

17 The Mustersan age at Gran Barranca: a review

Mariano Bond and Cecilia M. Deschamps

Abstract

The Mustersan South American Land Mammals Age (SALMA), based on the “Astraponotéen” of Ameghino (late Eocene), represents the first moment when native ungulate mammals showed an increase in the number of high-crowned taxa. Ameghino initially distinguished two levels in his “Astraponotéen”: the “Astraponotéen” and an “Astraponotéen le plus supérieur,” but later abandoned this subdivision. After Ameghino, other faunas came to be included in the “Astraponotéen,” such as those from Cerro del Humo and La Gran Hondonada. New collections made at Gran Barranca with precise stratigraphic control, isotopic dates, and magnetostratigraphy allow resuscitation of the “Astraponotéen le plus supérieur” and demonstrate its equivalence to the Tinguirirican of Chile, in both content and age. New studies show that many Mustersan ungulates with high-crowned cheek teeth come from the “Astraponotéen le plus supérieur.” This explains the mixture of faunas of notoungulates with different degrees of hypsodonty. The Mustersan SALMA is represented at Gran Barranca by assemblages from both the Rosado and Lower Puesto Almendra members, dated between 39.0 and 36.5 Ma. These members are separated by unconformities from the underlying Gran Barranca Member and the overlying Vera Member, containing faunas ascribed to the Casamayoran and “Astraponotéen le plus supérieur,” respectively. The classical Mustersan site at “Colhue-Huapi Norte” where several Mustersan taxa were found (among them the type of *Astraponotus asymmetrus*) is the same site as Cerro del Humo. The Rosado Member at Profile J (Gran Barranca) is here proposed as the source of the assemblage of taxa that serve as the type fauna of the Mustersan SALMA, because it has the characteristic taxa, precise upper and lower boundaries, and is placed within a well-dated and very complete mammal sequence.

Resumen

La Edad Mamífero Mustersense, basada en el “Astraponotéen” de Ameghino (Eoceno tardío), representa el primer momento en que los ungulados nativos muestran un incremento en el número de taxa de corona alta. Ameghino primero mencionó dos niveles el “Astraponotéen” y el “Astraponotéen le plus supérieur”, pero más

tarde abandonó esta subdivisión. Después de Ameghino se incluyeron en estas faunas, aquellas provenientes de otros sitios como Cerro del Humo o La Gran Hondonada. Nuevas colecciones realizadas en Gran Barranca con adecuado control estratigráfico, dataciones isotópicas y magnetostratigrafía, permitieron resucitar el “Astraponotéen le plus supérieur” y comprobar su equivalencia con el Tinguiririquense (Eoceno tardío-Oligoceno temprano) de Chile. Los nuevos estudios muestran que muchos de los ungulados Mustersenses con coronas más altas provienen del “Astraponotéen le plus supérieur”. Esto explica la supuesta mezcla de faunas de notoungulados con diferentes grados de hipsodoncia, considerada típica del Mustersense. La Edad Mustersense está representada en la Gran Barranca por el Miembro Rosado y el Miembro Puesto Almendra Inferior, datados entre 39,0 y 36,5 Ma. Estas unidades están separadas por dos discordancias del infrayacente Miembro Gran Barranca y el suprayacente Miembro Vera (que contienen faunas asignadas respectivamente al Casamayorense y al “Astraponotéen plus supérieur” = Tinguiririquense). También se comprobó que el sitio Mustersense clásico “Colhue-Huapi Norte”, de donde provienen varios de los taxones Mustersenses, entre ellos el tipo de *Astraponotus asymmetrus*, que da nombre al “Astraponotense” (=Mustersense), es sin duda el mismo que Cerro del Humo. Se propone considerar al Miembro Rosado, como nivel tipo de la Edad Mustersense debido a que tiene los fósiles característicos, cuenta con límites inferior y superior precisos y está incluido en una secuencia estratigráfica datada y muy completa.

Introduction

Since the work of Florentino Ameghino more than a century ago, many of the localities and the biostratigraphic and geochronologic units defined by him have received different denominations. Sometimes Ameghino’s units were neglected or joined together, and even the original concept was altered. As Simpson (1933) noted, the “Astraponotéen” of Ameghino, currently the Mustersan South American Land Mammals Age (SALMA), has been “happy” to receive little attention from researchers after Ameghino, as there was no multiplication of names that could confuse its original concept. However, the problem with the Mustersan arose at the very beginning by its original definition. In Ameghino’s original concept, this fauna apparently involved a “mixture”

of related taxa with very different degrees of hypsodonty, and he changed his mind about the existence of more than one level within the “Astraponotéen.” Even the original locality and assemblage used in its definition was not made clear. Gran Barranca was assumed to be the type locality, but as years passed, the concept of the Mustersan SALMA came to be based mainly on mammals from localities other than Gran Barranca. Thus, until very recently the faunal assemblage of the Mustersan SALMA, although defined or exemplified in new richer localities, continued being characterized by a mixture of taxa of different age.

The rediscovery that the Mustersan SALMA includes more than one faunal assemblage prompts us to review the Mustersan faunas at Gran Barranca. New collections with precise biostratigraphic context allow a revision of its faunal composition. Here we review this history in order to understand and interpret accurately the original concept in light of the new relationships among elements of this fauna, and propose a new type locality for the Mustersan.

The beginnings

Between 1887 and 1906, knowledge of the geology of the lower and middle Tertiary of Patagonia changed radically from what was known by D’Orbigny (1842), Darwin (1846), or Doering (1882). This change was almost solely due to the effort of the Ameghino brothers, Carlos in the field and Florentino in the cabinet (a museum’s cabinet or an adapted store room!). We owe an enduring debt to them for much of our understanding of the Cenozoic faunal succession in Patagonia. The succession they established is not only still in use in Argentina but has become the reference standard for SALMAs (Pascual *et al.* 1965, 1966; Marshall *et al.* 1983; Cione and Tonni 1995).

