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Original article

Biostratigraphy and biochronology of the Late Miocene of central Argentina: Evidence from rodents and taphonomy

Biostratigraphie et biochronologie du Miocène tardif de l'Argentine centrale : évidence d'après les rongeurs et la taphonomie

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Abstract

Biostratigraphy and biochronology of the Late Miocene of central Argentina is analyzed through evolutionary patterns of octodontoid rodents. The studied faunas were found in continental sediments assigned to the Cerro Azul and Saldungaray formations (La Pampa and Buenos Aires provinces, respectively). Taphonomic attributes of recovered mammals, linked mostly to the development of paleosols or to predators' activities, constraint the deposition lapse to short intervals. A biostratigraphic scheme based mainly on the anagenetic pattern of change in the octodontoid rodent lineage *Chasichimys-Xenodontomys* is proposed. Since there is no stratigraphic superposition among the studied levels, relationships among deposits are established through the polarity evidenced by the stage of evolution of chronomorphs of this lineage. Five new biozones for the Late Miocene of central Argentina are recognized. Evidence of other anagenetic sequences, and general trends of increasing hypsodonty in octodontoids, support this proposal. The results enhance the value of the "stage of evolution" concept as a correlation tool in biostratigraphic and biochronologic studies, mainly when applied through phyletic sequences.

Résumé

La biostratigraphie et la biochronologie du Miocène tardif d'Argentine centrale sont analysées à partir de l'évolution des rongeurs octodontoïdes. Les faunes étudiées proviennent de sédiments continentaux attribués aux formations Cerro Azul (province de La Pampa) et Saldungaray (Province de Buenos Aires). Les attributs taphonomiques des mammifères, liés principalement au développement des paléosols ou à l'activité des prédateurs, restreignent le temps de dépôt à des intervalles courts. Un cadre biostratigraphique basé sur le patron du changement anagénétique dans la lignée de rongeurs octodontoïdes *Chasichimys-Xenodontomys* est proposé. Comme il n'y a pas de superposition stratigraphique parmi les niveaux étudiés, les corrélations sont établies à partir de la polarité des changements mis en évidence dans les niveaux d'évolution de cette lignée. Cinq nouvelles biozones ont été reconnues pour l'intervalle Miocène tardif inférieur-Miocène terminal d'Argentine centrale. D'autres séquences anagénétiques, ainsi que la tendance générale à l'augmentation de l'hypsodontie chez les octodontoïdes, appuient cette proposition. Les résultats confortent la valeur du concept d'« état d'évolution » comme un outil de corrélation pour des études biostratigraphiques et biochronologiques, spécialement quand il est appliqué à des séquences phylétiques.

Keywords: Biostratigraphy; Biochronology; Taphonomy; Late Miocene; Argentina; Octodontoid rodents

Mots clés : Biostratigraphie ; Biochronologie ; Taphonomie ; Miocène tardif ; Argentine ; Rongeurs octodontoïdes

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1. Introduction

During the Late Miocene, important faunal turnovers associated to increasing aridity occurred worldwide (Janis, 1993). Records of these changes for southern South America are most clearly evidenced in the Pampean area of central Argentina (Vucetich et al., 1999 and literature therein). In the last 15 years we have performed studies on paleontology, taphonomy, biochronology and biostratigraphy in different Late Miocene-Pliocene outcroppings of central Argentina (e.g., Verzi et al., 1991, 1994, 1995, 2003; Goin et al., 2000; Montalvo, 2002; Deschamps, 2005). The analyzed deposits correspond to continental sediments of the Cerro Azul and Saldungaray formations (La Pampa and Buenos Aires provinces, respectively). These exposures and their faunal content belong to a sedimentary and faunistic cycle, which followed the withdrawal of a widespread marine transgression that extended from central Argentina to western Uruguay and southern Paraguay (“Mar Paranense”, see Pascual et al., 1985, 1996), or even farther north (Webb, 1995). The withdrawal of this sea would have been synchronous with a marked global sea level fall near 10 Ma (Haq et al., 1987; Verzi, 1999; Schultz et al., 2004).

The lithology of these mainly loessic postregression continental sediments in central Argentina is quite uniform, leading Fidalgo et al. (1975: 106) to group them as “Sedimentos Pampeanos”. This homogeneity has difficulted stratigraphic correlation based exclusively on geological data. As a consequence, the lithostratigraphic nomenclature is often based on the vertical (stratigraphic) or horizontal (geographic) distribution of the deposits, and not strictly on lithology (see Linares et al., 1980).

The Cerro Azul formation was assigned exclusively to the Huayquerian (Late Miocene; e.g., Montalvo and Casadío, 1988 and literature therein; Albino and Montalvo, 2006), whereas the Saldungaray formation was considered Montehermosan or even younger (Pliocene; e.g., Furque, 1967; González, 1984; Marshall et al., 1983; Verzi and Deschamps, 1996). However, recent biochronological data suggest a Chasicoan-Huayquerian age for the Cerro Azul Formation (Late Miocene; Verzi, 1999; Verzi et al., 2003, 2004b; Montalvo et al., 2005), and a Huayquerian age for the localities here studied of the Saldungaray Formation (Verzi et al., 2004b; Deschamps, 2005). In this paper, we propose a biochronology and biostratigraphy, including a biozonation, of these lithostratigraphic units. The analysis is based on taphonomy and the stage of evolution of Octodontoidea rodents, being the first attempt of this kind of analysis for southern South America. We discuss the contribution of the new scheme in the context of previous stratigraphic approaches.

