

MINERALOGY, GEOCHEMISTRY AND PALEOHISTOLOGY OF PLIOCENE MAMMALS FROM THE MONTE HERMOSO FORMATION (ARGENTINA). *PAEDOTHERIUM BONAERENSE* (NOTOUNGULATA, HEGETOTHERIIDAE) AS A CASE STUDY



RODRIGO L. TOMASSINI¹, CLAUDIA I. MONTALVO², TERESA MANERA³ AND GRACIELA VISCONTI²

¹INGEOSUR-CONICET. Departamento de Geología, Universidad Nacional del Sur, San Juan 670, B8000ICN Bahía Blanca, Buenos Aires, Argentina.

rodrigo.tomassini@yahoo.com.ar

²Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Av. Uruguay 151, L6300CLB Santa Rosa, La Pampa, Argentina.

cmontalvo@exactas.unlpam.edu.ar; gvisconti@exactas.unlpam.edu.ar

³INGEOSUR, San Juan 670, 8000 Bahía Blanca, Buenos Aires, Argentina. *tmanera@criba.edu.ar*

Abstract. We describe and analyze the mineralogical, geochemical and paleohistological characteristics present in hemimandibles of *Paedotherium bonaerense* (Ameghino) (Mammalia, Notoungulata, Hegetotheriidae). Remains were recovered from floodplain deposits of the Monte Hermoso Formation (early Pliocene). Francolite is the main mineral component in all hemimandibles, evidencing compositional changes in the internal crystalline structure during fossil-diagenesis. The similarity in the chemical composition of the fossils and the hosting rocks suggests that the enrichment of the remains with new elements was due to direct exchange with the sediments in which they were buried. Original bone microstructure shows good preservation, only affected by permineralization and microfissures. Manganese and iron oxides are the most abundant minerals infilling microstructural features and microfissures. The dark color identified on the outer surface of some remains is related to precipitation of manganese oxides. The results obtained allow us to establish the processes affecting the remains before and after burial, and thus interpret the different taphonomic histories. This work provides new information on a issue usually not considered in studies on vertebrate communities from the South American Neogene and at the same time it establishes a framework for the analysis of assemblages with similar characteristics.

Key words. Taphonomy. Mammals. *Paedotherium bonaerense*. Pliocene. Argentina.

Resumen. MINERALOGÍA, GEOQUÍMICA Y PALEOHISTOLOGÍA DE MAMÍFEROS PLIOCENOS DE LA FORMACIÓN MONTE HERMOSO (ARGENTINA). *PAEDOTHERIUM BONAERENSE* (NOTOUNGULATA, HEGETOTHERIIDAE) COMO CASO DE ESTUDIO. En la presente contribución se describen y analizan las características mineralógicas, geoquímicas y paleohistológicas presentes en hemimandíbulas de *Paedotherium bonaerense* (Ameghino) (Mammalia, Notoungulata, Hegetotheriidae), procedentes de los depósitos de llanura de inundación de la Formación Monte Hermoso (Plioceno temprano). En todos los ejemplares la francolita constituye el componente mineral principal, reflejando cambios composicionales en la estructura interna cristalina durante la fosildiagenésis. Las similitudes entre la composición química de los fósiles y de la roca hospedante indicarían que el enriquecimiento de los restos con nuevos elementos se produjo por un intercambio directo con los sedimentos donde los mismos fueron enterrados. La microestructura ósea original muestra una preservación muy buena, únicamente afectada por permineralización y el desarrollo de microfisuras. El relleno de los elementos microestructurales y de las microfisuras comprende principalmente óxidos de hierro y manganeso. La coloración oscura identificada en la superficie externa de algunos materiales está vinculada a la precipitación de óxidos de manganeso. Las observaciones realizadas permitieron establecer los procesos que afectaron a los restos tanto antes como después de su enterramiento y, a partir de ello, interpretar las diferentes historias tafonómicas. Este trabajo brinda información novedosa sobre una temática poco considerada en los estudios de las comunidades faunísticas de vertebrados del Neógeno de Sudamérica y, por otra parte, sirve como marco de referencia para el análisis de asociaciones con características similares.

Palabras clave. Tafonomía. Mamíferos. *Paedotherium bonaerense*. Plioceno. Argentina.

VERTEBRATE bones are composed by an organic phase mostly including collagen and lipids, and an inorganic phase mainly composed by hydroxyapatite [Ca₁₀(PO₄)₆(2OH)] (Lyman, 1994; Elorza *et al.*, 1999). As the bone microstructure is often preserved after death, the analysis of the microstructural features allows the interpretation of (1) aspects related to the

biology of organisms (Botha and Chinsamy-Turan, 2004; Chinsamy-Turan, 2005), and (2) processes that affected the remains (*e.g.*, replacement, permineralization, dissolution) along their taphonomic history (Cuezva and Élez, 2000; Pfretzschner, 2000).

The original mineralogical and geochemical composition

of skeletal elements is modified after death of the organism. In this sense, the enrichment with new chemical elements may be produced by (1) isomorphic replacements due to ionic substitutions in the crystalline structure; (2) precipitation of new mineral components in the cracks and bone voids, caused by loss of organic matter, due to fluids circulating in the host rocks; and (3) mineral accumulation by mechanical processes in pores and cracks, as a consequence of sediment compaction (Merino and Morales, 2006; Luque *et al.*, 2009).

These modifications depend on diverse factors. Some are intrinsic and referring to the properties of skeletal elements (*e.g.*, taxonomic group, size, bone density, integrity, porosity, molecular and chemical structure). Others are extrinsic and include pH and Eh conditions of the preserving environment, chemical characteristics of groundwater, inorganic components of host sediments, and the activity of bacteria and other microorganisms (Lyman, 1994; Luque *et al.*, 2009).

Work related to the evaluation of paleohistological, mineralogical and geochemical features of vertebrate fossil remains has increased notably over the past few decades. Such studies are a complementary tool to traditional taphonomic analyses. They allow interpretations on aspects related to the characteristics of the depositional environments and chemical con-

ditions of the host sediments and the circulating groundwater, among others (*e.g.*, Berreteaga *et al.*, 2004; Tütken *et al.*, 2008; Luque *et al.*, 2009; Pfretzschner and Tütken, 2011).

The Neogene fossil sites of the Pampean Region (Argentina) are characterized by their abundant and diverse remains of vertebrates, which favored the development of numerous detailed systematic and biochronostratigraphic studies (*e.g.* Cione and Tonni, 2005; Verzi *et al.*, 2008; Deschamps *et al.*, 2012; Tomassini *et al.*, 2013). Taphonomic studies involving these remains are still scarce (*e.g.*, Montalvo, 2004; Montalvo *et al.*, 2008; Tomassini, 2012; Tomassini and Montalvo, 2013). The main goal of this paper is to describe and interpret the mineralogical, geochemical and paleohistological features observed in fossils assigned to *Paedotherium bonaerense* (Ameghino, 1887) (Notoungulata, Hegetotheriidae) and collected in the fluvial deposits of the Monte Hermoso Formation (early Pliocene). This study allows to understand the changes that affected the remains before and after their burial, as well as the paleoenvironmental conditions under which these materials may have been preserved. The results can be extrapolated to other remains of the faunal assemblage recovered from the same beds, particularly those of micro-mammals.