Between 1889 and 1895 Carlos Ameghino discovered first in Chubut and later in Santa Cruz Province fossil mammals that became Florentino’s “*Pyrotherium* fauna” and the basis for his “Étage Pyrothéréen” (presently the Deseadan SALMA). This “Étage” was the first pre-Santacrucian biochronologic unit recognized in Patagonia. According to Simpson (1967a), the “*Pyrotherium* fauna” was found by Carlos Ameghino in his 1895–96 expedition (but perhaps even as early as 1893: Ameghino 1897), when he explored south of Lake Colhue-Huapi (Fig. 17.1). Only later, during his 1898–99 expedition, did Carlos realize that the original collection of fossils described as the *Pyrotherium* fauna actually included material of a distinctly older fauna from beds which eventually were named the “Couches à *Notostylops*.” Among the pre-Deseadan mammals described in 1897 from the “couches à *Pyrotherium*,” some may have been collected at Gran Barranca. In two letters to Florentino (15 February 1899 and 9 June 1899, in Ameghino 1900; Simpson 1967a) Carlos reported a good

exposure in “Colhue-Huapi” where the “*Notostylops*” and “*Pyrotherium*” beds were perfectly concordant stratigraphically but not “paleontologically” as there were sediments devoid of fossils between them (Fig. 17.2). But in his expedition of 1899–1900, he found mammals in beds he formerly supposed to be sterile. Florentino Ameghino (1901) named these new mammal-bearing beds and its fauna the “faune des couches à *Astraponotus*” and the corresponding stage as the “Étage Astraponotéen” (currently the Mustersan SALMA). However, he provided no precise geographic location. Consequently, we only know through specimen labels that the type of the taxon characterizing this stage, *Astraponotus asymmetricus* (Fig. 17.3A–C), was not collected at Gran Barranca but at “Colhue-Huapi Norte,” a locality north of Lake Colhue-Huapi, sometimes written as “Colhuapi” or “Coluapi Norte.” Thus, Carlos collected “Astraponotéen” fossils not only at Gran Barranca but also at other sites (Fig. 17.1).

All these mammal-bearing levels were included in Ameghino’s “Formation Guaranienne.” He still used the term “Formation” to mean a coeval group of beds or “couches,” or a chronological unit, but not as was beginning to be used worldwide following recommendations of geological congresses, a lithological unit of lower hierarchy. He also used the term “couches,” as a unit defined by fossils (nearly equivalent to biostratigraphic units), as did many authors at that time. Moreover, sometimes his “couches” were equivalent to a Substage or a Stage, representing an “Étage” with its corresponding “Age.”

Descriptions of the new taxa from the “Faune Astraponotéenne” and a faunal list were published in several papers (Ameghino 1901, 1902, 1904, 1905), but unfortunately without detailed geographic location. Nearly all of them were found in the “Couches à *Astraponotus*,” but three, *Pseudopachyrucos foliiformis*, *Interhippus deflexus*, and *Proplatyarthrus longipes* (Ameghino 1901, 1902, 1905) came from the “partie la plus supérieure des couches à *Astraponotus*.” Thus, between 1901 and 1906, F. Ameghino distinguished two fossil mammal-bearing levels within the “couches à *Astraponotus*.”

In his geology of Patagonia, Ameghino (1906) considered the “Astraponotéen” fauna transitional between the “*Notostylops*” and “*Pyrotherium*” faunas, and with “stratification parfaitement concordante.” “Astraponotéen” exposures around Lakes Musters and Colhue-Huapi were as extensive as those of the Notostylopéen, but because they were less fossiliferous it was difficult to determine the upper and lower boundaries of the “Astraponotéen” beds. The location of the outcrops in maps (Ameghino 1906) is far from exact. One of the localities, with molds of land snails (*Strophocheilus*), was figured on a profile on the left margin of the “río Chico del Chubut” on the upper third of its valley (Ameghino 1906) (Fig. 17.1). It was considered