2. Materials and methods

Octodontoidea rodents (Octodontidae, Echimyidae, and Abrocomidae) collected in different exposures of the Cerro Azul Formation (650 specimens) and Saldungaray Formation (22 specimens) are housed in Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, and Cátedra de Geología Histórica, Universidad Nacional del Sur, respectively. Other materials from these and other units of the Late Miocene of central Argentina deposited in Museo de La Plata, Museo Argentino de Ciencias Naturales “B. Rivadavia” (Buenos Aires) and Museo de Ciencias Naturales de Mar del Plata, were revised. The definition of biostratigraphic units, type areas and type sections follows the Código Argentino de Estratigrafía (Comité Argentino de Estratigrafía, 1992). Biostratigraphy and biochronology were mostly based on chronomorphs (sensu Martin, 1993) of the phyletic sequence of octodontid rodents *Chasichimys-Xenodontomys* (Verzi et al., 2004b). Additional systematic and evolutionary evidence of other octodontoid

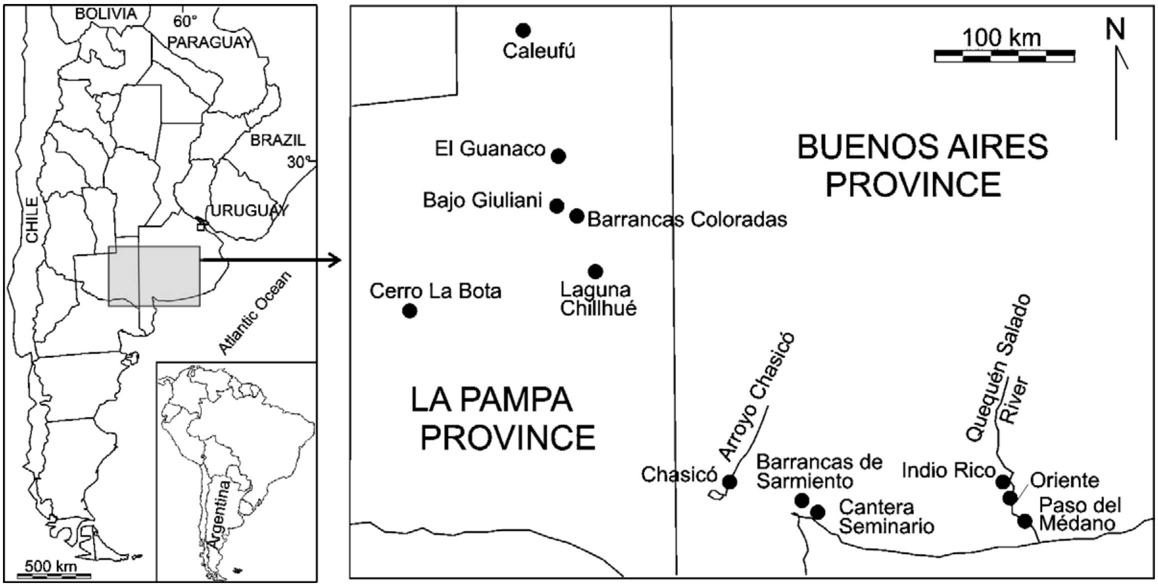

Fig. 1. Map showing localities mentioned in the text.
Fig. 1. Carte des localités décrites dans le texte.

rodents was also considered. Taphonomic attributes of recovered mammals were analyzed after Montalvo (2002).

3. Geological setting

The Cerro Azul formation is composed of massive brown reddish sandy silts, with loessic erosion (Linares et al., 1980). One upper level of calcrete (tosca) is usually present. This formation outcrops in central Argentina, mainly in eastern La Pampa province, and western Buenos Aires province (as ‘‘Epecuén Formation’’, sensu Pascual, 1961). A detailed description of the geology and stratigraphy of this formation can be seen in Linares et al. (1980) and Goin et al. (2000). In this study, the following exposures of the Cerro Azul Formation are included: Cerro La Bota, Laguna Chillhué, Bajo Giuliani, Barrancas Coloradas, El Guanaco, and Caleufú (Fig. 1). The levels exposed at Bajo Giuliani, Barrancas Coloradas, El Guanaco, and Caleufú correspond to eolian deposits with pedogenetic evidence. In Laguna Chillhué eolian and lacustrine deposits are intercalated, while Cerro La Bota represents an ephemerous fluvial event.

Exposures of the Saldungaray Formation (Furque, 1967; Deschamps, 2005) in Barrancas de Sarmiento and Cantera Seminario (Buenos Aires Province) are composed of reddish light brown silty fine sands and loessoid silts, partly friable and partly carbonated, with intercalations of paleosols and calcrete levels. Bioturbations, crotovines and escorias (impact glasses) are frequent (Deschamps et al., 1998; Verzi and Deschamps, 1996). Based on lithological evidence, González (1984) correlated Barrancas de Sarmiento with the Monte Hermoso Formation (see Zavala, 1993; Cione and Tonni, 1995a) and ‘‘Irene Formation’’ (Reig, 1955; Fidalgo et al., 1975).

We use here the original lithostratigraphic names for the Cerro Azul and Saldungaray formations because they have been formally described (Linares et al., 1980; Furque, 1967). But beyond these names, the lithologic uniformity makes the limits of these units rather confusing. In the particular case of the Cerro Azul Formation, it includes those levels described as the ‘‘Epecuén Formation’’ exposed at western Buenos Aires Province (Pascual, 1961), and it is even indistinguishable from the underlying sediments assigned to the Arroyo Chasicó Formation (Llambías in Linares et al., 1980: 107; see Goin et al., 2000).

4. Taphonomic attributes of samples

Mammal remains of all the samples show a high degree of weathering and breakage. They comprise especially mandible and maxilla fragments, isolated teeth, and postcranial bones (Fig. 2). Middle-large mammals (estimated mass over 5 kg; Montalvo, 2004b) were scarce except for xenarthran scutes. Consequently, the analysis of taphonomic attributes was focused on small-mammal remains, which were the most abundant and best preserved in all the studied assemblages (Table 1).

