fossil vertebrate locality GBV-60 El Nuevo at Profile M corresponds to Level 15 of Cifelli (1985). The distinctive stratum yielding the fossil vertebrates is in the Rosado Member (Bellosi Chapter 2, this book). The composition of the mammal assemblage based on our new collections includes some noteworthy differences from typical Barrancan taxa among Notoungulata (Reguero and Prevosti this book) and Didolodontidae (Gelfo this book).

Mustersan

Above El Nuevo occur levels of the Mustersan SALMA, which at Gran Barranca is between 38.7 and 37.0 Ma. Levels with Mustersan assemblages are found in the Rosado and Lower Puesto Almendra Members (Bond and Deschamps this book; Gelfo this book; López *et al.* this book; Reguero and Prevosti this book). Bond and Deschamps (this book) proposes that the Rosado Member at Gran Barranca become the type section for the Mustersan Age, given the presence of characteristic Mustersan taxa, precise upper and lower boundaries, and intermediate position within a well-dated mammal sequence. The composition of the Mustersan fauna at Gran Barranca is largely based on recent collections made by Duke/MLP expeditions at GBV-3 El Rosado and an American Museum of Natural History (AMNH) locality known as "Coley's Quarry," reviewed most recently by Bond and Deschamps (this book) and Gelfo (this book).

The locality GBV-3 El Rosado, just west of Profile J, is the richest Mustersan fauna at Gran Barranca and occurs in the Rosado Member. Cifelli (1985) recorded only two taxa in the AMNH collection from this locality, *Notostylops* sp. and *Antepithecus brachystephanus*, and on this basis included this level in his Barrancan Subage. Since that time, we have collected extensively at GBV-3 El Rosado and have recovered *Astraponotus*, cf. *Eopachyrucos*, in addition to *Periphragnis* and *Rhyphodon* (typical Mustersan isotemnids), and also possibly the notohippid *Puelia* (López *et al.* this book). The co-occurrence of *Notostylops* with *Astraponotus* at GBV-3 El Rosado is noteworthy, but this is not the first time *Notostylops* has been reported as part of an otherwise Mustersan assemblage (see Simpson n.d.) wherein he remarked that the Locality #5 (Cerro Blanco) fossils "en general son mamíferos típicos del Mustersense, pero no comprendo la presencia de *Notostylops*. Nunca he encontrado este género en situ junto con mamíferos parecidos" ["in general these are typical Mustersan mammals, but I don't understand the presence of *Notostylops*. I've never found this genus in situ together with such mammals"].

Coley's Quarry (GBV-64) is the *Astraponotus* quarry Coleman S. Williams worked at the base of Unit 1 of the Lower Puesto Almendra Member. The material includes *Astraponotus* and isotemnid taxa typical of Mustersan assemblages elsewhere in Patagonia. Also, AMNH material of *Periphragnis* sp. from Gran Barranca includes specimens from Coley's Quarry and from GBV-65 (the level of Simpson's #94), another possible Mustersan level.

It should be pointed out that the Rosado Member, GBV-3 El Rosado, and the Rosado Tuff are three different things. The Rosado Member is a distinctive lithostratigraphic unit comprising various strata described by Bellosi (Chapter 2, this book). GBV-3 El Rosado and GBV-60 El Nuevo are fossil vertebrate localities within the Rosado Member. The Rosado Tuff is a dated tuff sampled from the same stratum yielding the fossil mammals at GBV-3. The Rosado Member at Gran Barranca is not a synonym for the Mustersan fauna or the Mustersan SALMA. The Mustersan fossils from Coley's Quarry were collected at a stratigraphic level in the Lower Puesto Almendra Member between Profiles A and G. Thus, the Mustersan at Gran Barranca may be represented by fossil taxa from at least two levels, each in a different member. The faunule from GBV-60 El Nuevo appears to be of intermediate composition between more typical Barrancan and Mustersan assemblages at Gran Barranca, but the locality occurs within the Rosado Member.

La Cancha

Above the Mustersan is found a fauna that is similar in composition to the Chilean type fauna for the Tinguiririca SALMA (Flynn *et al.* 2003). Some characteristic elements of the fauna were known in Ameghino's time and described at the "Astraponotéen plus superior" (Bond and Deschamps this book). The Tinguiririca fauna at Gran Barranca is found in the Vera Member at a level dated to between 33.3 and 33.7 Ma. This age is similar to, but better constrained than the age of the Tinguiririca type fauna. While similar in many respects, the Chilean fauna contains the earliest record of rodents whilst the assemblage at GBV-4 La Cancha at Gran Barranca has yielded no rodents despite an intensive effort to recover small mammals. Almost all we know about the Tinguiririca at Gran Barranca is described in work reported here (Carlini *et al.* this book; Goin *et al.* this book; López this book; Reguero and Prevosti, this book).