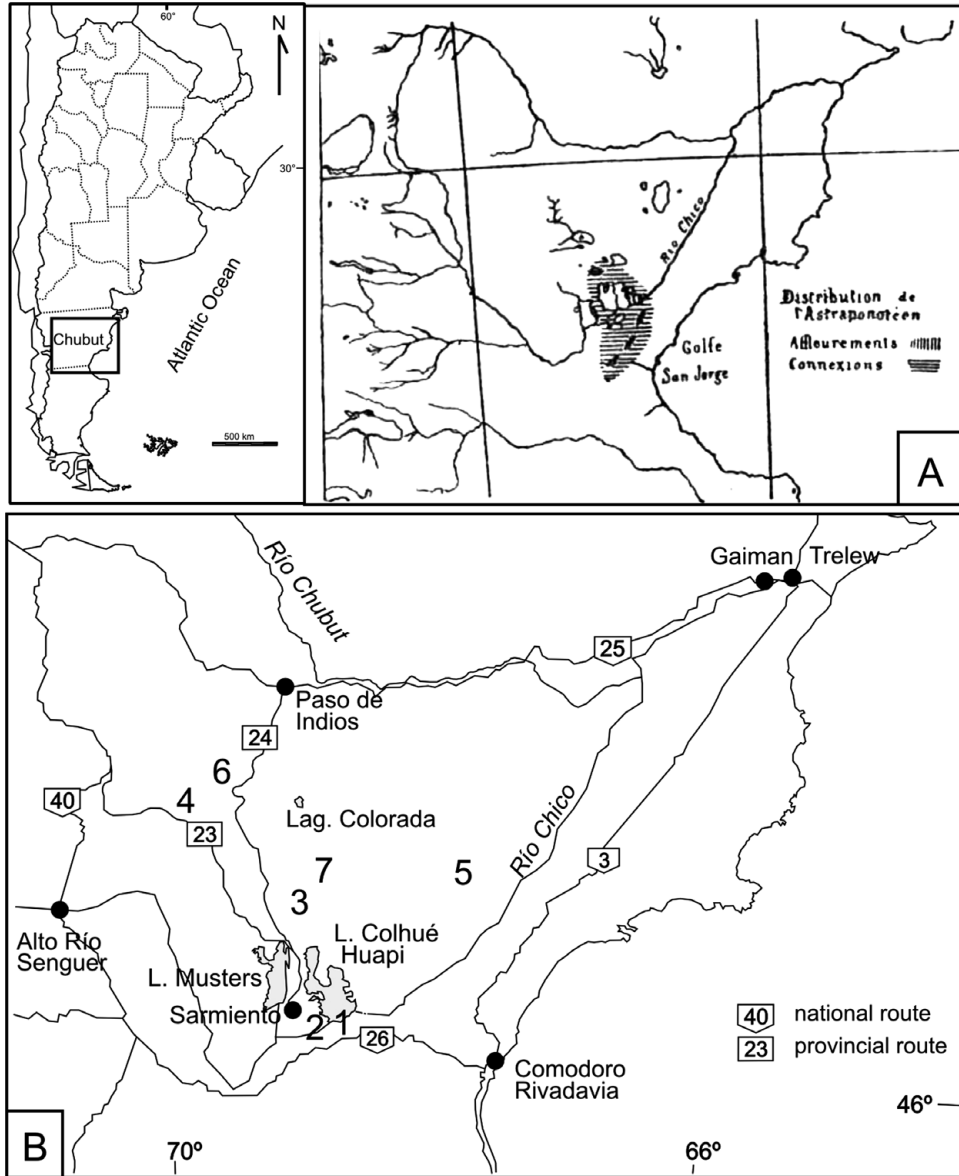


Fig. 17.1. Location map. (A) Original map of Ameghino; (B) localities mentioned in the text: 1, Gran Barranca; 2, Cerro Blanco (west flank of Gran Barranca); 3, Colhue-Huapi Norte = Cerro del Humo = Cretáceo superior del Lago Musters = El Pajarito; 4, Laguna del Mate; 5, Sierra Cuadrada; 6, Gran Hondonada; 7, Cerro Talquino.

important because carnivorous dinosaur remains (*Genyodectes serus*) were mentioned in the uppermost Notostylopéen or Astraponotéen beds. Ameghino (1906, Figs. 31, 58) included a profile of Gran Barranca (Fig. 17.2), based on field observations by Carlos, showing the “Astraponotéen” composed of greenish and whitish clays between the “notostylopéen supérieur” and the “pyrothéréen”, and below a mantle of eruptive basalt. In that paper, Florentino stated that the evolutionary transition between the *Astraponotus* and *Pyrotherium* faunas seemed to be very gradual and the temporal hiatus probably not very long. Hence,

Ameghino abandoned the intermediate level (“partie la plus supérieure des couches à *Astraponotus*”), but ambiguously said that a transitional fauna might be found. Instead, he found stronger evidence for a paleontological “hiatus” between the “Astraponotéen” and the underlying “Faunes Notostylopéennes.”

Ameghino (1906) characterized the “Faune Astraponotéenne” pointing out the independent appearance in many lineages of ungulates of a strong tendency toward molar hypselodonty (“vers l’hypselodontie”). Among other faunal distinctions, he reported the decrease in the diversity of

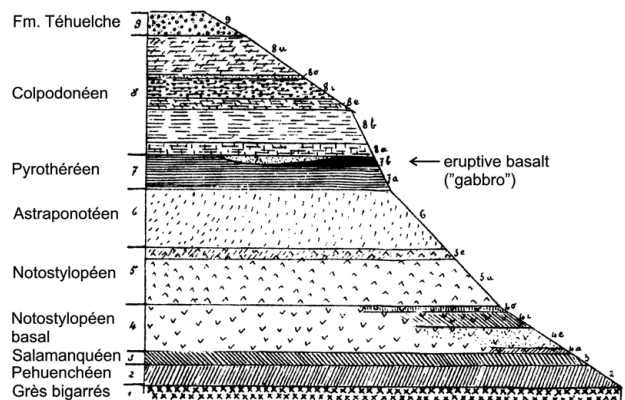


Fig. 17.2. Profile from the Gran Barranca, south of Lake Colhue-Huapi, according to C. Ameghino (from F. Ameghino 1906, figure 81, page 112).

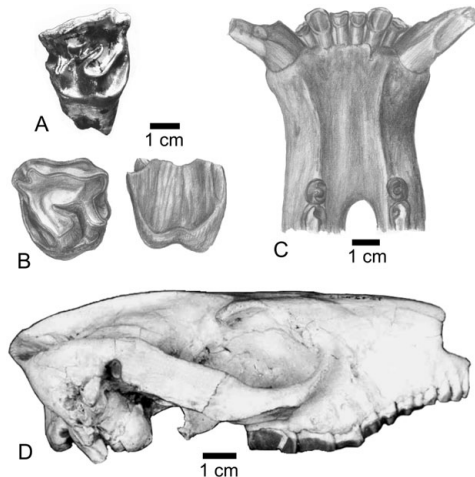


Fig. 17.3. Examples of typical Mustersan mammals. (A–C) *Astraponotus assymetrus* and (D) *Puelia coarctatus*. (A) Type of *Astraponotus dicksoni*, MLP 12–2217, right M1 or M2; (B) MLP 67-II-27–46, left M1 or M2; (C) MLP 82-V-7–2, mandibular symphysis with right and left I1–3, C1 and P2–3; (D) MLP 67-II-27–27, skull in lateral view.

“condylarths” and notostylopids and the appearance of the earliest pyrotheriids. Hence, the “Faune Astraponotéenne” appeared as an intermediate stage between the more brachyodont ungulates of the “Faunes Notostylopéennes” and the more hypsodont or even hypselodont (or euhypodont) taxa of the “Faune Pyrothéréenne.” Thus, as early as 1906 the stratigraphic position and general features of the “Faune Astraponotéenne” were established, but neither the precise location of its main localities nor the provenance of its original materials was ever reported.

How many of Ameghino’s fossil specimens of Mustersan age really came from Gran Barranca? At the time Carlos

Ameghino was collecting in the “Astraponotéen,” his rival Santiago Roth of the Museo de La Plata collected Mustersan mammals at three sites, especially one north of Lake Colhue-Huapi (called Musters by Roth). Like Carlos, Roth reported no precise locations for his Mustersan localities (Roth 1899, 1901, 1903), but later he indicated them on an unpublished map (Simpson 1936a). The fossils found in the most productive of these sites were labeled “C. S. M.,” “Cretáceo Superior Lago Musters,” as Roth thought these beds were much older (Simpson 1936a). Roth also collected at another locality, Cañadón Blanco (probably in central Chubut), that he supposed to be lower Tertiary in age, probably “Pyrothéréen.” Marshall (1982) confused Roth’s Cañadón Blanco with Simpson’s Mustersan locality of Cerro Blanco west of Colhue-Huapi (Fig. 17.1B).