Articulated skeletal elements were very scarce. Breakage shows smooth surfaces, suggesting it was produced on already mineralized remains. Only a few skeletal elements show spiral fractures suggesting prior to burial breakage [Fig. 3 (6–7)]. Gnawed bones and specimens with tooth marks were found in all the assemblages, but they were only frequent in Caleufú [Fig. 3(13)] and Bajo Giuliani (Table 1). Weathering evidence prior to burial is scarce; however, weathering stages one and two of Andrews (1990) are present. Fragments of upper and

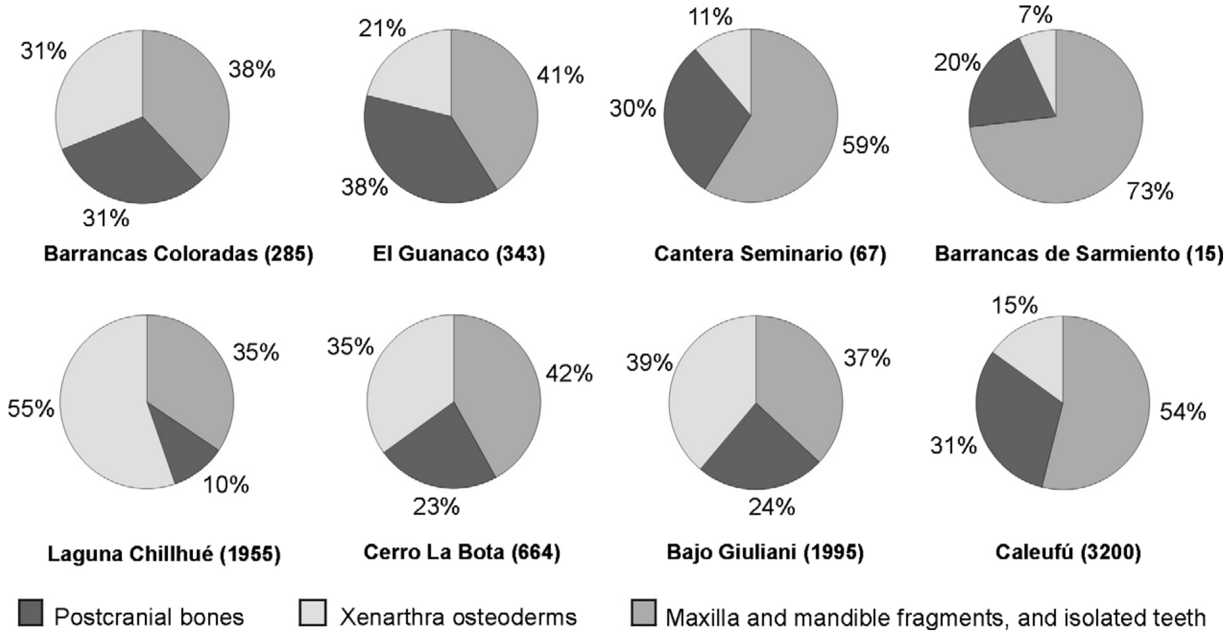

Fig. 2. Pie diagrams showing the relative frequencies (as percentages) of skeletal remains for each locality. In brackets are numbers of identifiable specimens (NISP) for each locality.

Fig. 2. Diagrammes gâteau montrant des fréquences relatives (comme pourcentages) des restes squeletaires de chaque localité. Les numéros de spécimens identifiables (NISP) de chaque localité sont entre parenthèses.