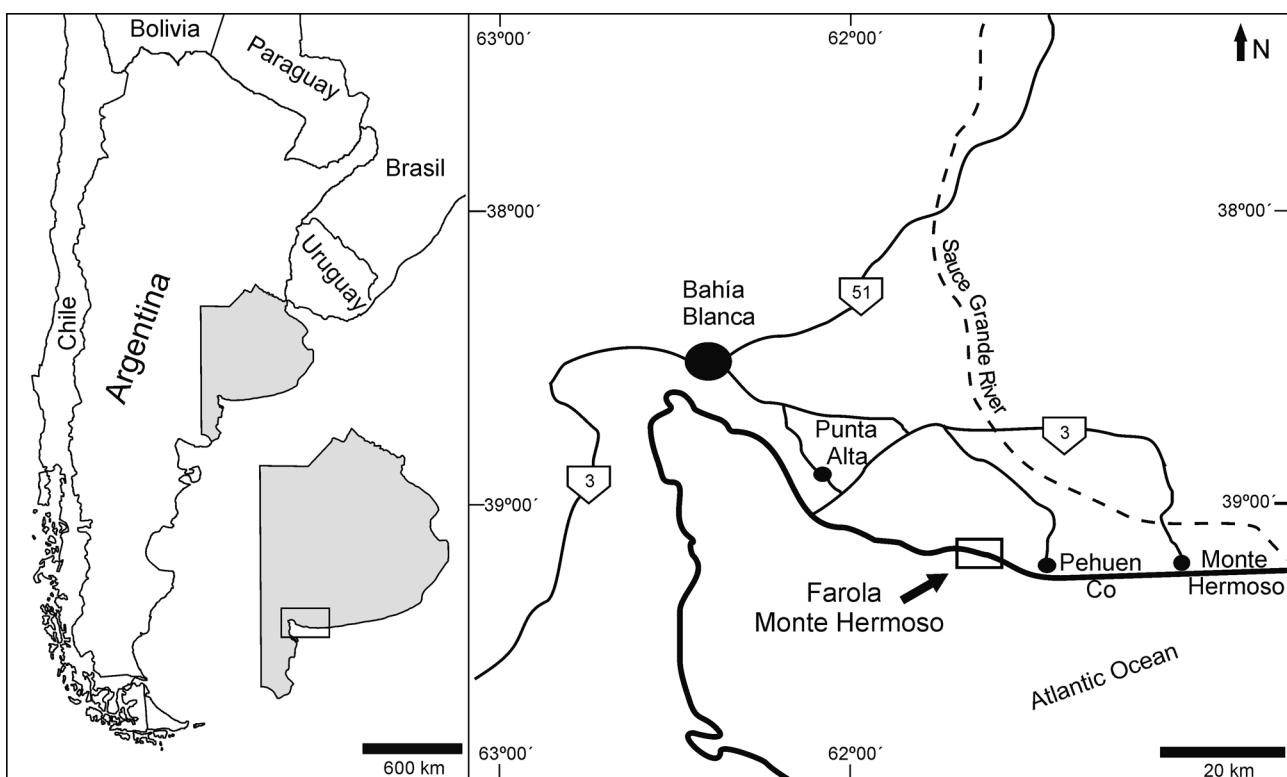


Figure 1. Location map showing Farola Monte Hermoso locality.

GEOGRAPHIC AND STRATIGRAPHIC SETTING

Farola Monte Hermoso ($38^{\circ} 58' 01''S$; $61^{\circ} 41' 43''W$) type locality of the Monte Hermoso Formation (Zavala, 1993)– is located on the Atlantic coast, 53 km SE from the city of Bahía Blanca, Buenos Aires Province, Argentina (Fig. 1). According to Zavala and Navarro (1993), the sediments originating the rocks assigned to this formation were accumulated in a dynamic fluvial environment of high-sinuosity rivers similar to those proposed by Miall (1985) as “muddy fine-grained rivers”. These authors recognized architectural elements of channels, lateral accretion deposits, and overbank deposits.

The hemimandibles studied in this work were recovered from a bed of silty mudstone, with colors ranging from reddish brown to yellowish brown (Fig. 2). This deposit shows a massive structure in the middle and upper portions, while the lower one is very finely laminated. Evidence of bioturbation by root activity was identified, particularly in the middle and upper portion. Remains of Osteichthyes, Aves, Amphibia, Reptilia and Mammalia are very abundant in this bed. In addition, coprolites produced by carnivore mammals, burrows produced by micro- and macromammals, fossil footprints of xenarthrans and invertebrates traces (e.g. *Taenidium* Heer 1877, *Beaconites* Vialov, 1962, *Skolithos* Haldeman, 1840) were also recorded in this level (Tomassini, 2012; Tomassini *et al.*, 2013).

The bed from which the analyzed material comes represents floodplain deposits originated from the settling of suspension material provided by the channel during flooding events (Tomassini, 2012; Tomassini and Montalvo, 2013). Lithology, sedimentary structures, vertebrate remains and fossil traces allow correlating this bed with facies Fl defined by Zavala and Navarro (1993) for the overbank deposits. On the basis of taphonomic features and sedimentary context in which the remains were preserved, Tomassini and Montalvo (2013) recognized a floodplain taphonomic mode (*sensu* Behrensmeyer, 1988) for these deposits. This taphonomic mode includes an assemblage mainly composed by re-sedimented remains, corresponding to different contexts (terrestrial and aquatic). The exposure time of the remains on the surface was relatively short and the burial occurred gradually. During this period, the remains were scarcely affected by destructive processes such as weathering, abrasion activity of predator/scavengers and trampling, among others. After burial, the remains were modified by mineralogical and geo-

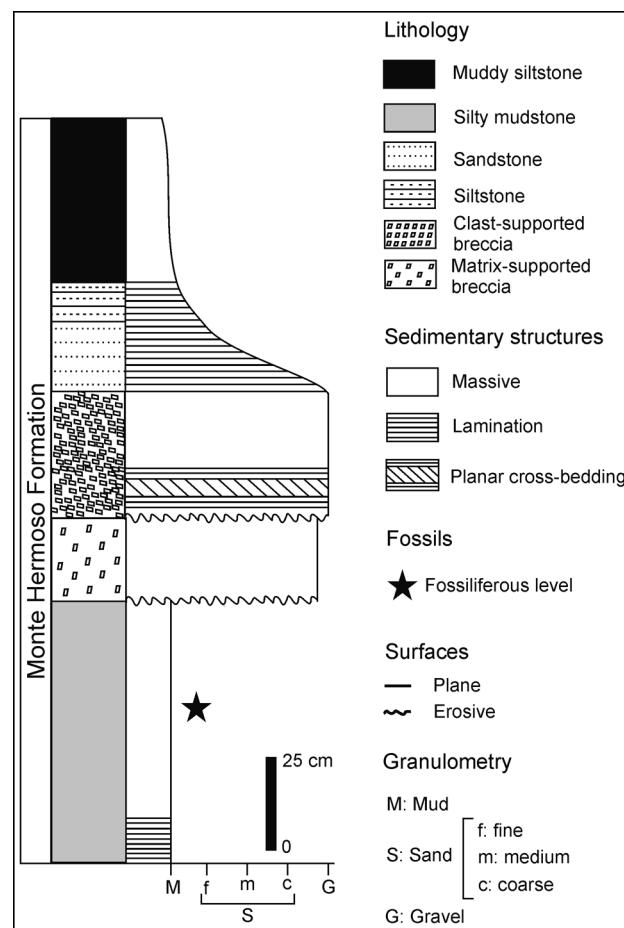


Figure 2. Stratigraphic section of the Monte Hermoso Formation. Modified from Tomassini (2012).

chemical changes and by bioerosion and corrosion processes.