The idea of a distinct faunal level called the "Astraponotéen plus superieur" began with Ameghino (1901) supported by evidence that accumulated piecemeal beginning with (1) the curious assemblage from Cañadón Blanco discovered by Roth in 1902, (2) the under-appreciated discovery of Profile K by Egidio Feruglio (Simpson 1936), (3) the collection of a few fossils in a similar stratigraphic context at Profile M by the Scarritt Expedition in 1930 (Simpson 1967), and (4) newer collections from diverse localities in Patagonia (Hitz *et al.* 2000; Croft *et al.* 2003; Reguero *et al.* 2003; Bond and Deschamps this book). A Tinguiririca SALMA was finally given substance by the remarkable fauna from Chile (Flynn *et al.* 2003). Now the presence of this distinctive faunal level at Gran Barranca has been confirmed by the rediscovery of GBV-4 La Cancha.

The vertebrate locality GBV-4 La Cancha occurs in the La Cancha bed, a distinctive stratum extending nearly unbroken between Profiles K and M. The La Cancha bed occurs within the otherwise nearly monotonous and lithologically homogeneous Vera Member (Bellosi Chapter 19, this book). GBV-4 La Cancha is a flat exposure with a surface area roughly that of a "soccer pitch" near the top of the Vera Member at Profile K. The Carlini Tuff outcrops near the base of the La Cancha bed. GBV-4 La Cancha at Gran Barranca is stratigraphically correlated with the levels at Profile M where Coley Williams collected *Eomorphippus*, and in clear stratigraphic and age relationships with older and younger assemblages referred to the Mustersan and Deseadan land mammal ages. Finally, GBV-4 La Cancha has been dated by an integrated magnetic polarity and Ar/Ar geochronology (Ré *et al.* Chapter 3, this book).

The marsupial faunas from the Tinguiririca levels represent a radical departure from any other known Paleogene marsupial faunas, although marsupials recovered from the GBV-3 El Rosado level at Gran Barranca are under study and could change that picture, as noted by Goin *et al.* (this book). Goin *et al.* (this book) call attention to a radical shift in the niche structure of the smaller marsupials in the Tinguiririca fauna at Gran Barranca and carried on in the slightly younger La Cantera fauna (see below). They note that in the Paleocene and Eocene, frugivorous, omnivorous, or insectivorous marsupials dominated. By contrast, many of the Tinguiririca and later early Oligocene marsupials (and by far the most commonly occurring ones) show more herbivorous feeding habits (seeds, hard fruits, and/or abrasive food items). Particularly *Hondonadia* and *Klohnia* have molar morphologies indicative of some side-to-side or anteroposterior masticatory movements and some degree of hypsodonty. Additionally, the newly described Argyrolagoidea developed a rodent-like molar pattern. The rodent-like adaptations among South American marsupials suggest a rapid response to more cool, open, and arid environments, which opened a new series of adaptive zones by the early Oligocene. The change in marsupial niche structure from the Eocene to the Oligocene is a distinctive feature of the La Cancha fauna as compared to other (older) Paleogene associations. Given our present state of knowledge, the La Cancha marsupials represent the most dramatic marsupial turnover of the South American Cenozoic, an event termed the *Bisagra Patagónica* ("Patagonian Hinge") by Goin and colleagues.

The composition of the southern ungulate assemblage from La Cancha was discussed by López *et al.* (2005) and more recently by Reguero and Prevosti (this book) and López *et al.* (this book). GBV-4 La Cancha has yielded fragmentary remains of the pyrothere *Propyrotherium* and considerable diversity among notoungulates. The assemblage of southern ungulates from GBV-4 La Cancha has its greatest taxonomic similarity with the fauna from Tinguiririca in central Chile, and on this basis alone the GBV-4 La Cancha fauna can be assigned to the Tinguiririca SALMA.

Carlini *et al.* (this book) add substantially to knowledge of Tinguiririca dasypodids at Gran Barranca, which look markedly different from those of older faunal levels. While stegotheriins carry over from lower levels, utaetins disappear and eutatins make their first appearance and are quite diverse (three genera and five species). Euphractins decline in diversity to a single species (compared with four in Mustersan levels).