After Ameghino: between Simpson and the SALMAs

For 20 years after 1906 nobody studied the “Faune Astraponotéenne.” Feruglio (1929) and Frenguelli (1930) used the term “Capas con *Astraponotus*,” but Kraglievich (1930) used “Mustersense,” and all later authors eventually accepted this name.

After the Ameghinos, George Gaylord Simpson is one of the most influential figures in the study of Patagonian Paleogene mammals. No other author has ever made such an exhaustive review of the early mammalian faunas of Argentina and South America. From 1930 to 1934 Simpson led the Scarritt Expeditions to Patagonia, making new collections from new localities and also from the classic ones of Ameghino and Roth, with accurate field notes and sketches of the geology and stratigraphy. (Curiously the first references of Simpson to the Mustersan were related to diseases or dinosaurs. Studying a pathological specimen of the Roth Collection in the Museo de La Plata from the “C. S. M.,” Simpson (1932a) said that it probably came from the *Astraponotus* beds near “El Pajarito,” west of Cerro del Humo (Fig. 17.1B). On the other hand, Simpson (1932b) disproved the occurrence of dinosaurs in the *Notostylops* and *Astraponotus* beds, which he considered as Tertiary in age.) Simpson (1933, 1940) accepted that the *Astraponotus* beds contained a distinctive fauna different from those of the “Notostylopéen” and “Pyrothéréen,” and “officialized” the use of Mustersan (also spelled Mustersian) for this Age and Stage, and suggested that it could be subdivided in minor “faunules or facies.” He proposed Musters Formation for the mammal-bearing sediments, as part of the Sarmiento Group. For Simpson (1941) the Mustersan fauna was a distinctive biostratigraphic zone, and as he supposed the Casamayoran as early Eocene, he assigned the Mustersan to the late Eocene. Some of the Mustersan exposures appear as channels cut into the underlying Casamayoran, and in

some localities it is absent between the Casamayoran and Deseadan; because of this, Simpson (1941, 1948) inferred a temporal hiatus separating the Mustersan from the Deseadan fauna. Simpson (1940, 1941) considered that the Mustersan fauna was represented at Cerro del Humo, Colhue-Huapi (Gran Barranca), Cañadón Colorado and perhaps other sites. In his study of the Roth collections from the “C. S. M.” and “Cañadón Colorado” Simpson (1936a, 1967a) found that many of the taxa were synonyms of those of Ameghino, and that other different taxa were represented in collections made by Carlos Ameghino at Colhue-Huapi Norte. Simpson (1936a) concluded that the “C. S. M.” was the same as his Cerro del Humo and also probably “Colhue-Huapi Norte,” although Carlos emphatically denied this (Simpson 1967a).

Later, Simpson (1967b) did not recognize distinct levels within the Mustersan, despite the fact that these had been mentioned by F. Ameghino, and Simpson’s own statements of 1933 and 1940. He included some taxa from “Cañadón Blanco” in the Mustersan fauna, even though they were more evolved than those from typical Mustersan levels of Cerro del Humo and Colhue-Huapi Norte. The bulk of Simpson’s Mustersan specimens come from Cerro del Humo, but some from Gran Barranca, Cerro Blanco (on the westward flank), Profile A, and the upper levels of Profile M (Simpson 1930).

Shortly after Simpson, Bordas (1943, 1945) made a good collection of Mustersan fossils at Cerro del Humo, Gran Barranca, Sierra Cuadrada, and especially at Cerro Talquino (Fig. 17.1B). Feruglio’s (1949) geological description of Patagonia did not change what was previously known for the Mustersan.

Sometime before 1946, Tomás Suero, a geologist of the national petroleum company (YPF) discovered a locality in central Chubut (El Pozón or La Gran Hondonada) (Fig. 17.1B), that proved to be extremely rich in fossil mammals. During the 1960s and early 1970s, this locality, and the nearby Laguna del Mate (Fig. 17.1B), were intensively prospected and rich collections of Mustersan mammals were made (Odreman Rivas 1978; Cladera *et al.* 2004). In their classic work about Tertiary vertebrate evolution of Argentina, Pascual and Odreman Rivas (1971) (see also Pascual 1970; Pascual *et al.* 1965) considered the Mustersan to be middle Eocene, as they regarded the “Divisaderan” as late Eocene and the Deseadan as early Oligocene (see López this book, concerning the Divisaderan fauna). Their faunal list was based almost solely on fossil mammals from Cerro del Humo, Colhue-Huapi Norte, and La Gran Hondonada. This faunal list is nearly the same as that of Simpson (1967b), and also includes a mixture of related taxa with high-crowned to brachyodont cheek teeth. Pascual and Odreman Rivas (1971, 1973) interpreted the absence of reptiles in the Mustersan as due to more temperate climates than those of the Casamayoran. They interpreted the presence

of hypsodont notoungulates as an indication of a herbaceous steppe paleoenvironment. The discontinuous distribution of Mustersan sediments and the presence of channel-beds cutting the underlying Casamayoran suggested that the low flat plains of the Casamayoran had been modified by an uplift-induced erosion event (Pascual and Odreman Rivas 1973).

The new Mustersan fossil localities of La Gran Hondonada and Laguna del Mate gradually enlarged the mammal list of this SALMA, which became more and more based on remains from these localities and Cerro del Humo. For example, in the *Stratigraphical Lexicon of the Argentine Republic* (Servicio Geológico Nacional 1976), Gran Barranca is only secondarily mentioned as an exposure for the Mustersan.

Spalletti and Mazzoni (1979) studied the stratigraphy of the Sarmiento Formation at Gran Barranca; they mention Casamayoran and Deseadan fossils, but they do not mention Mustersan ones.