From a biostratigraphic point of view –according to the scheme proposed by Cione and Tonni (2005)– two temporally successive biozones are represented in the Monte Hermoso Formation. The *Trigodon gaudryi* Biozone (late Miocene–early Pliocene) comprises the lower and middle levels of this formation and represents the basis for the Montehermosan Stage/Age. This biozone includes the bed bearing the analyzed fossils. The *Neocavia depressidens* Biozone (early Pliocene) comprises the upper levels of this formation and represents the basis for the lower Chapadmalalan Stage/Age. However, Tomassini *et al.* (2013) indicated that the faunal variations between the different levels of this formation are minimal and do not reflect significant chronological differences. Thus a subdivision into two different biostratigraphic units is not be justified. On this basis, these authors proposed a new scheme for the Monte Hermoso Formation, with the recognition of a single biostratigraphic unit, the *Eumysops laeviplicatus* Range

Zone (early Pliocene). This unit, comprising the whole thickness of the formation, corresponds to the early Pliocene and constitutes the basis for the Montehermosan Stage/Age.

MATERIALS AND METHODS

Mineralogical, geochemical and paleohistological analyses were performed in nine hemimandibles of the hegetotheriine notoungulate *P. bonaerense*. All of them were found in the floodplain deposits of the Monte Hermoso Formation. We chose to select the hemimandibles of this taxon as case study because they are very abundant in this unit and because they have a preservation pattern similar to that of most fossils from the same bed.

The study included only the evaluation of the bone component itself, not considering the components of the teeth (enamel, dentine and cement). To discard possible biases related to taxonomic and ontogenetic aspects, only adult specimens were selected. Additionally, other taphonomic attributes such as weathering, abrasion, disarticulation, corrosion, bioerosion and type of fracture were also analyzed. The color of the outer surface was determined following the Rock Color Chart (Goddard *et al.*, 1948). One of the most evident macroscopic attributes that distinguishes most of the materials from the Monte Hermoso Formation is the partially or totally black color of their outer surface (Tomassini, 2012). We analyzed three light brown (5YR 6/4) specimens, three totally black (N1), and three light brown (5YR 6/4) with black spots (N1) variable in size and intensity and with dendrite habit in some sectors.

The main mineral components of the host rocks were identified with a Leica MS 5 binocular light microscope. Mineralogy of fossils was determined through analysis of X-ray diffraction using a Rigaku D-Max III-C diffractometer,

at the Departamento de Geología, Universidad Nacional del Sur (UNS). The elemental chemical composition –both of fossils and host rocks– was determined through EDX (Energy Dispersive X-ray) analysis using an EDAX, DX-4. This analysis was performed in different sectors of the samples. Some specimens were photographed using a JEOL 35 CF SEM scanning electron microscope. Both equipments belong to the Unidad de Administración Territorial del Centro Científico y Tecnológico CONICET Bahía Blanca (CCT-CONICET-BB).

Thin transverse and longitudinal sections of all hemimandibles were made at the second molar (m_2) level, in order to assess the preservation of the original bone microstructure and mineralogical features. These sections were made at the Laboratorio de Petrotomía of the INGEOSUR (CONICET), Departamento de Geología, Universidad Nacional del Sur (UNS), following the methodology suggested by Tomassini (2012), and were analyzed under a Nikon Eclipse E400 POL petrographic polarizing microscope.

All the materials and thin sections are housed in the collection of the Museo Municipal de Ciencias Naturales “Carlos Darwin”, Punta Alta (Buenos Aires Province), under the acronym MD-FM.

RESULTS

The hemimandibles of *P. bonaerense* were isolated and disarticulated (*sensu* Behrensmeyer, 1991). Six specimens presented no evidence of weathering (stage 0 of Andrews, 1990); however, the other three showed slight splitting of bones, chipping of teeth and splitting of dentine (stage 1 of Andrews, 1990). No signs of abrasion were recognized (category 1 of Alcalá, 1994). All the remains showed some degree of breakage affecting mainly the portion of the ascendant ramus. Al-



Figure 3. Color variations of the outer surface of the hemimandibles of *Paedotherium bonaerense*; **1**, MD-FM 05-138, light brown; **2**, MD-FM 13-59, black; **3**, MD-FM 13-38, light brown with black spots. Scale bar= 2 cm.

though the fractures were mainly stepped, with an irregular fracture surface, two specimens showed smooth perpendicular fractures (Marshall, 1989). Corrosion marks (*e.g.*, degradation and partial dissolution of the outer bone layer) and traces produced by root growth assigned to the *Corrosichnia* ethological category (Mikuláš, 1999) were also identified.

As stated above, concerning the color of the remains, we analyzed three light brown specimens, three black, and three light brown with black spots (Fig. 3.1–3). In some remains the dark color was superimposed to the traces produced by roots (Fig. 4.1), whereas in others the dark color was altered by posterior corrosion processes (Fig. 4.2).

Studies using X-ray diffraction revealed that francolite [$\text{Ca}_5(\text{PO}_4\text{CO}_3)_3(\text{F}, \text{OH})$] was the main mineral component of the materials (Fig. 5). Besides, EDX analysis corroborated the phosphate-calcite composition of the remains, on the basis of the identification of P and Ca (Fig. 6.1–3). In all cases F, C, O, Na, Mg, Al, Si and K (the last seven not plotted in the diagrams) were also recorded. Iron (Fe) was only detected in two light brown specimens (Fig. 6.1). Manganese (Mn) was

identified in all specimens either black or light brown with black spots (Fig. 6. 2–3). In the former, Mn was detected in all sectors of the sample whereas in the latter it was detected mainly in the areas with spots. On the contrary, as shown in Figure 6.1, this element was absent in all analyzed sectors of the outer surface of the light brown specimens.

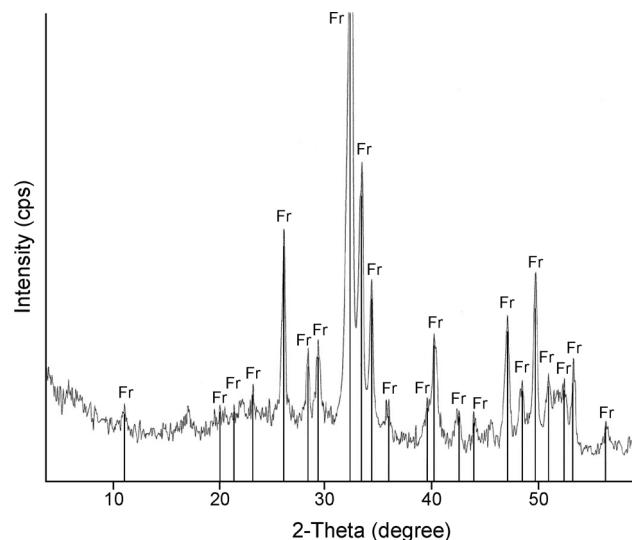


Figure 5. X-ray diffractogram of a hemimandible of *Paedotherium bonaerense* showing the francolite (Fr) peaks.