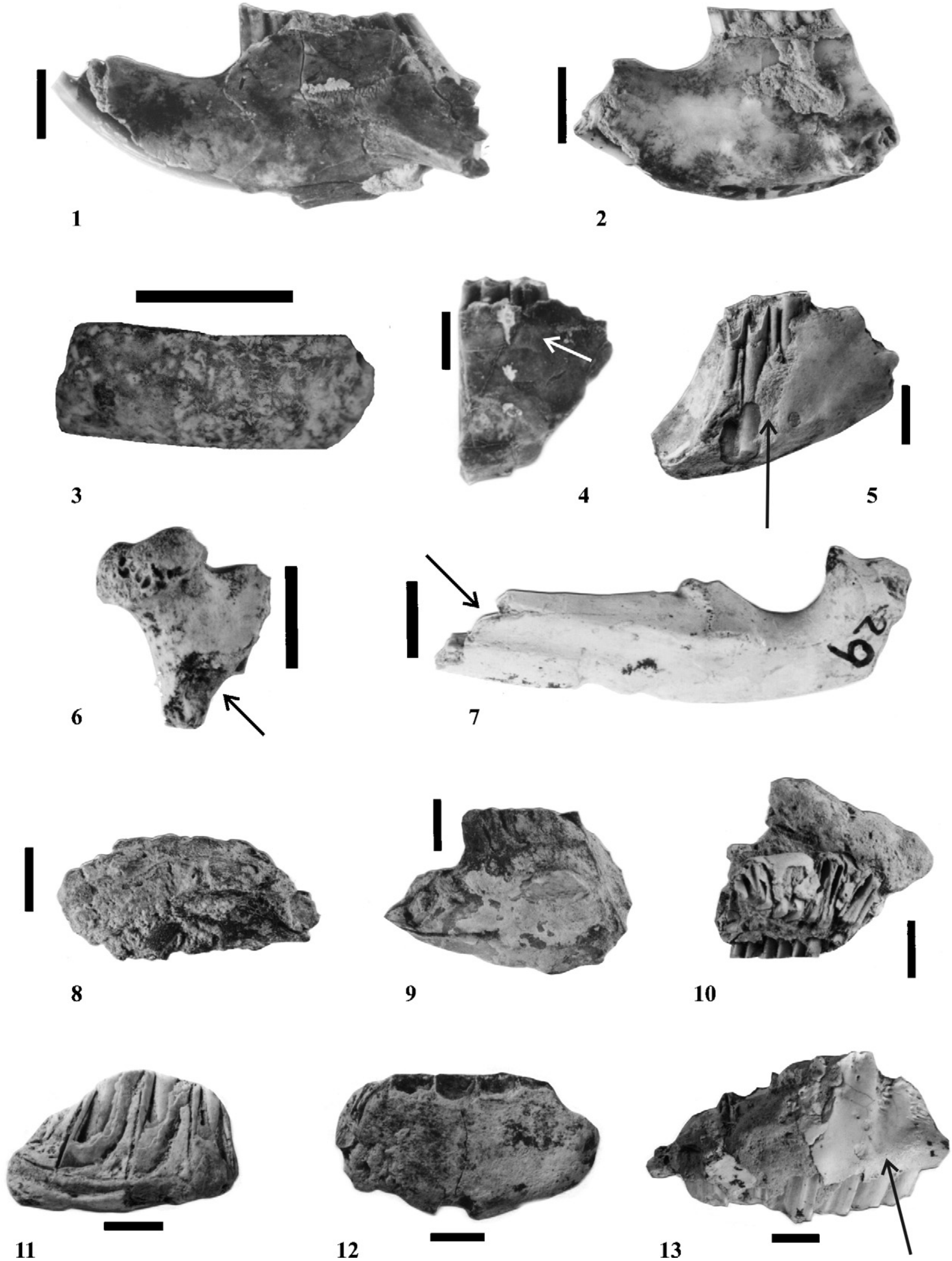

Fig. 3. Taphonomic attributes of mammal remains from Cerro Azul Formation. **1, 2**. Impregnations with manganese oxide in left mandibles of Octodontinae (1. GHUNLPam 19782; 2. GHUNLPam 21212); **3–5**. Corrosion on molar (3. GHUNLPam 5286) and mandibles (4. GHUNLPam 21419; 5. GHUNLPam 19187) of *Paedotherium minor*; **6, 7**. Spiral breakage on small-mammal bones (6. Proximal end of right femur GHUNLPam 21566/28; 7. Proximal end of left ulna GHUNLPam 19874/29); **8**. Coprolith (GHUNLPam 21516); **9**. Patina on left mandible of *Orthomyctera* sp. (GHUNLPam 21873); **10.** Calcareous concretion on a palate of *Neocavia* cf. *lozanoi* (GHUNLPam 21346); **11, 12.** Abrasion on left mandibles of *Paedotherium minor* (11. GHUNLPam 345; 12. GHUNLPam 5278); **13.** Tooth marks on a palate of *Paedotherium minor* (GHUNLPam 19209). 1, 2, 4–10, and 13, remains from Caleufú; 3, 11, 12, remains from Cerro La Bota. Scale: 5 mm.

Table 1
Taphonomic attributes of the small-mammals for each locality. Number of identifiable specimens (NISP)
Tableau 1
Attributs taphonomiques des petits mammifères de chaque localité. Numéro de specimens identifiables (NISP)

	Barrancas Coloradas	El Guanaco	Cantera Seminario	Barrancas de Sarmiento	Laguna Chillhué	Cerro La Bota	Bajo Giuliani	Caleufú
NISP	196	271	67	15	779	308	1194	2442
Skeletal articulation	≤1%	1%	≤1%	1%		≤1%	1%	4%
Breakage	82%							
Tooth or gnaw marks	≤1%					1%	2%	6%
Digestion	none						1%	3%
Abrasion	none					84%	none	1%
Corrosion	15%	1%			12%	78%	18%	27%
Manganese oxide staining	80%							
Crust development	10%	2%	5%		17%	5%	15%	
Concretions	3%	none			81%	4%	5%	85%
Rhizoliths	1%			none	1%			4%

lower jaws, teeth, carpal and tarsal bone fragments were the most abundant identifiable skeletal elements. Taphonomic features related to pedogenetic processes such as rhizoliths, corrosive marks produced by roots, acids, and microorganisms, and different degrees of stains of manganese oxides, were frequent in every assemblage [Table 1 and Fig. 3(1–4)]. Specimens with fine micrite coating were abundant [Fig. 3(9, 10)], probably related to evaporation and evapo-transpiration processes within the soil.

The fossil assemblages of Barrancas Coloradas, El Guanaco, Barrancas de Sarmiento, and Cantera Seminario were recovered from small areas in which remains were scattered with low areal density. The number of specimens collected in each association was low (Table 1) and the taxonomic representation was poor. Most skeletal elements were found disarticulated and very fragmented; mandibles, isolated teeth and some postcranial bones (metapods and phalanxes) prevail. The taphonomic analysis suggests that these associations would have resulted from attritional mortality. The remains would have been exposed during a relatively short lapse, as suggested by the low pre-burial weathering. The genesis of these associations would be restricted to the time of soil formation.

Remains from Cerro La Bota show similar taphonomic characters as those of the mentioned assemblages, but with slight to strong abrasion signs (wear and polishing) affecting already mineralized remains [Table 1 and Fig. 3(11, 12)]. They would have undergone successive accumulation, transport and burial events. However, there is no evidence of mixture, sensu Fernández-López (2000), namely assemblages formed by biological entities from different environments.

The bearing levels at Laguna Chillhué are lacustrine sediments (Montalvo et al., 1995; Goin et al., 2000), exposed in a wide area of the cliffs of a modern lagoon. Taphonomic features of remains are similar to those described for the previous localities. Specimens with attributes related to pedogenetic processes were scarce, and no abrasion evidence suggesting remain mobility was found.

Assemblages of Bajo Giuliani and Caleufú were abundant and taxonomically diverse, distributed in a small area (Montalvo, 2002). They have the pre- and post-burial attributes present in the other faunas. Additional features of the sample from Caleufú suggest that micromammals were accumulated by predators' activities (Montalvo, 2002, 2004a). A process of prey selection is suggested by the predominance of remains of a few species of small rodents and notoungulates, high percentage of juveniles, breakage pattern and tooth marks. Coprolites with strongly digested bones were found (Fig. 3(8); Montalvo, 2004a, 2004b). Although a detailed taphonomic analysis of the assemblage of Bajo Giuliani is still in progress (Montalvo, in prep.), its major features suggest a similar genesis to that of Caleufú. Both assemblages would have been formed in a very short lapse, corresponding to a period of predators' activities (Behrensmeyer and Chapman, 1993).

5. Paleontological evidence: evolution of octodontoid rodents

Most octodontoid rodents used in this analysis were found in the Cerro Azul formation, where they are highly diverse (e.g., Montalvo and Casadío, 1988; Montalvo et al., 1998; Vucetich, 1995; Verzi et al., 1994, 1995, 1999). The study of this diversity is in progress and many taxa still remain unpublished (Verzi, 2002). In this formation, the group shows an evolutionary pattern characterized by parallel trends toward increasing molar hypsodonty in different lineages. This could be studied in detail in the phyletic sequence of the octodontids *Chasichimys*-*Xenodontomys*. Both gross morphology and microstructure of molars of this lineage show patterns of change related to hypsodonty through successive chronomorphs (Verzi, 1999; Verzi et al., 2003, 2004b). Similar evolutionary patterns have also been detected in the echimyid *Reigechimys* (Verzi et al., 1994) and in the lineage of *Neophanomys*, related to *Chasichimys* (Montalvo and Verzi, 2002). In addition to the evidence of these lineages, the whole octodontoid fauna of the Cerro Azul Formation shows increasing hypsodonty. As a result of this general trend, the Echimyidae developed highly hypsodont, although always protohypsodont, morphotypes strikingly convergent with octodontids (Verzi et al., 1994).