La Cantera

The next younger fauna at Gran Barranca is the La Cantera fauna (GBV-19) in Unit 3 of the Upper Puesto Almendra Member, constrained in age to between 31.1 and 29.5 Ma – at least 2.2 million years younger that the Tinguiririca at Gran Barranca, and certainly older than well-dated Deseadan faunas at Salla, Bolivia, and Scarritt Pocket and other Deseadan localities in Patagonia. La Cantera could justifiably be proposed as a SALMA of its own. Among the La Cantera marsupials, Goin *et al.* (this book) note the last record of rosendolopids and polydolopimorphians. Argyrolagoids continue in small numbers and the paucituberculate diversification continued. Large borhyaenids are represented for the first time by *Pharsophorus*. Several other characteristic elements of the Deseadan SALMA appear but many characteristically Tinguiririca elements persist, especially marsupials that do not survive in the typical Deseadan faunas of Patagonia, Brazil, and Bolivia (Carlini *et al.* this book; Goin *et al.* this book; López *et al.* this book; Reguero and Prevosti this book; Vucetich *et al.* Chapter 13, this book).

Xenarthrans are represented at La Cantera by one stegotheriin, as in the Tinguiririca, and the same three genera of eutatins are represented. On the other hand, the composition of the euphractine fauna is quite different, with just one species possibly in common: *Parutaetus chilensis*. Two other Tinguiririca euphractine genera drop out and two genera are added: *Archaeutatus* and *Prozaedyus* (Carlini *et al.* this book).

The rodent fauna in the La Cantera level is the oldest in Argentina and morphologically most primitive in South America (Vucetich *et al.* Chapter 13, this book). The represented taxa include three octodontoids, one cavioid, one dasyproctid, and one possible chinchilloid. All species have low-crowned teeth (brachydont) except the chinchilloid which displays an incipient unilateral hypsodonty. The absence of rodents in well-documented Tinguiririca levels at Gran Barranca suggests rodents arrived from the north during the early Oligocene. Based on their similarity with African rodents of the late Eocene, rodents arrived in South America as immigrants from Africa perhaps in the middle to late Eocene.

The ungulate fauna from La Cantera contains elements of the Tinguiririca fauna along with a significant number of more evolutionarily advanced taxa that are known from Deseadan faunas (*Scarrittia*, *Henricofilholia*) including guide fossils for this SALMA. Sixty percent (60%) of the remains collected at La Cantera are clearly referable to the Leontiniidae, characteristic elements in Deseadan faunas of Patagonia. Of the leontiniid material from GBV-19 La Cantera the most abundant taxa are new species only known from this locality, e.g. *Scarrittia barranquensis* and *Henricofilholia vucetichia* (Ribeiro *et al.* this book).

The family Notohippidae is represented at GBV-19 La Cantera also by two new species, *Patagonhippus canterensis* and *Patagonhippus dukei*, closely related to well-known taxa from La Flecha and Cabeza Blanca, but more primitive morphologically (López *et al.* this book).

To date, Toxodontidae are represented only by rare upper molars generally comparable in morphology to *Proadinotherium* from Deseadan assemblages in Argentina, Chile, Bolivia, and Colombia. Toxodontidae appear abruptly at La Cantera, with as yet no plausible ancestor in older levels or faunas anywhere in Patagonia.

The typotherians include a small *Trachytherus* (Mesotheriidae) and *Prohegetotherium* (Reguero and Castro 2004; Reguero and Cerdeño 2005). Archaeohyracidae include material of either *Archaeotypotherium* or *Archaeohyrax*, and *Protarchaeohyrax gracilis*. Material of Interatheriidae from GBV-19 is similar in size and morphology to *Eopachyrucos pliciferus*.

In general, Hegetotheriidae, Mesotheriidae, and Leontiniidae are present at La Cantera but not at GBV-4 La Cancha and between Isotemnidae and Notohippidae, more primitive taxa are recorded at GBV-4 La Cancha. Among typotherians, both Notopithecinae and Interatheriinae are present at GBV-4 La Cancha, but only relatively derived Interatheriinae occur at GBV-19 La Cantera.