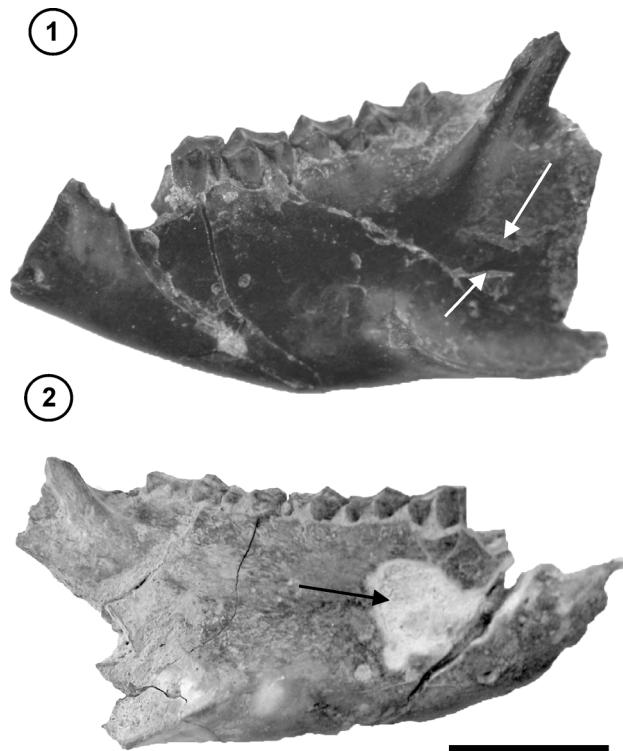


Figure 4. Taphonomic modifications of the hemimandibles of *Paedotherium bonaerense*; **1**, MD-FM-13-44, dark color superimposed on traces produced by roots growth; **2**, MD-FM 13-48, alteration of the dark color by effects of corrosion. Scale bar= 2 cm.

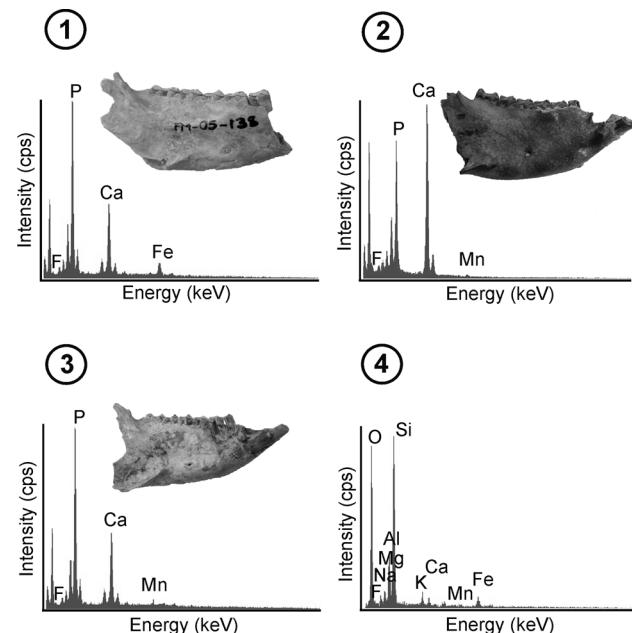


Figure 6. Elemental chemical composition of the hemimandibles of *Paedotherium bonaerense* and the host rock; **1**, light brown specimen, the presence of Fe stands out; **2**, black specimen, the presence of Mn stands out; **3**, light brown with black spots specimen, the presence of Mn stands out; **4**, sample of host rock.

Main mineral components of the host rocks include quartz, plagioclase, biotite, iron and manganese oxides, amphibole, pyroxene and volcanic ash. Except for P, in the EDX analysis of the rocks the same chemical elements of the hemimandibles were identified (Fig. 6.4).

In the thin sections, the microstructural features of these skeletal elements were recognized (Fawcett, 1995; Paniagua, 1996). In this sense, we identified a cortical bone tissue with presence of trabeculae (Fig. 7.1–3).

Primary osteons were recognized. In all cases these osteons showed their typical constitution, which includes a vascular canal surrounded by concentric bone lamella with a centripetal disposition. Other vascular canals, without concentric bone lamellae were also present (Fig. 7.2–4). In both cases lenticular or fusiform osteocyte lacunae were identified (Fig. 7.2–4). With high magnification it was possible to see the thin and branched canaliculi that communicate these osteocyte lacunae. In some sectors, oblique or transverse canals were recognized, traversing the lamellae of the osteons and connecting to each other the vascular canals previously men-

tioned. These were interpreted as Volkmann canals (Fig. 7.2–4). Other variably sized cavities, quite larger than the described vascular canals, were interpreted as canals for the passage of larger vessels (Fig. 7.3).

The small cavities interpreted as vascular canals, osteocyte lacunae and canaliculi were infilled mainly with manganese oxides, and in a lower proportion with iron oxides (Figs. 7.4, 8). In all samples, most cavities were completely full. In those cases with partial infilling, this was covering the margins of the cavities (Figs. 7.4, 8). On the other hand, in the larger cavities interpreted as canals for large vessels the infilling was composed of a muddy clastic material with crystals of quartz, plagioclase, iron and manganese oxides, calcite and volcanic ash, among others (Fig. 7.3). The composition of this infilling was similar to that of the host rocks. Finally, this type of infilling was also recognized in the spaces of the alveolar cavities, between the hemimandible itself and the teeth (Fig. 7.3).

In 75% of the thin sections, microfissures were observed. These were mainly on the lower portion of the hemimandible and had variable direction and width (Fig. 7.5). Most of them