Fig. 3. Attributs taphonomiques des restes de mammifères de la Formation Cerro Azul. **1, 2**. Imprégnations d'oxyde de manganèse aux mandibules gauches à Octodontinae (1. GHUNLPam 19782 ; 2. GHUNLPam 21212) ; **3–5**. Corrosion de la molaire (3. GHUNLPam 5286) et mandibules (4. GHUNLPam 21419 ; 5. GHUNLPam 19187) à *Paedotherium minor* ; **6, 7**. Fracture en spiral aux os des petits mammifères (6. Extrémité proximal du fémur droit GHUNLPam 21566/28 ; 7. Extrémité proximal de l'ulna gauche GHUNLPam 19874/29) ; **8**. Coprolite (GHUNLPam 21516) ; **9**. Patine de la mandibule gauche à *Orthomyctera* sp. (GHUNLPam 21873) ; **10**. Concrétion calcaire au palais de *Neocavia* cf. *lozanoi* (GHUNLPam 21346) ; **11, 12**. Abrasion des mandibules gauches à *Paedotherium minor* (11. GHUNLPam 345 ; 12. GHUNLPam 5278) ; **13**. Traces dentaires au palais à *Paedotherium minor* (GHUNLPam 19209). 1, 2, 4–10, et 13, restes provenant de Caleufú ; 3, 11, 12, restes provenant de Cerro La Bota. Échelle : 5 mm.

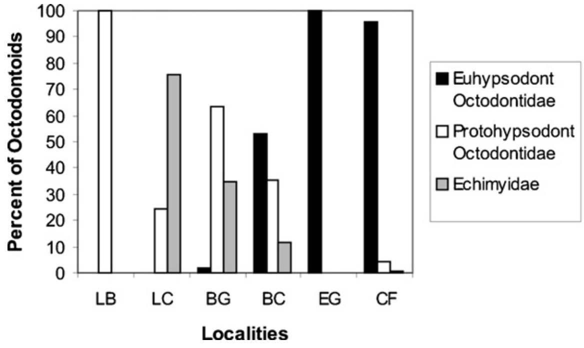

Fig. 4. Changes in the composition of the octodontoid communities from the Cerro Azul Formation (updated from Verzi, 1999). The relative abundance of each octodontoid group is expressed as percent of the total of octodontoid specimens. Protohypsodont octodontoids are represented by Octodontidae and Echimyidae; euhypsodont octodontoids are only Octodontidae. BC, Barrancas Coloradas; BG, Bajo Giuliani; CF, Caleufú; EG, El Guanaco; LB, Cerro La Bota; LC, Laguna Chillhué.

Fig. 4. Changements de la composition des communautés des octodontoïds de la Formation Cerro Azul (actualisé de Verzi, 1999). L'abondance relative de chaque group d'octodontoïds est indiquée comme pourcentage du total de spécimens d'octodontoïds. Octodontoïds protohypsodontes sont représentés par Octodontidae et Echimyidae ; octodontoïds euhypsodontes sont seulement Octodontidae. BC, Barrancas Coloradas ; BG, Bajo Giuliani ; CF, Caleufú ; EG, El Guanaco ; LB, Cerro La Bota ; LC, Laguna Chillhué.

The Octodontidae acquired rootless molars, resulting in the differentiation of the modern representatives of the subfamilies Ctenomyinae and Octodontinae (Verzi, 1999).

From the oldest exposure of the Cerro Azul formation in Cerro La Bota (Verzi, 1999) to the youngest one in Caleufú (Verzi et al., 2003, see below), Octodontidae with rootless molars increase in number while protohypsodont Octodontidae and Echimyidae decrease (Fig. 4). A slight reversion of this trend occurs in Caleufú, but this is probably due to taphonomic causes, since this locality has the highest fossiliferous richness (Fig. 2 and Table 1), the genesis of which is interpreted as an accumulation by predators' activity. This trend toward increasing hypsodonty was probably a response to increasing aridity and consequent development of open environments, such as steppes or savannas, during the Late Miocene (Verzi, 1999). Available data show the global character of this Late Miocene cooling and drying trend, which triggered the differentiation of savanna-adapted mammals in different continents (e.g., Janis, 1993; Leakey et al., 1996; MacFadden and Cerling, 1996; Pascual and Ortiz Jaureguizar, 1990).

6. Biostratigraphy of the upper Miocene in central Argentina

Since there is no stratigraphic superposition among the studied levels, the following scheme of biostratigraphic and biochronological correlation among the bearing units is based on the stage of evolution of octodontoid rodents above mentioned, as proposed by Verzi (1999) and Verzi et al. (2003, 2004b). The relationship among deposits is established especially through the polarity evidenced by the anagenetic evolutionary pattern of the *Chasichimys-Xenodontomys* lineage. The following range zones are determined, from oldest to youngest.

6.1. *Zone of* Chasichimys bonaerense

Age: Early Chasicoan (early Late Miocene).

Reference section: The type area and section is Cerro La Bota (37° 22′ S–65° 28′ W, Utracán Department, La Pampa Province, Fig. 1). The stratotype is the lower level of the Cerro Azul Formation outcropping at this locality (Fig. 5).

Characteristic assemblage: Exclusive of this zone is an undescribed octodontoid (as "*Chasichimys bonaerense*" in Pascual, 1967; see Verzi, 1999). This zone includes the first record of the dasypodids (Xenarthra) *Chasicotatus ameghinoi* and *Macrochorobates scalabrinii* (Urrutia, 2004).

Remarks: This zone is also recognized in the Vivero Member of the Arroyo Chasicó Formation (Arroyo Chasicó, Buenos Aires Province, Fig. 1), and correlates with the Zone of *Chasicotherium rothi* sensu Cione and Tonni (2001).

6.2. *Zone of* Chasichimys scagliai

Age: Late Chasicoan or Early Huayquerian? (Late Miocene, see below).