Two subfamilies of Astrapotheriidae are present at La Cantera; Astrapotheriinae comparable to *Parastrapotherium* (it should be noted that material of large astrapotheriine is known to occur as float down slope from both Colhuehuapian and Deseadan levels) and Albertogaudryiinae, represented by a large form comparable to *Albertogaudrya* (a genus otherwise known from Casamayoran and Mustersan levels in Patagonia) and a smaller taxon recently described by Kramarz and Bond (2009).

Some mandibular fragments from GBV-19 La Cantera can be referred to Litopterna, but generally poor preservation, makes their identification problematical, but are reminiscent of the enigmatic genus *Protheosodon* (Proterotheriidae?).

Deseadan

Until now, the Deseadan at Gran Barranca has been elusive. Marshall *et al.* (1986) complained that the precise stratigraphic context of Deseadan taxa was not recorded and Cifelli had trouble pinning it down stratigraphically based on Simpson's otherwise well-documented collection of fossil mammals at the AMNH. Since long before the time of Simpson, and as early as the work of Carlos and Florentino Ameghino, the presence of a Deseadan or "*Pyrotherium*" level at Gran Barranca has never been convincingly or adequately documented. Three localities in the Upper Puesto Almendra Member at Gran Barranca have yielded useful assemblages of fossil mammals (GBV-1, GBV-34 in Unit 3, and GBV-35) that although of limited diversity, have taxonomic compositions reminiscent of the type Deseadan fauna at La Flecha and the best-known Deseadan assemblage at Cabeza Blanca. Four new isotopic dates (26.3 to 29.2 Ma) are available for basalts in the Upper Puesto Almendra Member indicating that multiple flows are represented with relatively brief intervening periods of local erosion (Ré *et al.* Chapter 4, this book). Local unconformities occur both at the base (D7) and at the top of the basalts (D8). The Deseadan localities come from within Unit 3 of the Upper Puesto Almendra Member in association with basalts but the stratigraphic relationship between them and their associated unconformities is obscure (Ré *et al.* Chapter 3, this book).

The most abundant material from these localities are isolated specimens (mostly teeth) of large Leontiniidae and Astrapotheriidae. The leontiniid material is referred to *Scarrittia barranquensis*, and *Scarrittia* cf. *S. canquelensis* (Ribeiro *et al.* this book), and the astrapotheriid to *Parastrapotherium crassum* (Kramarz and Bond this book).

Remains of *Pyrotherium* are rare at Gran Barranca. Simpson (1930, p. 75) observed only "a few fragments, none . . . happen to have been in place." A single lower milk molar of *Pyrotherium sorondoi* (FMNH P 15068) is the only material of *Pyrotherium* collected by the Riggs expedition at Gran Barranca. The most complete material known to date are the two specimens of *Pyrotherium* collected by Alejandro Bordas in 1939, including MACN 12410, a left maxilla with M1 and M2 from Km 163 (a classic geographic place name associated with Gran Barranca that indicates nothing about its stratigraphic provenance). Bordas (1945) published a profile of a 130-m thick exposure of the Sarmiento Formation at Gran Barranca onto which he indicates the *Pyrotherium* zone just below a basalt somewhere at the west end of Gran Barranca.

No rodents or xenarthrans have been recorded from Deseadan levels at Gran Barranca.

Colhuehuapian

After a considerable temporal hiatus (in faunal representation though not necessarily in deposition) there occurs the Lower Fossil Zone of the Colhue-Huapi Member, the type fauna of the Colhuehuapian SALMA, between 20.0 and 20.2 Ma. A number of chapters in this book summarize our current state of knowledge about this faunal zone (Carlini *et al.* this book; Czaplewski this book; Kay this book; Kramarz and Bond this book; Reguero and Prevosti this book; Ribeiro *et al.* this book; Vucetich *et al.* Chapter 14, this book) and Goin *et al.* (2007) reported previously on the marsupial fauna.

Among dasypodine armadillos, astegotheriins (*Pseudostegotherium*) reappear for the first time since the Barrancan with a very tiny species (*Pseudostegotherium glangeaudi*). *Stegotherium* is present and abundant. Among Euphractinae is one species of Eutatini *Proeutatus*, and one of the Euphractin *Prozaedyus* both also known from the "Pinturan" levels (Carlini *et al.* this book).