Then, Marshall *et al.* (1983), in a classic synthesis of the geochronology of the mammal-bearing Tertiary of South America, tentatively assigned the Mustersan to the middle Eocene. They repeated the misunderstanding that the “*Astraponotus* fauna” was first found and recognized by specimens collected by Carlos Ameghino in his 1895–96 expedition, and suggested Gran Barranca as the type locality of the Mustersan “land-mammal age,” also because a “majority” of Ameghino’s specimens came from there.

In a biostratigraphic study of the Casamayoran, Richard Cifelli (1985) had access to Simpson’s unpublished field notes of Gran Barranca. He reported two sites with Mustersan mammals, the first in his Profile I (Simpson’s Profile A as in this book) occurs in the base of Simpson’s Channel Series, and the second in Profile V (Simpson’s Profile M as in this book) with the notohippid *?Eomorphippus pascuali* collected above and below an unconformity 20 m higher than the Channel Series of Profile V (= Profile M). The unconformity corresponds to the erosional base of Simpson’s Upper Channel Beds (Simpson 1967b) currently assigned to the Tinguirirican SALMA.

Legarreta and Uliana (1994), clearly influenced by the observations of earlier authors on the channel series of Gran Barranca, stated again that the Mustersan beds were filling channels incised in the Casamayoran, with hiatuses between the Upper Casamayoran (Barrancan) and the Deseadan. These authors considered the Mustersan to be late middle Eocene in age and referred it to the Bartonian.

Flynn and Swisher (1995) assigned the Mustersan to the interval 45–50 Ma. These authors commented on the new fauna from Tinguiririca in central Chile which eventually led to the recognition of a new interval of time, the Tinguirirican SALMA, not younger than 31.5 Ma (Wyss *et al.* 1994; Flynn *et al.* 2003). This new SALMA filled the gap between the Mustersan and the Deseadan, traditionally

filled in part by the controversial “Divisaderan” SALMA (López this book). At about the same time, restudy of the Ameghino and Roth collections led Bond *et al.* (1996, 1997) to resuscitate Ameghino’s original subdivision of the “Astraponotéen” and to recognize that many of the mammals with a higher degree of hypsodonty probably came from levels higher than those yielding the original “Astraponotéen” fauna. These higher levels could be equivalent to the upper levels of “Cañadón Blanco” and to the Tinguirirican SALMA. The revival of the “Astraponotéen le plus supérieur” and recognition of its equivalence to the Tinguirirican make clear that the supposed mixture of notoungulates with very different degrees of hypsodonty is the result of joining two different faunas from different stratigraphic levels and ages.

Gran Barranca revisited and the Mustersan site

Recently, a series of joint expeditions from Duke University and the Museo de La Plata, together with the Museo Argentino de Ciencias Naturales and Universidad de Buenos Aires, have made new collections of fossils with stratigraphic and geochronologic control. The completeness of the fossil record of Gran Barranca, together with the new geochronology, clarify the timing of the faunal succession between the Barrancan and Tinguirirican SALMAS.

In 1999, a revised geochronology at Gran Barranca using new isotopic age determinations, indicated an age for the Barrancan between 35.3 and 37.6 Ma (see Kay *et al.* 1999), that is late Eocene. This would imply that the Mustersan was late Eocene and the “Astraponotéen plus supérieur” early Oligocene. Recently, additional isotopic determinations indicate an older age for the Barrancan of 42.1–38.3 Ma, or middle Eocene (Ré *et al.* Chapter 4, this book). The Tinguirirican SALMA or “Astraponotéen plus supérieur” at Gran Barranca is present in the Vera Member (Bellosi and Madden 2005; Bellosi this book), estimated as not older than 33.3 Ma (Ré *et al.* Chapter 4, this book). Many of the taxa described by Roth from “Cañadón Blanco” that were placed in synonymy with taxa described by Ameghino from “Collhue-Huapi” (Gran Barranca?) are now in fact recorded from the Vera Member. Among them, *Eomorphippus* is very common. The Mustersan SALMA is represented in the Rosado and Lower Puesto Almendra members (Ré *et al.* Chapter 3, this book).

Unraveling systematics and provenance

The systematic history of some notoungulates illustrates the causes of the confusion concerning the Mustersan concept.

Ameghino (1901) described *Eomorphippus obscurus*, as coming from his “Couches à *Astraponotus*” without further

details as to provenance, but it is noteworthy that the original material (MACN 10917) comes from a level very rich in manganese. This taxon shows molar crowns higher than any other Mustersan toxodontid. Simpson (1967b) considered *Eomorphippus obscurus* as senior synonym of *Pseudostylops subquadratus* Ameghino 1901, *Eurystomus stehlini* Roth 1901, and *Lonkus rugei* Roth 1901. The last two taxa come from the Roth’s “Formación terciaria inferior” of Cañadón Blanco, which he said it was clearly different and younger than his “C.S.M.,” the designation for fossils that later became the most representative example of the Mustersan fauna. Because of this synonymy, Simpson (1967b) listed *Eomorphippus obscurus* in the Mustersan, disregarding the stratigraphic provenance which Roth gave for the junior synonyms *Eurystomus* and *Lonkus*. *Eomorphippus* was also found in upper levels of the putative Mustersan at Gran Barranca, in a section where the Italian geologist Egidio Feruglio (1927) had also found it (Simpson 1936b). The notohippid ?*Eomorphippus pascuali*, relatively lower-crowned than *E. obscurus* but more advanced than the reputedly ancestral notohippid *Puelia* (see below), was also found stratigraphically higher than the levels with the “typical” Mustersan fauna (Simpson 1967b; Cifelli 1985).

Ameghino (1902) described the notohippid *Interhippus deflexus* as coming from the “partie la plus supérieure des couches à *Astraponotus*.” Simpson (1967b) said that it could have been collected from the overlaying Deseadan beds, and thus he listed it with doubt in the Mustersan fauna.

Ameghino (1902) reported the Archaeohyracidae “*Archaeohyrax sulcidens*” (“*Bryanpattersonia sulcidens*”, Simpson 1967b) as coming from the “Couches à *Astraponotus*.” This species is a synonym of “*Archaeohyrax gracilis*” Roth 1903 (= *Protarchaeohyrax gracilis*: Reguero *et al.* 2003a) from his “Formación terciaria inferior” at Cañadón Blanco. As Roth considered the fossils from Cañadón Blanco to be Deseadan in age, Simpson (1967b) concluded that this fauna probably included a mixture of Casamayoran, Mustersan, and Deseadan fossils based also on Bryan Patterson’s personal communication (Simpson, 1967b).