Reference section: The type area and section is Laguna Chillhué (37° 17′ S–64° 09′ W, Guatraché Department, La Pampa Province; Fig. 1), and the stratotype is recognized in the lower levels of the Cerro Azul Formation in this locality (Fig. 5).

Characteristic assemblage: The echimyid *Reigechimys plesiodon* is exclusive of this zone (Verzi et al., 1994). Also, the echimyids *Pampamys emmonsae* (Verzi et al., 1995) and *Eumysops* are first recorded. Among non-rodent mammals, the marsupial *Thylamys pinei* is recorded.

Remarks: The holotype of *C. scagliai* (=*Pattersomys scagliai* sensu Pascual, 1967) was found in the Arroyo Chasicó Formation with uncertain stratigraphic provenance (Verzi, 1999). Nevertheless, its grade of dental evolution indicates that it was very probably found in levels younger than the Vivero Member (Verzi, 1999). *Chasicotatus ameghinoi* and *Macrochorobates scalabrinii* are also recorded in this zone (Urrutia, 2004).

6.3. *Zone of* Chasichimys *morphotype a*

Age: Late Huayquerian (Late Miocene).

Reference section: The type area and section is Bajo Giuliani (36° 43′ S–64° 18′ W, Capital Department, La Pampa Province, Fig. 1). The stratotype is recognized in the levels of the Cerro Azul Formation outcropping at this locality (Fig. 5).

Characteristic assemblage: The octodontids *Palaeoctodon* aff. *simplicidens* and *Neophanomys biplicatus*, and the most hypsodont species of the echimyid *Reigechimys*, *R. octodontiformis*, are exclusive of this zone (Montalvo and Casadío, 1988; Verzi et al., 1994, 1999). The echimyid *Pampamys emmonsae* is also recorded. The exclusive marsupial taxa *Zygolestes tatei*

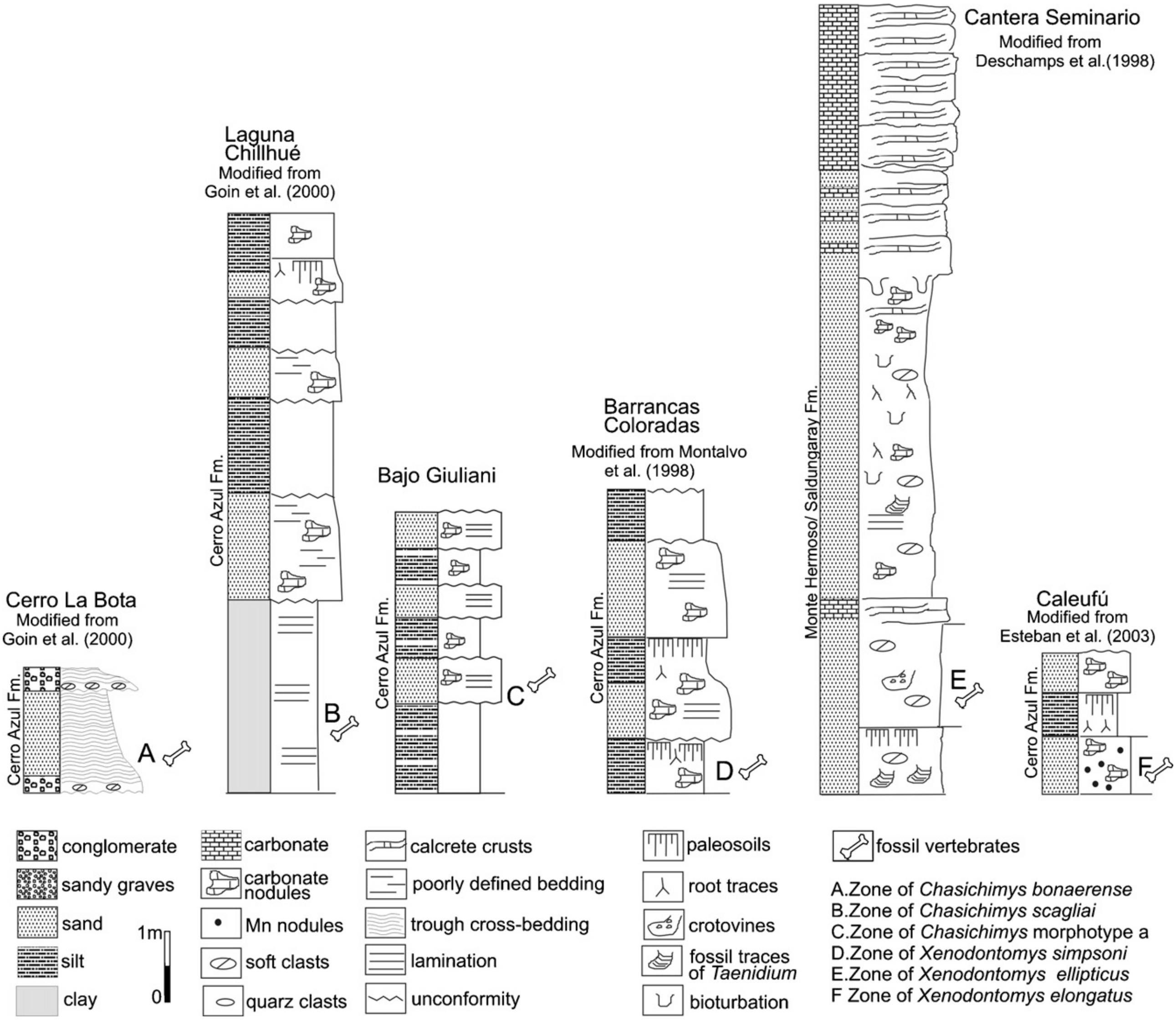

Fig. 5. Stratigraphic profiles of the localities showing the record of *Chasichimys-Xenodontomys* lineage and corresponding zones.
Fig. 5. Colonnes stratigraphiques montrant la répartition de la lignée *Chasichimys-Xenodontomys* et les biozones correspondantes.

and *Pliolestes venetus* are recorded; also *Microtragulus rusconii* and *Thylamys pinei* are present (Goin et al., 2000).

6.4. *Zone of* Xenodontomys simpsoni

Age: Late Huayquerian (Late Miocene).