Goin *et al.* (2007) revised the Colhuehuapian Didelphimorphia and Sparassodonta. The Colhuehuapian levels of Gran Barranca are the richest ones in marsupials of this age, including 15 species referred to six families of these two orders only. Among the most important results, they recognized the oldest record of Didelphoidea including the oldest Caluromyidae, and a great diversity of carnivores including the oldest Thylacosmilidae. They described a new species of *Necrolestes*, an unusual Santacrucian mammal of uncertain affinities, with "pretribosphenic" molar pattern. Although not revised in the context of this project, other groups of marsupials are recorded in the Colhuehuapian levels at Gran Barranca: microbiotheriids, caenolestids, and abderitids (Marshall 1976; Pascual *et al.* 1996). A wide variety of microbiotheriids, several argyrolagid taxa, and an impressive diversity of paucituberculatans (Caeonolestidae, Palaeontentidae, and Abderitidae) have been recognized (F. Goin pers. comm.).

Vucetich *et al.* (Chapter 14, this book) describe a remarkable rodent fauna from the Colhuehuapian SALMA. Strikingly, the Colhuehuapian rodents are more diverse than from any other rodent fauna in the Cenozoic. Some of the diversity is accounted for by *in situ* evolution of Deseadan Patagonian taxa whilst other lineages appear without obvious Patagonian antecedents and likely originated from northern subtropical regions after the Deseadan. The diversity of rodent cheek tooth designs including crown complexity, increased crown height, and a broader size range compared with Deseadan rodents shows that Colhuehuapian caviomorphs had already developed considerable dietary niche breadth. Especially notable are the richness of small octodontoids and the great diversity of possibly arboreal erethizontids that have their acme at this time. Many

Colhuehuapian rodent lineages had gone extinct in Patagonia after the middle Miocene; only eocardiids and chinchillids are certainly closely related to extant representatives. They note that the differences between the Gran Barranca Colhuehuapian fauna and those from other well-known Colhuehuapian sites are minor and may result largely from environmental variations.

Primates are rare elements of the Gran Barranca fauna, being found only in the Colhuehuapian (Kay this book). Kay describes a new genus, *Mazzonicebus*. The addition of this taxon brings the known diversity of Colhuehuapian primates to three genera. *Mazzonicebus* is closely related to *Soriacebus* from the younger Miocene rocks of the Pinturas Formation in Santa Cruz Province, but not recorded at Gran Barranca. The two offer the first well-documented sister-taxon relationship between a Colhuehuapian and a "Pinturan" (some times considered as early Santacrucian) primate, spanning ~3 m.y. *Mazzonicebus* and *Soriacebus* show specializations for fruit husking and seed predation, a dietary niche similar to that seen in the more derived members of the living platyrrhine subfamily Pitheciinae (sakis and uakaries), a fact that has led some researchers to conclude that *Soriacebus* is an early representative of that clade. However, the more primitive characters of the dentition of *Mazzonicebus* compared with *Soriacebus* further document and reinforce the hypothesis that these two Argentine early Miocene taxa are an independently evolved clade that is an ecological "vicar" of the extant platyrrhine seed predation dietary niche.

Bats are another rare element of the Gran Barranca fauna known from the Colhuehuapian. *Mormopterus barrancae* is a new species of phyllostomine Molossidae. A more primitive species of this genus is found in the Deseadan of Brazil. A single tooth, 20–30% smaller than *M. barrancae*, represents a second smaller species in the Colhuehuapian of Gran Barranca. The presence of the Phyllostominae suggests a warm moist climate and the availability of lowland forest habitat in the Colhuehuapian, consistent in part with habitats inferred from early Miocene rodents and primates.

Colhuehuapian notoungulates seem poorly diversified for a fauna otherwise so rich. Only five species referable to four families occur in the Lower Fossil Zone (Reguero and Prevosti this book). Kramarz and Bond (2005) and Soria (2001) list four taxa of Proterotheriidae (Litopterna) from the Colhuehuapian of the Sarmiento Formation without specifying whether from Gran Barranca or elsewhere in Patagonia: *Lambdaconus lacerum*, *Paramacrauchenia inexspectata*, *Paramacrauchenia scamnata*, and *Prolicaphrium specillatum*. Finally, there are at least three taxa of Astrapotheriidae in the Colhuehuapian at Gran Barranca, *Parastrapotherium symmetrum*, *Parastrapotherium martiale*, and *Astrapotherium? ruderarium* and possibly a fourth uruguaytheriine (Kramarz and Bond this book).