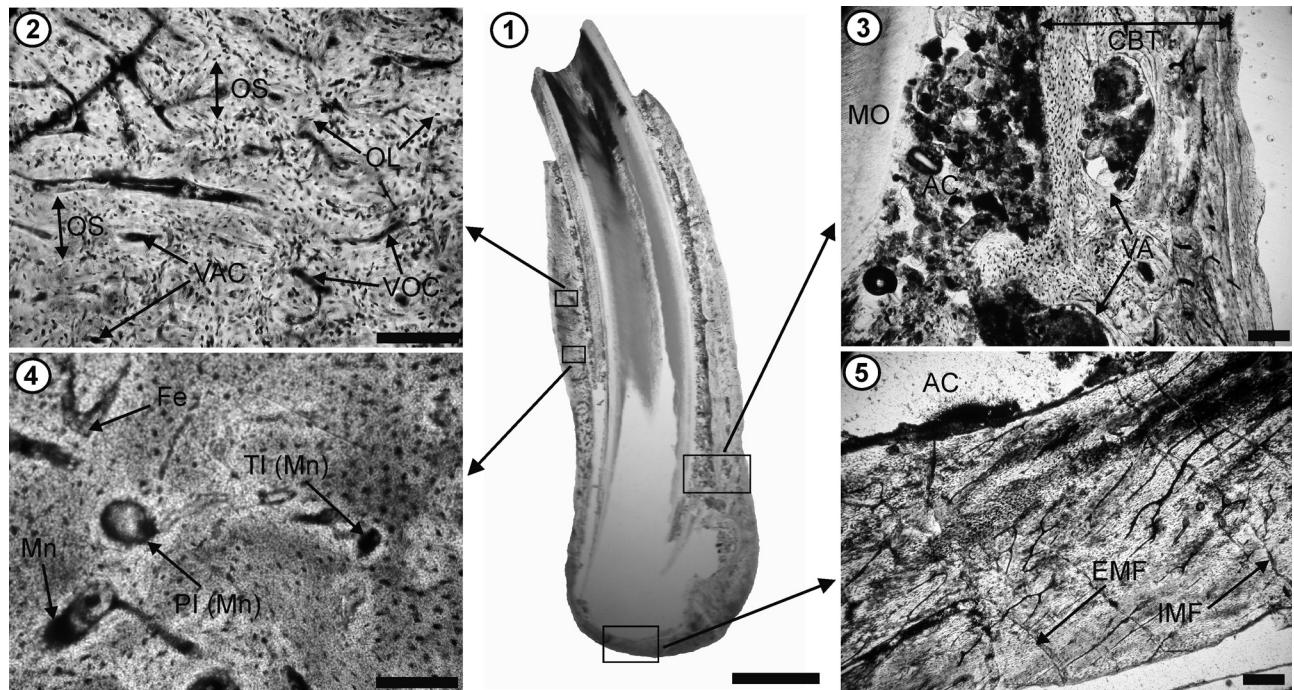


Figure 7. Transverse section of a hemimandible of *Paedotherium bonaerense*, analyzed with petrographic microscope; **1**, detail of the section at the level of m2, scale bar= 2 mm; **2**, features of the bone microstructure; **3**, cavities interpreted as canals for vessels, infilled with muddy clastic material; **4**, microstructural features infilled with iron and manganese oxides; **5**, microfissures at the lower portion of the skeletal element. Abbreviations: **AC**, alveolar cavity; **CBT**, compact bone tissue; **EMF**, empty microfissure; **Fe**, iron oxide; **IMF**, infilled microfissure; **Mn**, manganese oxide; **MO**, molariform; **OL**, osteocyte lacunae; **OS**, osteon; **PI**, partial infilling; **TI**, total infilling; **VAC**, vascular canal; **VOC**, Volkmann canal. Scale bar= 100 μ m.

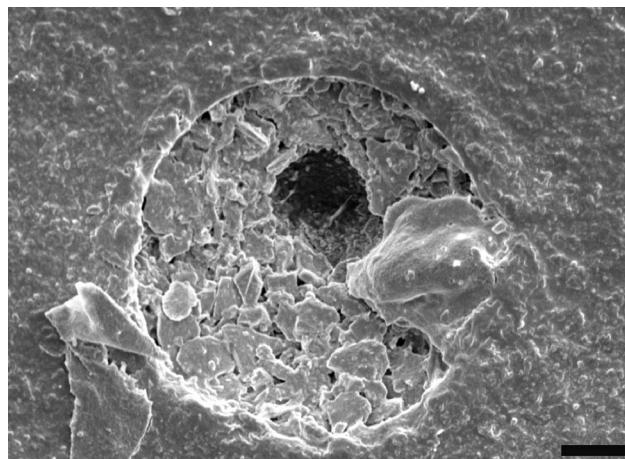


Figure 8. Transverse section of a hemimandible of *Paedotherium bonaerense*, analyzed with scanning electron microscope. A vascular canal partially infilled may be observed. Scale bar= 10 µm

were infilled, partial or totally, with manganese and iron oxides. No microfissures with muddy clastic infilling were identified. Some of the microstructural features (*e.g.*, vascular canals) infilled with oxides were cut by empty microfissures (Fig. 7.5).

DISCUSSION

Paedotherium bonaerense is a small rodentiform ungulate, with an estimated body mass less than 2 kg, herbivorous and with digging habits, typical of open areas such as herbaceous and shrubby steppes (Bond *et al.*, 1995; Giallombardo *et al.*, 2002; Elissamburu, 2012). This species is the most derived of the genus and its stratigraphic range is Pliocene–early Pleistocene (Bond *et al.*, 1995; Cerdeño and Bond, 1998).

The remains of *P. bonaerense* and *P. typicum* Ameghino, 1887—the other Pliocene species— are very abundant in different beds of the Monte Hermoso Formation (Tomassini, 2012; Tomassini *et al.*, 2013). As the analyzed hemimandibles are part of a significant sample of *P. bonaerense* from the floodplain deposits and because of their characteristics they are representative of all typical taphonomic attributes of these beds, they can be used as case study.

Evidence of slight weathering allows estimating a relatively short period of surface exposure (Andrews, 1990), during which the skeletons were disarticulated and the bones dispersed. The absence of abrasion signs, together with the low energy inferred for the host deposits, suggest that the remains were not exposed a long time to the abrasive action of sedimentary particles (Behrensmeyer, 1991) and probably suffered

little or null transport. The stepped fractures would be associated with processes occurring when the materials were still on the surface, whereas the smooth perpendicular fractures would have been caused by processes acting after burial, when bones were mineralized (Behrensmeyer *et al.*, 1989; Alcalá and Martín Escorza, 1998). Corrosion marks—similar to those described in other materials from the same beds (Tomassini, 2012)—may have been produced either by fungal or bacterial activity or by the action of soil acids. According to Montalvo (2002), root traces assigned to *Corrosichnia* indicate a temporary shallow burial in a substrate supporting vegetation.

Francolite was identified as the main mineral component of all the materials from the floodplain deposits of the Monte Hermoso Formation. This suggests that they were affected by compositional changes that determined the substitution of the original biogenic hydroxyapatite by a more physically and chemically stable material. This phenomenon is one of the most frequent mineralogical modification of vertebrate remains and occurs during the of early fossil-diagenesis by isomorphic replacement without alteration of the internal crystalline structure of ions PO_4^{3-} and OH^- by ions CO_3^{2-} and F^- respectively (Tuross *et al.*, 1989; Elorza *et al.*, 1999; Lecuyer *et al.*, 2003; Luque *et al.*, 2009; Merino and Buscalioni, 2013).

Similarities between chemical composition of the materials and the host rocks would indicate that the incorporation of new elements in the remains was produced during the fossil-diagenetic stage by a direct exchange with the sediments. In this way, the fossilization process was conditioned by particular characteristics (*e.g.*, lithology, texture, structure) of the microenvironment of preservation. The new chemical elements would have been mobilized and provided by groundwater circulating in the host deposits. This interpretation suggests, in agreement with the type of deposit and with the previous analysis of other taphonomic attributes (Tomassini, 2012; Tomassini and Montalvo, 2013), that the remains from the floodplain beds were not affected by re-elaboration processes (*sensu* Fernández-López, 2000).