In this way, the Mustersan became a mixed assemblage of taxa from different stratigraphic levels, notably, the higher-crowned taxa came from “Cañadón Blanco” or from geographically imprecise and stratigraphically poorly documented “Astraponotéen” levels.

Another interesting case is that of *Astraponotus*. This genus is represented by a few remains from the Mustersan beds at Gran Barranca and from other places. By contrast, *Astraponotus* is very common in the Mustersan beds at Laguna del Mate, La Gran Hondonada (Cladera *et al.* 2004), and Cerro del Humo. Whilst revising the old collections, I have observed that the type of *Astraponotus assymetrus* from Ameghino’s “Collhue-Huapi Norte” is the same

individual as a specimen collected by Roth in the “C. S. M.” (Cerro del Humo of Simpson). This demonstrates that Cerro del Humo and “Colhue-Huapi Norte” are certainly a single locality, and confirms Simpson’s suspicion (1967a).

The Mustersan fauna at Gran Barranca

Based on new collections made in the Rosado Member, Carlini *et al.* (2005a) recorded Dasypodidae: Dasypodinae: Stegotheriini, Astegotheriini (with a new species of *Stegosimpsonia*), Euphractinae: Euphractini, Eutatini (*Meteutatus* cf. *attonsus*), and also larger xenarthrans as the glyptodontoid *Machlydotherium*.

The Astrapotheria are represented by fragmentary isolated teeth of *Astraponotus assymetrus* and by the Trigonostylopidae *Trigonostylops gegembauri* (Roth 1899), very similar to and comparable in size to the larger specimens of *T. wortmanni*. The type of *T. gegembauri* comes from the Mustersan of “C. S. M.”

The Litopterna are represented by fragmentary remains, mainly isolated teeth of a medium to large brachyodont and bunodont taxon similar to *Xesmodon* and *Decaconus* (Proterotheriidae). There are also remains similar to *Lambdaconus*, a medium- to large-sized didolodontid “condylarth.” The Mustersan is the last moment in which these bunodont forms are recorded (see Gelfo this book).

The Notoungulata are represented by several groups. The Notostylopidae are represented by *Otronia muhlbergi* (described by Roth (1901) from “C. S. M.”), and the Isotemnidae (basal toxodontids) by fragmentary remains of *Periphragnis* and *Rhyphodon*, two common taxa in beds of Mustersan age.

Another Mustersan notoungulate present at Gran Barranca is *Puelia* originally described by the type species *P. plicata* Roth 1899 from “C. S. M.”. New material from the Mustersan beds at La Gran Hondonada, allowed us to refer another species to this genus, *P. coarctatus* (Fig. 17.3D) (Bond and López 1993). Both species are present in the Rosado Member. They have been considered either as notoungulates *incertae sedis*, isotemnids similar to or somehow related to the Notohippidae (Simpson 1967b), either as basal Notohippidae (Bond and López 1993) or basal Toxodontia (Shockey 1997). Whatever their phylogenetic position, these species have been recorded so far only in Mustersan beds. Their morphology is what might be expected for a structural ancestor of generalized Notohippidae such as the Tinguirirican *Eomorhippus obscurus*.

Other notoungulates recorded in the Rosado Member are Oldfieldthomasiidae, Archaeohyracidae, and notopithecine Interatheriidae. The Oldfieldthomasiidae probably pertain to the *Ultrapithecus-Tsamnichoria* group. The archaeohyracids are represented by *Pseudhyrax* sp. and *P. strangulatus*, a mesodont form, very frequent and typical of the Mustersan SALMA, also recorded in the Tinguirirican SALMA

(Croft *et al.* 2003). Notopithecine Interatheriidae is represented by *Guilielmoscottia*, typical of the Mustersan SALMA (Simpson 1967b).

The only incongruence in the Rosado fauna is the presence of an interatheriid Interatheriinae, cf. *Eopachyrucos*, which is a hypsodont taxon characteristic of the Tinguirirican SALMA (Hitz *et al.* 2003; Reguero *et al.* 2003b). If its provenance is confirmed, it will represent the oldest record of an advanced interatheriid.

Conclusions

Although Florentino Ameghino stated that the “Couches à *Astraponotus*” and the “Astraponotéen” were recognized in a section of the Gran Barranca found by Carlos Ameghino, from this review it is clear that the bulk of fossil mammals that were used to define the Mustersan SALMA came from the localities of Cerro del Humo (or Colhue-Huapi Norte), and later from Cerro Blanco, Cerro Talquino, La Gran Hondonada, and Laguna del Mate (Fig. 17.1B). The case of the holotype of *Astraponotus assymetrus* mentioned above proves that the concept of “Astraponotéen” was constructed mainly on the basis of materials coming from north of Lake Colhue-Huapi and not from Gran Barranca. As we have also seen, some of the taxa reported by Ameghino for the “Astraponotéen” which very probably came from Gran Barranca have been recognized as components of the Tinguirirican SALMA or “Astraponotéen le plus supérieure.” The recognition of the “Astraponotéen plus supérieur” or Tinguirirican fauna as distinct from those of the Mustersan, and their stratigraphic and temporal separation, allows discrimination of the more advanced higher-crowned taxa of the Tinguirirican from the lower-crowned taxa from the Mustersan and the Barrancan, and documents the transition of these faunas to more open and grass-dominated habitats.

The type locality of the Mustersan Stage/Age should be defined at Gran Barranca – the locality with the best and continuous mammal record for the middle Eocene – early Miocene – in Profile J (Bellosi this book) where the Rosado Member has both the characteristic fossils and well-defined upper and lower limits.

ACKNOWLEDGEMENTS

The authors thank the editors for the invitation to contribute with this chapter, M. Reguero and A. Kramarz for access to the collections of the Museo de La Plata and the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” respectively and information supplied, R. H. Madden for information on some aspects of the material, and M. G. Vucetich and R. F. Kay for valuable comments on the manuscript. Field research was supported by US National Science Foundation grants EAR-0087636, BCS-0090255, and DEB-9907985 to Richard F. Kay and Richard H. Madden.