"Pinturan"

Near the top of the Sarmiento Formation in the Upper Fossil Zone of the Colhue-Huapi Member between 19.7 and 18.7 Ma, there occurs a still poorly represented fauna that while resembling the Pinturan fauna from Santa Cruz Province, may be at least 1.5 m.y. older (Kramarz *et al.* this book). Although notoungulate and litoptern material from the "Pinturan" levels at Gran Barranca is fragmentary, three typotherians are present (*Interatherium*, *Protypotherium*, *Pachyrukhos*) and a fragmentary upper molar has been assigned to *Tetramerorhinus* (Proterotheriidae) (Kramarz *et al.* this book). Rodents are represented at least by seven genera of five families, including the otherwise exclusively "Pinturan" *Prostichomys*. Edentates are also diverse, represented by dasypodids, glyptodonts, and tardigrades, this latter through a single mandible fragment.

Regional and global climatic influences

Southern South America was likely influenced by worldwide and southern hemisphere climate trends and events during the middle Cenozoic. These might include (1) the period of cooling after the Mid-Eocene Climate Optimum (MECO), (2) the Eocene–Oligocene transition (EOT), and (3) the early Miocene warming trend leading to the Middle Miocene Climate Optimum (MMCO) (Lear *et al.* 2000; Zachos *et al.* 2001).

Our suspicion that biotic evidence bearing on these three events should be preserved in the terrestrial fossil record of the Sarmiento Formation at Gran Barranca (Fig. 29.3) is based on the fact that oceanic climate prevails today across Patagonia, with characteristically moderated seasonal atmospheric temperature extremes closely tied to sea-surface temperatures in the adjacent southern oceans. Proximity to Antarctica brings colder temperature extremes during the austral winter when colder polar air migrates northward, and similar such phenomena may have intensified with the onset and variation in the intensity of Antarctic glaciation. Today the Andes interrupts the westerly flow of atmospheric moisture across Patagonia, producing a pronounced orographic effect. However, the present morphology of the Patagonian Andes seems to postdate the early Miocene such that orographic influence on rainfall must have been less strongly felt when the Sarmiento Formation was deposited. The low altitude and flatness of central Patagonia makes the peninsula susceptible to sea-level change at epoch-scale and shorter durations (Miller *et al.* 2005; Pekar and Christie-Blick 2008). The surface area of the peninsula changed with sea level and parts of Patagonia may have become isolated from the rest of the continent (Bellosi Chapter 2, this book; Guerstein *et al.* this book; Kohn *et al.* this book). Beyond the reductions and increases in the appearance of high-crowned teeth among herbivorous marsupials as well (Goin *et al.* this book).

Early to middle Miocene climate amelioration

Oxygen isotope curves for the Neogene (Zachos *et al.* 2001) indicate a prominent period of ice-free conditions extending from the late Oligocene to the MMCO, corresponding to the interval between the Colhuehuapian and the Colloncuran in Patagonia, i.e. between 20.4 and 15.7 Ma.

The oldest record of primates in the Patagonian fossil record is in the Lower Fossil Zone of the Colhue-Huapi Member at Gran Barranca at about 20.2 Ma (Kay this book). Thereafter, primates occur continuously in the Patagonian fossil record until their latest known occurrence in the Colloncuran (Kay *et al.* 1998a). Primates were present in Patagonia throughout the 4.5-million-year interval between 20.2 and 15.7 Ma. Given the modern association between primates, humid environments, and subtropical climate conditions at their southernmost occurrences today (*Alouatta caraya* at 28° S in Argentina, and 30° S in Brazil), Patagonian climate must have been warm (mean annual temperature >19 °C) and humid (mean annual precipitation >1100–1400 mm) during the interval between 20.4 and 15.7 Ma.

The fossil record for the Colhuehuapian at Gran Barranca is especially rich in small marsupials and rodents. Goin *et al.* (2007) reviewed all the published evidence for Colhuehuapian climates in Patagonia and concluded that central Patagonia supported a regionally heterogeneous vegetation that included wet forests, palm-tree associations, restricted grassy environments, and flooded or paludal areas on variable topography. Most climate indicators accord with the view that Patagonian climates at this time were warm and humid during all or most of the year at a time when the Patagonian Andes did not act as an orographic barrier to moisture-laden winds. These benign conditions are reflected especially in the richness of brachydont octodontoids and erethizontid rodents (Vucetich *et al.* Chapter 14, this book). Also, asthegotheriin dasypodine armadillos reappear again in Patagonia after a 20-Ma hiatus (Carlini *et al.* this book).