Despite the mineralogical and geochemical changes that affected the materials, the paleohistological analysis showed a very good preservation of the bone microstructure. In this sense, the analyzed samples may be included in category 5 of the histological index proposed by Hedges *et al.* (1995), *i.e.*, with an integrity percentage higher than 95%. Microstructural

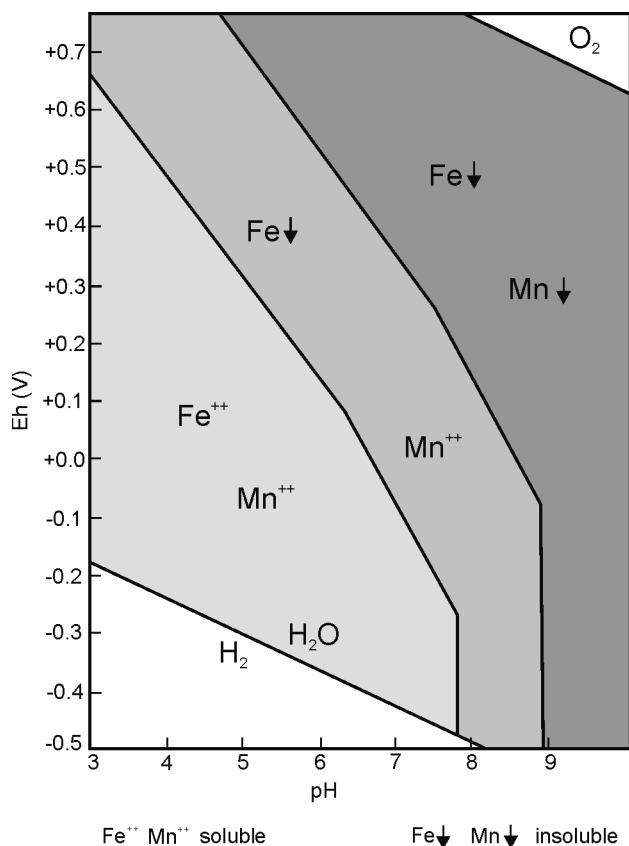


Figure 9. Eh/pH stability diagram for Mn and Fe forms. Modified from Dorronsoro *et al.* (2006).

features were affected only by permineralization (infilling of histological structure cavities with crystalline or amorphous mineral substances; *sensu* Fernández-López, 2000) and the development of microfissures. The evidence from the different types of infilling reveals two temporally different events of permineralization.

During the first event of permineralization –before the remains were completely buried– the muddy clastic material mobilized by water action during the flooding events infilled the alveolar cavities of the bones and the cavities identified as canals for the larger vessels, occupying the empty spaces generated by degradation of the organic matter. The grain-size of this infilling prevented it from spreading into the small cavities.

In the second event of permineralization, once the remains were completely buried, the circulation of fluids rich in Mn and Fe favored the infilling of the smallest and narrowest cavities such as the vascular canals, osteocyte lacunae and canaliculari. During periods of water saturation, manganese and

iron remained in their soluble and mobile forms (Mn^{++} and Fe^{++}), while during periods of drought and aridity these elements precipitated as oxides (Buol *et al.*, 1991; Kemp and Zárate, 2000; Pereda-Suberbiola *et al.*, 2000; Dorronsoro *et al.*, 2006; Luque *et al.*, 2009). Based on the stability fields defined for the different forms of manganese and iron, depending on the Eh and pH (Fig. 9), it is considered that the precipitation of these oxides reflects an increase in the alkaline conditions and the oxidizing conditions of the preservation microenvironment. Although in this case the oxides could not be determined with certainty, pyrolusite (MnO_2) and hematite (Fe_2O_3) are often two of the most common autogenic minerals in the fossil remains preserved in this kind of deposits (Pfretzschner, 2004).

According to several authors (*e.g.*, Pfretzschner, 2001, 2004; Luque *et al.*, 2009; Pfretzschner and Tütken, 2011), for fossil remains preserved in continental environments the oxide precipitation in the cavities of different microstructural features generally occurs once the organic matter is completely degraded. At this time, the chemical milieu changes from being controlled by the conditions inside the bone to depend on the external conditions of the microenvironment of preservation. The permineralization process would have favored the preservation of the bone microstructure against the destructive taphonomic processes (*e.g.*, corrosion) that acted afterwards on the materials.

The characteristics of the microfissures suggest that they originated after burial, probably due to the lithostatic load generated by overlying sediments. Most microfissures may have been produced before permineralization and their infilling possibly occurred simultaneously with that of the cavities of the bone microstructure. However, other microfissures are empty and cut the microstructural features infilled with oxides. This suggests that they were produced after permineralization. The presence of numerous fractures and microfissures of diagenetic origin would be related to the morphological characteristics of the hemimandibles of *Paedotherium*, *i.e.*, elongated, narrow, and with a very thin bone layer in their lower portion. These characteristics make them susceptible to break easily with little pressure (Montalvo, 2004).

As indicated, the outer bone surface of some of the analyzed materials shows a dark color. Tomassini (2012) indicated that this attribute is present in approximately 86% of the total of specimens recovered from the floodplain deposits of this

formation. Even Darwin (1846, p. 81) noted that many of the remains of this unit were “(...) as black as jet”.

In this study case we consider that impregnation due to the precipitation of manganese oxide is responsible for the color change. This interpretation is based on the fact that (1) in the black as well as in the light brown with black spots specimens, the infilling of the cavities of microstructural features includes mainly manganese oxides. The EDX analysis of these samples showed the presence of Mn in all the outer surface sector; (2) although in the black and light brown with black spots specimens the infilling of cavities of microstructural features also includes iron oxides, these mineral represent a minor percentage. In addition, EDX analysis of these samples reflected the absence of Fe in all analyzed sectors of the outer surface; (3) dark spots showed a dendritic habit, characteristic of manganese coating; and (4) although in the light brown specimens the infilling of the cavities of microstructural features is also mainly by manganese oxides, EDX analysis revealed the absence of Mn in all analyzed sectors of the outer surface.

Several authors (*e.g.*, Shahack-Gross *et al.*, 1997; López-González *et al.*, 2006; Marín Arroyo *et al.*, 2008; Tomassini *et al.*, 2010) made reference to manganese enrichment and subsequent precipitation as oxides as one of the main processes by which bone materials are impregnated and acquire a dark color. Identification of these impregnations superimposed to traces produced by root growth (Corrosichnia) indicates that they were developed after the burial of the remains, from the manganese provided by water circulating through the host deposits and under the chemical conditions mentioned above.

CONCLUSIONS

Results obtained in this work allowed to assess the importance of some of the taphonomic processes affecting the hemimandibles of *Paedotherium bonaerense* recovered from the floodplain deposits of the Monte Hermoso Formation. During the time that remains were exposed on the surface, the organic matter was degraded and the larger cavities of bone microstructure were infilled with muddy clastic material mobilized by water during the flooding events. After burial, the remains were affected by compositional changes in the crystalline structure that determined the substitution of the original biogenic hydroxyapatite by francolite. The precipitation of manganese and iron oxides favored the infilling

of the smallest cavities of bone microstructure and, in some specimens, also the microfissures originated by lithostatic load. The impregnation with manganese oxides produced a dark color in the outer bone surface of some remains.

In addition, the data obtained suggest the paleoenvironmental conditions under which the materials were preserved. The presence of manganese and iron oxides suggests periods of drought and aridity, associated with an increase in the alkaline conditions and the oxidizing conditions of the microenvironment of preservation.

These interpretations may be extrapolated to other remains of the assemblage recovered from the floodplain level of this formation, particularly those corresponding to micro-mammals. They also provide new information on a topic scarcely considered in the study of vertebrate faunal communities from the Neogene of South America. This information aids in establishing a framework for the comparison and assessment of other vertebrate assemblages preserved in fluvial environments. The latter includes, for example, different fossil beds from the Arroyo Chasicó, Cerro Azul and Chapatmal formations, corresponding to the late Miocene–late Pliocene of the Pampean Region (Argentina); the remains recovered from these units show many of the characteristics mentioned in this work.