Reference section: The type area and section is Barrancas Coloradas (36° 41′ S–64° 11′ W, Capital Department, La Pampa Province, Fig. 1). The stratotype is recognized in the lower levels of the Cerro Azul Formation in this locality (Fig. 5).

Characteristic assemblage: The octodontid *Phtoramys hidalguense* and the echimyid aff. *Clyomys* (Montalvo et al., 1998) are recorded. Non-rodent mammals include *Microtragulus rusconii*.

Remarks: This zone is also recognized in the lower levels of the Cerro Azul Formation at El Guanaco (36° 17′ S–64° 16′ W, La Pampa Province, Fig. 1). But the chronomorph of *X. simpsoni* recorded in El Guanaco is slightly more derived, suggesting that these bearing levels are younger than those outcropping at Barrancas Coloradas (Verzi et al., 2004a, 2004b). *Chasicotatus ameghinoi* is also recorded in this zone (Urrutia, 2004).

6.5. *Zone of* Xenodontomys ellipticus

Age: Late Huayquerian (Late Miocene).

Reference section: The type area and section is Cantera Seminario (38° 45′ S–62° 11′ W, Buenos Aires Province, Fig. 1); the stratotype is recognized in Level 2 of the Saldungaray Formation (Deschamps et al., 1998; Fig. 5).

Characteristic assemblage: The octodontid *Phtoramys* cf. *hidalguense* is recorded (Deschamps et al., 1998).

Remarks: This zone is also recognized in the lower levels of the Saldungaray formation at Barrancas de Sarmiento (Buenos Aires Province, Fig. 1), and in the ‘‘Irene Formation’’ (*partim*) outcropping at the area of Quequén Salado River (Arroyo Indio

Rico, Irene, Paso del Médano and Oriente localities; Buenos Aires Province, Fig. 1). The chronomorph of *X. ellipticus* recorded at "Irene Formation" is more derived in molar gross morphology and enamel microstructure than the specimens found at Barrancas de Sarmiento and Cantera Seminario (Verzi et al., 2004b), suggesting that the bearing levels of "Irene Formation" are younger.

6.6. *Zone of* Xenodontomys elongatus

Age: Late Huayquerian (Late Miocene).

Reference section: The type area and section is Caleufú (35° 41′ S–64° 40′W, Rancul Department, La Pampa Province, Fig. 1). The stratotype is recognized in the lower levels of the Cerro Azul Formation in this locality (Fig. 5).

Characteristic assemblage: A new chronomorph of the octodontid *Neophanomys*, more derived than *N. biplicatus*, is exclusive of this zone (Montalvo and Verzi, 2002). The octodontid *Phtoramys homogenidens*, the dasypodid *Ringueletia simpsoni*, and the holarctic immigrants to South America of the families Cricetidae and Mustelidae (Verzi and Montalvo, in prep.), are first recorded. The dasypodid *Chasicotatus ameghinoi* is last recorded (Urrutia, 2004).

Remarks: The faunistic turnover recorded in Caleufú also includes the first record of euhypsodont Octodontinae in the Pampean area.

7. Biochronology

Taphonomic results suggest that each studied assemblage supporting the proposed biozones would be reliably synchronous from a stratigraphic point of view. The genesis of the associations of Barrancas Coloradas, El Guanaco, Cerro La Bota, Barrancas de Sarmiento, and Cantera Seminario are related to the development of paleosols, which constraints their time of accumulation to a lapse of 10^3–10^4 years (Behrensmeyer and Chapman, 1993; Bown and Kraus, 1981). Analogously, the association of Laguna Chillhué would have been formed by attritional mortality but within a wider area. The assemblages of Caleufú and Bajo Giuliani would also have been formed in a very short lapse, corresponding to that of predators' activities (Behrensmeyer and Chapman, 1993). Although remains show some evidence of transport in Cerro La Bota, no faunal component contradicts contemporaneity (see Verzi, 1999).

Both the pattern of dental evolution of the *Chasichimys-Xenodontomys* lineage and other evidence of octodontoid evolution suggest chronological differences among zones. Since the Zone of *Chasichimys bonaerense* is represented in the lower Vivero Member of the type area of the Arroyo Chasicó Formation, it was assigned to the Early Chasicoan Age (Fig. 6, Verzi et al., 1999). Radiometric data constrain the Early Chasicoan Age to *ca*. 9.3 Ma (Schultz et al., 2004). According to the evolutionary grade of *Chasichimys*, the Zone of *C. scagliai* is younger than the Zone of *C. bonaerense*. However, the uncertain stratigraphic position of the holotype of *C. scagliai* in the Arroyo Chasicó area (Verzi, 1999) precludes a reliable temporal assignment within the span Late Chasicoan-Early Huayquerian sensu Cione and Tonni (2001).

The remaining zones have been interpreted as different stages of the Late Huayquerian Age (Late Miocene; Verzi, 1999; Verzi et al., 2003, 2004a, 2004b). The record of *Neophanomys biplicatus* in the Zone of *Chasichimys* morphotype a, constrains the age of these zones to *ca*. 6.02 Ma (Fig. 6; Verzi et al., 1999). In the youngest Zone of *X. elongatus*, in Caleufú, a remarkable faunal turnover is recorded. In this locality, the first holarctic immigrants to South America of the families Cricetidae and Mustelidae are present, together with a

Ma	Epoch	South-American Ages	Biozones	Type Localities	Lithostratigraphic Units	Other Octodontoids	Other taxa
5.3	Early Pliocene	Montehermosan	*Trygodon gaudry*	Monte Hermoso	Monte Hermoso Fm		
	Late Miocene	Late Huayquerian	*Xenodontomys elongatus*	Caleufú	Cerro Azul Fm	*Neophanomys* nov. *Phtoramys homogenidens*	*Ringueletia simpsoni* *Chasicotatus ameghinoi* Muridae Mustelidae
			Xenodontomys ellipticus	Cantera Seminario	Saldungaray Fm	*Phtoramys cf. hidalguense*	
			Xenodontomys simpsoni	Barrancas Coloradas	Cerro Azul Fm	*Phtoramys hidalguense* *aff. Clyomys*	*Microtragulus rusconii* *Chasicotatus ameghinoi*
? 6.02			*Chasichimys* morphotype a	Bajo Giuliani		*Reigechimys octodontiformis* *Neophanomys biplicatus* *Palaeoctodon aff. simplicidens* *Pampamys emmonsae*	*Pliolestes venetus* *Zygolestes tatei* *Thylamys pinei* *Microtragulus rusconii*
		?	*Chasichimys scagliai*	Laguna Chillhué		*Reigechimys plesiodon* *Pampamys emmonsae* *Eumysops*	*Thylamys pinei* *Chasicotatus ameghinoi* *Macrochorobates scalabrinii*
9.3		Early Chasicoan	*Chasichimys bonaerense*	Cerro La Bota			*Chasicotatus ameghinoi* *Macrochorobates scalabrinii*

Fig. 6. Stratigraphic chart of the Late Miocene of central Argentina (chronology not in scale).