Geographic isolation

The South American mammal fauna evolved in geographic isolation from other continents through most of the middle Cenozoic (Simpson 1950, 1980; Patterson and Pascual 1968). The available evidence from age-calibrated molecular phylogenetics and paleontology suggests that continental South American land mammals became isolated from Antarctica sometime prior to about 36 Ma (Springer *et al.* 1998; Reguero *et al.* 2002; Nilsson *et al.* 2004). This biogeographic separation of South America from Antarctica occurred prior to the opening of Drake Passage to deep-water circulation sometime between the EOT and about 28 Ma (Lawver and Gahagan 2003; Livermore *et al.* 2005).

In terms of faunal composition through the middle Cenozoic, continued geographic proximity between South America and Antarctica was less meaningful than South America's geographic proximity to Africa. Despite the progressive widening of the South and Equatorial Atlantic, waif immigration of small mammals from Africa to South America contributed rodents and primates to the South American fauna. Rodents first appear in the South American fossil record in dated context at about 31.5 Ma (Wyss *et al.* 1993) and shortly thereafter in Patagonia (Vucetich *et al.* 2004, Chapter 13, this book). The existence of caviomorphs in South America sometime prior to these dated occurrences, while logical, has yet to be adequately age-calibrated (Vucetich and Ribeiro 2003; Frailey and Campbell 2004). The geographic spread of caviomorph rodents to southern South America may not have occurred very rapidly. An example may be provided by the Sigmodontinae. Fully 6 million years elapsed between a molecular-clock divergence date for the clade Sigmodontinae between 12.3 and 13.1 Ma (Steppan *et al.* 2004) and their first appearance in the South American fossil record at 30° S latitude at about 6 Ma (Verzi and Montalvo 2008). During their accommodation to South American environments, Sigmodontinae achieved higher taxonomic level diversification (tribe) encompassing variation in locomotor and digestive anatomy (Voss 1988), cranial morphology and tooth crown shape and height (Steppan 1995), and a body size range from the smallest *Calomys musculinus* 8.2–21.2 g to largest *Holochilus magnus* 227–250 g (Carleton and Musser 1984; Patterson 1999; Williams and Kay 2001), plausibly constrained by competition with caviomorphs (Patterson and Wood 1982; Wood and Patterson 1959; Walton 1997).

The oldest known primate in South America is *Branisella* in Bolivia at tropical latitudes at about 26.0 Ma (Kay *et al.* 1998b, 2001; Takai *et al.* 2000). The impact of primates on the native South American fauna will be difficult to assess without a more continuous record from tropical latitudes. Nevertheless, their presence in Patagonia during a substantial interval of the early to middle Miocene is thought to have influenced ecological vicars, among them caenolestoid marsupials (Strait *et al.* 1990). Primates appear to have been excluded from Patagonian environments prior to the beginning of the Miocene Climatic Optimum.

Within Patagonia, a reduction of geographic area and possibly subdivision by marine barriers may have accompanied middle Cenozoic marine transgressions. Guerstein *et al.* (this book) review the history of marine deposits and sea-level variation affecting the surface area of Patagonia. A tentative geochronology for middle Cenozoic Patagonian transgressions can be established using age-calibrated sea-level curves (Miller *et al.* 2005) and their correlation with discontinuities and temporal hiatuses in sedimentation between members of the Sarmiento Formation. Not all of these highstands are preserved in marine sediments in the vicinity of Gran Barranca, nor in the dinoflagellate record described by Guerstein *et al.* (this book). Nevertheless, middle Cenozoic transgressions may have influenced mammalian evolution through their influence on the relationship between habitable area and the area of pyroclastic sediment accumulation (Ardolino *et al.* 1999; Malumián 1999).