ACKNOWLEDGEMENTS

To R. Caputo, director of the Museo Municipal de Ciencias Naturales “Carlos Darwin”, for access to material; to V. Sorrius for help in the EDX analysis and SEM photographs; to H. Ortiz for his collaboration with thin sections; and to C. Deschamps for the English translation. Comments and suggestions by A. Mancuso and J.L. Prado (reviewers) and by D. Pol (editor) certainly improved the manuscript. This paper was funded by CONICET and grants PICT 2012-2674 and PGI 24/H119, and FCEyN (UNLPam) 209.

REFERENCES

- Alcalá, L. 1994. *Macromamíferos neógenos de la fosa de Alfambra-Teruel*. Instituto de Estudios Turolenses y Museo Nacional de Ciencias Naturales, Teruel, 554 p.
- Alcalá, L. and Martín Escorza, C. 1998. Modelling diagenetic bone fractures. *Bulletin de la Société Géologique de France* 169: 101–108.
- Ameghino, F. 1887. Apuntes preliminares sobre algunos mamíferos extinguidos del yacimiento de Monte Hermoso existentes en el Museo de La Plata. *Extracto de la 1^a entrega del Tomo I del Boletín del “Museo de La Plata”*: 1–20.
- Andrews, P. 1990. *Owls, caves and fossils. Predation, preservation, and accumulation of small mammal bones in caves, with the analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset, UK*. The University of Chicago Press, Chicago, 231 p.
- Behrensmeyer, A.K. 1988. Vertebrate preservation in fluvial channels. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63: 183–189.
- Behrensmeyer, A.K. 1991. Terrestrial vertebrate accumulations. In: P.A. Alli-

- son and D.E.G. Briggs (Eds.), *Taphonomy: Releasing the Data Locked in the Fossil Record*. Plenum Press, New York, p. 291–335.
- Behrensmeyer, A.K., Gordon, K. and Yanagi, G. 1989. Nonhuman bone modification in Miocene fossils from Pakistan. In: R. Bonnichsen and M. Sorg (Eds.), *Bone Modification*. Institute for Quaternary Studies, University of Maine, Orono, p. 99–120.
- Berreteaga, A., Badiola, A., Astibia, H., Pereda-Süberbiola, X., Elorza, J., Etxebarria, N. and Álvarez, A. 2004. Estudio geoquímico de fósiles de vertebrados de varias localidades del Cretácico Superior y Paleógeno de los Pirineos occidentales. *Geogaceta* 36: 171–174.
- Bond, M., Cerdeño, E. and López, G. 1995. Los ungulados nativos de América del Sur. In: T. Alberdi, G. Leoni and E.P. Tonni (Eds.), *Evolución biológica y climática de la región pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo occidental*. Monografías del Museo Nacional de Ciencias Naturales y Consejo Superior de Investigaciones Científicas, Madrid, p. 257–275.
- Botha, J. and Chinsamy-Turan, A. 2004. Growth and life habits of the Triassic cynodont *Tritylodon*, inferred from bone histology. *Acta Palaeontologica Polonica* 49: 619–627.
- Buol, S.W., Hole, F.D. and Mac Cracken, R.J. 1991. *Génesis y clasificación de suelos*. Editorial Trillas, México D.F., 417 p.
- Cerdeño, E. and Bond, M. 1998. Taxonomic revision and phylogeny of *Paedotherium* and *Tremacillus* (Packyrukhinae, Hegetotheriidae, Notoungulata) from the Late Miocene to the Pleistocene of Argentina. *Journal of Vertebrate Paleontology* 18: 799–811.
- Chinsamy-Turan, A. 2005. *The microstructure of dinosaur bone*. The Johns Hopkins University Press, Baltimore and London, 194 p.
- Cione, A.L. and Tonni, E.P. 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la Provincia de Buenos Aires, Argentina. In: R.E. de Barrio, R.O. Etcheverry M.F. Caballé and E. Llambías (Eds.), *Geología y Recursos Minerales de la Provincia de Buenos Aires* (La Plata), Relatorio del 8º Congreso Geológico Argentino: p. 183–200.
- Cuezva, S. and Élez, J. 2000. Estudio preliminar de la microestructura de los huesos fósiles de mamíferos de Somosaguas (Mioceno medio, Madrid). *Coloquios de Paleontología* 51: 137–157.
- Darwin, Ch. 1846. *Geological observations on South America*. Smith, Elder & Co., London, 279 p.
- Deschamps, C.M., Vučetić, M.G., Verzi, D.H. and Olivares, A.I. 2012. Biostratigraphy and correlation of the Monte Hermoso Formation (early Pliocene, Argentina): the evidence from caviomorph rodents. *Journal of South American Earth Science* 35: 1–9.
- Dorronsoro, B., Aguilera, J., Dorronsoro-Díaz, C., Stoops, G., Sierra, M., Fernández, J. and Dorronsoro-Fernández, C. 2006. Hidromorfia en suelos. Curso de Edafología, Universidad de Granada: <http://edafologia.ugr.es/hidro/concept.htm>.
- Elissamburu, A. 2012. Estimación de la masa corporal en géneros del Orden Notoungulata. *Estudios Geológicos* 68: 91–111.
- Elorza, J., Astibia, H., Murelaga, X. and Pereda-Süberbiola, X. 1999. Franclite as a diagenetic mineral in dinosaur and other Upper Cretaceous reptile bones (Lano, Iberian Peninsula): microstructural, petrological and geochemical features. *Cretaceous Research* 20: 169–187.
- Fawcett, D. 1995. *Tratado de histología*. Interamericana McGraw-Hill, Madrid, 1047 p.
- Fernández-López, S. 2000. *Temas de Tafonomía*. Departamento de Paleontología, Universidad Complutense de Madrid, Madrid, 167 p.
- Giallombardo, A., Castro, P., Ortiz Jaureguizar, E. and Bond, M. 2002. Estimación de la masa corporal de los Pachirukhinae (Notoungulata, Hegetotheriidae) y análisis de su patrón a través del tiempo. 8º Congreso Argentino de Paleontología y Bioestratigrafía (Corrientes), Actas: 100.
- Goddard, E., Trask, P., De Ford, R., Rove, O., Singewald, J. and Overbeck, R. 1948. *Rock Color Chart*. National Research Council, Washington, 8 p.
- Haldeman, S.S. 1840. *Supplement to number one of "monograph of the Limnades, or freshwater univalve shells of North America", containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in *Paludina* and *Anculosa**. J. Dobson, Philadelphia, 3 p.
- Hedges, R.E., Millard, A.R. and Pike, A.W. 1995. Measurements and relationship of diagenetic alteration of bone from three archaeological sites. *Journal of Archaeological Science* 22: 201–209.
- Heer, O. 1877. *Flora fossili Helvetiae. Die vorweltliche Flora der Schweiz*. J. Wüster, Zürich, 182 p.
- Kemp, R.A. and Zárate, M.A. 2000. Pliocene pedosedimentary cycles in the southern Pampas, Argentina. *Sedimentology* 47: 3–14.
- Lécuyer, C., Bogey, C., García, J.P., Grandjean, P., Barrat, J.A., Floquet, M., Bardet, N. and Pereda-Süberbiola, X. 2003. Stable isotope composition and rare earth element content of vertebrate remains from Late Cretaceous of northern Spain (Laño): did the environmental record survive? *Palaeogeography, Palaeoclimatology, Palaeoecology* 193: 457–471.
- López-González, F., Grandal-d'Anglade, A. and Vidal-Romaní, J. 2006. Deciphering bone depositional sequences in caves through the study of manganese coatings. *Journal of Archaeological Science* 20: 1–11.
- Luque, L., Alcalá, L., Mampel, L., Pesquero, M.D., Royo-Torres, R., Cobos, A., Espílez, E., González, A., Ayala, D., Aberasturi, A., Marzo, P. and Alloza, R. 2009. Mineralogical, elemental and chemical composition of dinosaur bones from Teruel (Spain). *Journal of Taphonomy* 7: 151–178.
- Lyman, R.L. 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge, 524 p.
- Marín Arroyo, A.B., Landete Ruiz, M.D., Vidal Bernabeu, G., Seva Román, R., González Morales, M.R. and Straus, L.G. 2008. Archaeological implications of human-derived manganese coatings: a study of blackened bones in El Mirón Cave, Cantabrian Spain. *Journal of Archaeological Science* 35: 801–813.
- Marshall, L. 1989. Bone modification and “The laws of burial”. In: R. Bonnichsen and M. Sorg (Eds.), *Bone modification*. Institute for Quaternary Studies, University of Maine, Orono, p. 7–24.
- Merino, L. and Buscalioni, A.D. 2013. Mineralogía y cambios composicionales en fragmentos óseos atribuidos a un dinosaurio ornitópodo del yacimiento barremiense de Buenache de la Sierra (Formación Calizas de la Huérquina, Cuenca, España). *Estudios Geológicos* 69: 193–207.
- Merino, L. and Morales, J. 2006. Mineralogía y geoquímica del esqueleto de los mastodontes de los yacimientos Batallones 1, 2 y 5. Implicaciones tafonómicas. *Estudios Geológicos* 62: 53–64.
- Miall, A.D. 1985. Architectural-element analysis: a new method of facies analysis applied to fluvial deposits. *Earth Science Reviews* 22: 261–308.
- Mikulás, R. 1999. Notes to the concept of plant trace fossils related to plant-generated sedimentary structures. *Bulletin of the Czech Geological Survey* 74: 39–42.
- Montalvo, C.I. 2002. Root traces in fossil bones from the Huayquerian (Late Miocene) faunal assemblage of Telén, La Pampa, Argentina. *Acta Geologica Hispanica* 37: 37–42.
- Montalvo, C.I. 2004. [Paleobiología de la asociación faunística de Caleufú (La Pampa, Formación Cerro Azul, Mioceno superior-Plioceno inferior) a través de análisis tafonómicos: La Plata, Argentina]. Tesis Doctoral, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 251 p. [Unpublished].
- Montalvo, C., Melchor, R., Visconti, G. and Cerdeño, E. 2008. Vertebrate taphonomy in loess-palaeosol deposits: A case study from the late Miocene of central Argentina. *Geobios* 41: 133–143.
- Paniagua, R. 1996. *Citología e histología vegetal y animal. Biología de las células y tejidos animales y vegetales*. Interamericana McGraw-Hill, Madrid, 807 p.
- Pereda-Süberbiola, X., Astibia, H., Murelaga, X., Elorza, J.J. and Gómez-Alday, J.J. 2000. Taphonomy of the Late Cretaceous dinosaur-bearing beds of the Laño Quarry (Iberian Peninsula). *Palaeogeography, Palaeoclimatology, Palaeoecology* 157: 247–275.
- Pfretzschner, H.U. 2000. Microcracks and fossilization of Haversian bone. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 216: 413–432.
- Pfretzschner, H.U. 2001. Iron oxides in fossil bone. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 220: 417–429.
- Pfretzschner, H.U. 2004. Fossilization of Haversian bone in aquatic environments. *Comptes Rendus Palevol* 3: 605–616.
- Pfretzschner, H.U. and Tütken, T. 2011. Rolling bones - Taphonomy of Jurassic dinosaur bones inferred from diagenetic microcracks and mineral infillings. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310: 117–123.
- Shahack-Gross, R., Bar-Yosef, O. and Weiner, S. 1997. Black-colored bones