REFERENCES

- Ameghino, F. 1897. Mammifères crétacés de l'Argentine: deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. *Boletín del Instituto Geográfico Argentino*, **18**, 406–521.
- Ameghino, F. 1900–02, l'Age des formations sédimentaires de Patagonia. *Anales del la Sociedad Científica Argentina*, **50**, 109–130, 145–165, 209–229; **51**, 20–39, 65–91; **52**, 189–197, 244–250; **54**, 161–180, 220–249, 283–342.
- Ameghino, F. 1901. Notices préliminaires sur de ongulés nouveaux de terrains crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba*, **16**, 349–426.
- Ameghino, F. 1902. Notice préliminaire sur des mammifères nouveaux des terrains crétacés de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba*, **17**, 5–70.
- Ameghino, F. 1904. Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina*, **56**, 193–208; **57**, 162–175, 327–341; **58**, 35–71, 182–192, 225–291.
- Ameghino, F. 1905. La faceta articular inferior única del astrágalo de algunos mamíferos no es un carácter primitivo. *Anales del Museo Nacional de Buenos Aires*, **3**, 1–64.
- Ameghino, F. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie avec un parallèle entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires*, **15**, 1–568.
- Bellosi, E. S. and R. H. Madden 2005. Estratigrafía física preliminar de las secuencias piroclásticas terrestres de la Formación Sarmiento (Eoceno-Mioceno) en la Gran Barranca, Chubut. *Actas XVI Congreso Geológico Argentino*, **4**, 427–432.
- Bond, M. and G. M. López 1993. El primer Notohippidae (Mammalia, Notoungulata) de la Formación Lumbrera (Grupo Salta) del noroeste argentino: consideraciones sobre la sistemática de la familia Notohippidae. *Ameghiniana*, **30**, 59–68.
- Bond, M., G. López, and M. A. Reguero 1996. "Astraponotéen plus supérieure" of Ameghino: another interval in the Paleogene record of South America. *Journal of Vertebrate Paleontology*, **16**(Suppl. 3), 23A.
- Bond, M., M. A. Reguero, G. M. López, A. A. Carlini, F. J. Goin, R. H. Madden, M. G. Vucetich, and R. F. Kay 1997. The "Astraponotéen plus supérieur" (Paleogene) in Patagonia. *Ameghiniana*, **34**, 533.
- Bordas, A. F. 1943. Contribución al conocimiento de las bentonitas argentinas. *Revista Minera, Geología y Mineralogía*, **14**, 1–60.
- Bordas, A. F. 1945. Geología estratigráfica de algunas zonas de Patagonia. *Anales del Museo de la Patagonia*, **1**, 139–184.
- Carlini, A. A., M. Ciancio, and G. J. Scillato-Yané 2005a. Los Xenarthra de Gran Barranca: más 20 Ma de Historia. *Actas XVI Congreso Geológico Argentino*, **4**, 419–424.
- Cifelli, R. L. 1985. Biostratigraphy of the Casamayoran, Early Eocene, of Patagonia. *American Museum Novitates*, **2820**, 1–26.
- Cione, A. L. and E. P. Tonni 1995. Chronostratigraphy and "Land-Mammal Ages" in the Cenozoic of southern South America: principles, practices and the "Uquian" problem. *Journal of Paleontology*, **69**, 135–159.
- Cladera, G., E. Ruigomez, E. Ortiz Jaureguizar, M. Bond, and G. M. López 2004. Tafonomía de La Gran Hondonada (Formación Sarmiento, edad-mamífero Mustersense, Eoceno Medio) Chubut, Argentina. *Ameghiniana*, **41**, 315–330.
- Croft, D. A., M. Bond, J. J. Flynn, M. A. Reguero, and A. R. Wyss 2003. Large archaeohyracids (Tpyotheria, Notoungulata) from Central Chile and Patagonia, including a revision of *Archaeotpyotherium*. *Fieldiana, Geology*, n.s., **49**, 1–38.
- Darwin, C. R. 1846. *Geological Observations on South America, being the Third Part of the Geology of the voyage of Beagle, under the Command of Captain Fitzroy, R. N. during the Years 1832 to 1836*. London: Smith Elder and Co.
- D'Orbigny, A. 1842. *Voyage dans l'Amérique Méridionale* vol. 3, Geologie. Paris: P. Bertrand.
- Doering, A. 1882. Geología. *Informe Oficial de la Comisión Científica Agregada al Estado Mayor General de la Expedición al Río Negro*, **3**, 299–530.
- Feruglio, E. 1929. Apuntes sobre la constitución geológica del la region del Golfo de San Jorge. *Anales de la Sociedad Argentina de Estudios Geográficos "Gaea"*, **3**, 395–486.
- Flynn, J. J. and C. C. Swisher III 1995. Chronology of the Cenozoic South American Land Mammal Ages. In Berggren, W. A., Kent, D. V., Aubry, M. P., and Hardenbol, J. (eds.), *Geochronology, Time-Scales, and Global Stratigraphic Correlation*, Special Publication no. 54. Tulsa, OK: Society for Sedimentary Geology, pp. 317–333.
- Flynn, J. J., A. R. Wyss, D. A. Croft, and R. Charrier 2003. The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal 'Age'. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 229–259.
- Frenguelli, J. 1930. Nomenclatura estratigráfica patagónica. *Anales de la Sociedad Científica de Santa Fé*, **3**, 1–117.
- Hitz, R. B., M. A. Reguero, A. R. Wyss, and J. J. Flynn 2000. New Interatheriines (Interatheriidae, Notoungulata) from the Paleogene of Central Chile and Southern Argentina. *Fieldiana, Geology*, n.s., **42**, 1–26.
- Kay, R. F., R. H. Madden, M. G. Vucetich, A. A. Carlini, M. M. Mazzoni, G. H. Ré, M. Heizler, and H. Sandeman 1999. Revised geochronology of the Casamayoran South Land-Mammal Age: climatic and biotic implications. *Proceedings of the National Academy of Sciences USA*, **96**, 13 235–13 240.
- Kraglievich, L. 1930. La Formación Friaseana del río Frías, río Fénix, Laguna Blanca, etc. y su fauna de mamíferos. *Physis*, **10**, 127–161.
- Legarreta, L. and M. A. Uliana 1994. Asociaciones de fósiles y hiatos en el Supracretácico–Neógeno de Patagonia: una perspectiva estratigráfico–secuencial. *Ameghiniana*, **31**, 257–281.