Faunal hypsodonty and the establishment of grass-dominated ecosystems

The evolution of high-crowned teeth was a major feature of mammal evolution in South America throughout the Cenozoic, as a general faunal trend of increasing proportions of taxa with high-crowned teeth, as successive independent radiations within clades, and as events of coincident increase involving diverse clades. The evolution of high-crowned teeth in the middle Cenozoic of Patagonia occurs in diverse lineages of herbivorous mammals, including marsupials (Goin *et al.* this book), as many as six clades of native ungulates (Pascual *et al.* 1996; Reguero *et al.* this book), and several clades of rodents (Vucetich *et al.* Chapters 13 and 14, this book), all documented by the fossil record at Gran Barranca. The general trend of increasing faunal hypsodonty in the middle Cenozoic appears to have started among notoungulates in Patagonia as early as 43 Ma when lophodont ungulates begin to replace bunodont forms. By 38 Ma 23% of notoungulate genera were hypsodont (Kohn *et al.* 2004) and this trend culminated in at least 44% of genera sometime prior to 33 Ma in the early Oligocene. The first appearance of herbivorous marsupials with high-crowned teeth seems to have been at the EOT (Goin *et al.* this book). Rodents in the early Oligocene at GBV-19 La Cantera had notably more low-crowned teeth than their Deseadan (late Oligocene) and Colhuehuapian (early Miocene) successors. Notable examples of independent lineages evolving *in situ* towards higher crowns during the Deseadan to Colhuehuapian interval include Toxodontidae, Notohippidae, and Caviodea. Thus, the general faunal trend, multiple examples of the independent radiation of hypsodont taxa within clades, and several events of coincident accelerated increase in hypsodonty in Patagonia significantly antedate the initiation and early middle Cenozoic trends in faunal hypsodonty in North America (Prothero and Heaton 1996) and Europe (Collinson and Hooker 1987; Legendre 1989).

As documented at Gran Barranca, in the middle Cenozoic in Patagonia, there occurred several events of accelerated increase in crown height within the larger trend toward higher proportions of herbivore taxa with high-crowned teeth. These events occurred between 39 and 38 Ma, again between 32 and 26 Ma, and between 22 and 20 Ma. The occurrence of hypsodonty (Pascual and Ortíz-Jaureguízar 1990) in sediments containing grass phytoliths (Mazzoni 1979) has traditionally been understood to reflect the establishment of widespread grass-dominated ecosystems in South America (Jacobs *et al.* 1999). This plant–animal interaction assumes that herbivores evolve high-crowned teeth in response to the silica content of grass in the diet. However, in North America, phytoliths of open-country grasses become dominant in the Great Plains 6 million years before horses evolved hypsodonty (Strömberg 2002, 2004, 2005), and long after faunal hypsodonty became the dominant evolutionary trend among terrestrial mammalian herbivores. At Gran Barranca, grass phytoliths are abundant in the Gran Barranca Member (Zucol *et al.* this book) at least 1.5 million years before the oldest coincident increase in hypsodonty in Notohippidae, Archaeohyracidae, and Interatheriidae between 39 and 38 Ma. All this indicates that herbivores either did not exploit grasses or were adapting to some other source of dietary abrasives.

Summing up

Despite the fact that more than 100 years of research has been undertaken at Gran Barrranca, much remains to be done. The research in the present volume highlights as much about what we do not know as what we do know. The record of biotic evolution is as yet dimly perceived. Yet the collective efforts of the contributors to this book have moved forward on many questions. We now know roughly the stratigraphy of Gran Barranca and something about its mode of deposition. We have a more detailed understanding of the chronological ages of most of the vertebrate faunas. We have filled in some gaps. Most notably we have better documented the faunas clustered around the Eocene–Oligocene boundary. The work done up to now shows very clearly that it is misleading to assume that we can predict what occurred in Patagonia from global proxies of climate change, e.g. in sea-surface temperatures, or even regional effects like Andean uplift, sea-level fluctuations, the onset of Antarctic glaciation, or the opening of circumpolar oceanic circulation. What is especially clear is that different mammal groups responded in different ways to the same effects. For example, it appears that increased cheek-tooth crown height (hypsodonty) occurred over a long period of time and occurred in some taxonomic groups earlier than in others, and at different rates.

There are many gaps in our knowledge that could be addressed relatively easily. To cite a few examples, we have only begun to study the micro-plant remains despite the abundance of phytoliths through the section. Much more needs to be done with stable isotopes as proxies of climate change. And more intensive efforts must be made to recover small mammals, especially in the Gran Barranca Member. Other gains will come only with considerably more effort. Learning about the paleobiology of the mammalian species will be and temporal hiatuses in sedimentation between members of the Sarmiento Formation. Not all of these highstands are preserved in marine sediments in the vicinity of Gran Barranca, nor in the dinoflagellate record described by Guerstein *et al.* (this book). Nevertheless, middle Cenozoic transgressions may have influenced mammalian evolution through their influence on the relationship between habitable area and the area of pyroclastic sediment accumulation (Ardolino *et al.* 1999; Malumián 1999).

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