Fig. 6. Tableau stratigraphique du Miocène tardif de l'Argentine centrale (la chronologie n'est pas à l'échelle).

sudden and massive record of euhypsodont octodontines previously restricted to western Argentina (Verzi and Montalvo, in prep.). We suggest that this turnover could be coeval with the glacial event detected for the latest Miocene, both at global (*ca.* 5.7–5.8 Ma, Opdyke, 1995) and regional (> 5.04, Ton-That et al., 1999) scale. Accordingly, the presence in Caleufú of some species (e.g., the octodontoid *Phtoramys homogenidens*) shared with the fauna of Montehermosan Age (Early Pliocene; Zone of *Trigodon gaudryi* sensu Cione and Tonni, 1995a) supports a latest Huayquerian Age, near the Mio-Pliocene boundary (*ca.* 5.3; Berggren et al., 1995), for the mentioned zone.

The correlation and age of the ''Irene Formation'', where the Zone of *X. ellipticus* is recorded, is still uncertain. So far, this ''formation'' has been assigned to the Montehermosan (Early Pliocene) and/or Chapadmalalan (Early-Middle Pliocene; see review in Goin et al., 1994). Goin et al. (1994: 19) assigned the fauna of this formation to the Lower Chapadmalalan (sensu Cione and Tonni, 1995b; Early Pliocene); but these authors pointed that: "El análisis preliminar de los vertebrados en la ''Formación'' Irene resulta ambiguo en términos de correlación." We believe that in view of the wide distribution along the Quequén Salado river and the thickness of the river bank deposits, probably more than one stage/age may be represented in this formation. According to our results (Verzi et al., 2003), at least the levels bearing *X. ellipticus* in Irene, Arroyo Indio Rico, Paso del Médano and Oriente localities, belong to the Late Huayquerian (Late Miocene).

8. Discussion

In the standard of the South American stages/ages, the span between the Chasicoan and Montehermosan, is known traditionally as Huayquerian. But the faunas of the Huayquerian stratotype, in the Huayquerías de San Carlos (Mendoza province, western Argentina), are poorly known. In spite of this, we keep the term ''Huayquerian'', commonly used in South American stratigraphy and chronology, to designate the latest Miocene. Currently, the best represented fauna of this age in southern South America is that of central Argentina. Particularly the mammal faunas of the Cerro Azul Formation, including those of the ''Epecuén Formation'' (Goin et al., 2000), have been traditionally considered as Huayquerian in age (e.g., Pascual and Bocchino, 1963; Ortega Hinojosa, 1967; Pascual and Bondesio, 1982; Montalvo and Casadío, 1988; Verzi et al., 1991, 1994, 1995; Goin et al., 2000; Cione and Tonni, 2001). However, according to the evidence of the octodontoids, the Cerro Azul Formation also includes the Early Chasicoan, represented by the Zone of *Chasichimys bonaerense*. This zone correlates with the Zone of *Chasicotherium rothi* proposed by Cione and Tonni (2001), as the base for the Lower Chasicoan substage. The scarce and poorly known record of the octodontoid fauna of the Arroyo Chasicó Formation precludes correlation of the other zones here proposed with the zones of *Chasicotatus ameghinoi* and *Macrochorobates scalabrinii* proposed by Cione and Tonni (2001) for the upper levels of the Chasicó area. Moreover, both dasypodid species that give name to these zones representing the Upper Chasicoan and Lower Huayquerian substages, respectively, have a wide stratigraphic distribution in the Cerro Azul Formation (Fig. 6). In our scheme, both *M. scalabrinii* and *C. ameghinoi* appear together in the Zone of *C. bonaerense* of Early Chasicoan age, these being their oldest records. Both taxa are also recorded in the Zone of *C. scagliai*. *Chasicotatus ameghinoi* is recorded also in the zones of *X. simpsoni* and *X. elongatus*. This suggests that the record of these dasypodids in the Chasicó area is biased.

According to the above mentioned biochronologic and radiometric evidence, the zones of *Chasichimys* morphotype a to *X. elongatus* represent successive episodes of the Late Huayquerian, but probably only partially comparable with the Upper Huayquerian substage sensu Cione and Tonni (2001).

In view of these results, the sequence *Chasichimys-Xenodontomys* seems to be a valuable correlation tool for the Late Miocene of central Argentina. Lindsay (1990) revised the usefulness of the ''stage of evolution'' as strategy for assigning an age to mammal faunas. Our results support particularly the value of the concept of ''stage of evolution'' in phyletic sequences of increasing hypsodonty. The non-reversible nature, namely unequivocal polarity, of such sequences implies a valuable attribute as correlation tool when there is no stratigraphic superposition of the bearing levels. However, given that preservation and detection of these sequences is frequently limited by taphonomic causes, even in these cases the most common strategy is the analysis of changes in whole faunas. Nevertheless, faunal turnovers (Vrba, 1992) used in biostratigraphic and biochronologic studies include speciation, migration and extinction events. Such events lack unequivocal polarity, so the assessment of the ''stage of evolution'' in these cases may not be clear (see discussion in Cione and Tonni, 1995c). As stated by Lindsay (1990), efforts should be focused on analyses of ''stage of evolution'' in several taxa. Even in such cases, the non-reversible grades of phyletic sequences (anagenetic patterns) provide reliability to correlation analyses.

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