- Marshall, L. G., R. Hoffstetter, and R. Pascual 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing tertiary of south america. *Palaeovertebrata, Mémoire Extraordinaire*, 1–93.
- Odreman Rivas, O. 1978. Sobre la presencia de un Polydolopidae (Mammalia, Marsupialia) en capas de Edad Mustersense (Eoceno Medio) de Patagonia. *Obra del Centenario del Museo de La Plata*, **5**, 29–38.
- Pascual, R., E. J. Ortega Hinojosa, D. Gondar, and E. P. Tonni 1965. Las Edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio bonaerense. *Anales de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires*, **6**, 165–193.
- Pascual, R. 1970. Evolución de las comunidades, cambios faunísticos e integraciones biocenóticas de los vertebrados cenozoicos de Argentina. *Actas IV Congreso Latinoamericano de Zoología*, **2**, 991–1088.
- Pascual, R. and O. Odreman Rivas 1971. Evolución de las comunidades de los vertebrados del Terciario argentino: los aspectos paleozoogeográficos y paleoclimáticos relacionados. *Ameghiniana*, **8**, 372–421.
- Pascual, R. and O. Odreman Rivas 1973. Las unidades estratigráficas del Terciario portadoras de mamíferos, su distribución y sus relaciones con los acontecimientos diastróficos. *Actas V Congreso Geológico Argentino*, **3**, 293–338.
- Pascual, R., E. J. Ortega Hinojosa, D. Gondar, and E. P. Tonni 1966. Las Edades del Cenozoico mamalífero de la Provincia de Buenos Aires. In *Paleontografía Bonaerense Vertebrata*. Buenos Aires: Comisión de Investigaciones Científicas, vol. 4, pp. 1–27.
- Reguero, M. A., D. A. Croft, J. J. Flynn, and A. R. Wyss 2003a. Small archaeohyracids (Tyotheria, Notoungulata) from Chubut Province, Argentina, and Central Chile: implications for Trans-Andean temporal correlation. *Fieldiana, Geology*, n.s., **48**, 1–17.
- Reguero, M. A., M. Ubilla, and D. Perea 2003b. A new species of Eopachyrucos (Mammalia, Notoungulata, Interatheriidae) from the Late Oligocene of Uruguay. *Journal of Vertebrate Paleontology*, **23**, 445–457.
- Roth, S. 1899. Aviso preliminar sobre Mamíferos Mesozoicos encontrados en Patagonia. *Revista del Museo de La Plata*, **9**, 381–388.
- Roth, S. 1901. Notas sobre algunos nuevos mamíferos fósiles. *Revista del Museo de La Plata*, **10**, 251–256.
- Roth, S. 1903. Noticia preliminar sobre nuevos mamíferos fósiles del Cretáceo Superior y Terciario Inferior de la Patagonia. *Revista del Museo de La Plata*, **11**, 133–158.
- Servicio Geológico Nacional 1976. *Léxico Estratigráfico de la República Argentina*. Buenos Aires: Secretaría de Estado de Minería, Servicio Geológico Nacional.
- Shockey, B. J. 1997. Two new notoungulates (Family Notohippidae) from the Salla Beds of Bolivia (Deseadan: Late Oligocene): systematics and functional morphology. *Journal of Vertebrate Paleontology*, **17**, 584–599.
- Simpson, G. G. 1930. *Scarritt-Patagonian Exped. FieldNotes*. New York: American Museum of Natural History. (Unpublished.) Available at <http://paleo.amnh.org/notebooks/index.html>.
- Simpson, G. G. 1932a. The most ancient evidence of diseases among South American mammals. *American Museum Novitates*, **543**, 1–4.
- Simpson, G. G. 1932b. The supposed association of dinosaurs with mammals of Tertiary type in Patagonia. *American Museum Novitates*, **566**, 1–21.
- Simpson, G. G. 1933. Stratigraphic nomenclature of the early Tertiary of Patagonia. *American Museum Novitates*, **644**, 1–13.
- Simpson, G. G. 1936a. Notas sobre los mamíferos más antiguos de la Colección Roth. *Instituto del Museo de la Universidad Nacional de La Plata, Obra del Cincuentenario*, **2**, 63–94.
- Simpson, G. G. 1936b. A specimen of Pseudostylops subquadratus Ameghino. *Memoria dell' Instituto Geologico Reale Universita di Padova*, **11**, 1–12.
- Simpson, G. G. 1940. Review of the mammal-bearing Tertiary of South America. *Proceedings of the American Philosophical Society*, **83**, 649–709.
- Simpson, G. G. 1941. The Eocene of Patagonia. *American Museum Novitates*, **1120**, 1–15.
- Simpson, G. G. 1948. The beginning of the Age of Mammals in South America. I. *Bulletin of the American Museum of Natural History*, **91**, 1–232.
- Simpson, G. G. 1967a. The Ameghinos' localities for early Cenozoic mammals in Patagonia. *Bulletin of the Museum of Comparative Zoology*, **136**(4), 63–76.
- Simpson, G. G. 1967b. The beginning of the Age of Mammals in South America. II. *Bulletin of the American Museum of Natural History*, **137**, 1–259.
- Spalletti, L. A. and M. M. Mazzoni 1979. Estratigrafía de la Formación Sarmiento en la barranca sur del Lago Colhué Huapí, provincia del Chubut. *Revista de la Asociación Geológica Argentina*, **34**, 271–281.
- Wyss, A., J. J. Flynn, M. A. Norell, C. C. Swisher III, M. J. Novacek, M. C. McKenna, and R. Charrier 1994. Paleogene mammals from the Andes of Central Chile: a preliminary taxonomic, biostratigraphic, and geochronologic Assesment. *American Museum Novitates*, **3098**, 1–31.