- in Hayonim Cave, Israel: differentiating between burning and oxide staining. *Journal of Archaeological Science* 24: 439–446.
- Tomassini, R.L. 2012. [Estudio tafonómico y bioestratigráfico de los vertebrados de la Formación Monte Hermoso (Plioceno) en su localidad tipo, provincia de Buenos Aires. Tesis Doctoral, Universidad Nacional del Sur, Bahía Blanca, 300 p. Unpublished.].
- Tomassini, R.L. and Montalvo, C.I. 2013. Taphonomic modes on fluvial deposits of the Monte Hermoso Formation (early Pliocene), Buenos Aires Province, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 369: 282–294.
- Tomassini, R.L., Montalvo, C.I., Deschamps, C.M. and Manera, T. 2013. Biostratigraphy and biochronology of the Monte Hermoso Formation (early Pliocene) at its type locality, Buenos Aires Province, Argentina. *Journal of South American Earth Sciences* 48: 31–42.
- Tomassini, R.L., Montalvo, C.I., Manera, T. and Oliva, C. 2010. Estudio tafonómico de los mamíferos pleistocenos del yacimiento de Playa del Barco (Pehuen Co), Provincia de Buenos Aires, Argentina. *Ameghiniana* 47: 137–152.
- Tuross, N., Behrensmeyer, A.K., Eanes, E.D., Fisher, L.W. and Hare, P.E. 1989. Molecular preservation and crystallographic alterations in a weathering sequence of wildebeest bones. *Applied Geochemistry* 4: 261–270.
- Tütken, T., Vennemann, T.W. and Pfretzschner, H.U. 2008. Early diagenesis of bone and tooth apatite in fluvial and marine settings: constraints from combined oxygen isotope, nitrogen and REE analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266: 254–268.
- Verzi, D.H., Montalvo, C.I. and Deschamps, C.M. 2008. Biostratigraphy and biochronology of the Late Miocene of central Argentina: evidence from rodents and taphonomy. *Geobios* 41: 145–155.
- Vialov, O.S. 1962. Problemática de the Beacon Sandstone at Beacon Heights, West Antarctica. *New Zealand Journal of Geology and Geophysics* 5: 718–732.
- Zavala, C. 1993. Estratigrafía de la localidad de Farola Monte Hermoso (Plioceno-Reciente), Provincia de Buenos Aires. *12º Congreso Geológico Argentino y 2º Congreso de Exploración de Hidrocarburos* (Mendoza), Actas 2: 228–235.
- Zavala, C. and Navarro, E. 1993. Depósitos fluviales en la Formación Monte Hermoso (Plioceno inferior-medio). Provincia de Buenos Aires. *12º Congreso Geológico Argentino y 2º Congreso de Exploración de Hidrocarburos* (Mendoza), Actas 2: 236–244.

doi: 10.5710/AMGH.01.07.2014.2737

Recibido: 14 de abril de 2014

Aceptado: 01 de julio de 2014