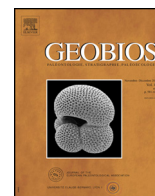




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## Original article

# Quaternary biostratigraphy and biogeography of mountain region of Córdoba, Argentina<sup>☆</sup>



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## ABSTRACT

In Argentina, Quaternary paleontological and biostratigraphic studies were mainly conducted in the Pampas plains of the provinces of Buenos Aires, Córdoba, Formosa and Santa Fe. The aim of the present study is to analyse the Pleistocene-Holocene record of the high plains of mountain in Córdoba in order to make interpretations on their biostratigraphical, geochronological, and paleobiogeographical significance. Representatives of 20 extinct and four living mammal species are listed, documenting the existence of two successive Assemblage Zones: *Scelidotherium leptocephalum*-*Glyptodon reticulatus* (between  $37,095 \pm 2020$  and  $14,040 \pm 785$  years BP) and *Panochthus-Equus* (*Amerhippus*) (between  $14,040 \pm 785$  and 9181 years BP). The presence of supposed Ensenadan or Bonaerian taxa (e.g., *Mesotherium* sp., *Catonyx tarijensis*, *Megatherium americanum*, and *Glossotherium* sp.) in late Pleistocene sediments suggests that the mountainous area of Córdoba has acted as a refuge area or reservoir. The Quaternary faunas recorded in the Pampean highlands, Pampean flats, and western and northern regions of Argentina do not show differences in the morphological characteristics and numbers of taxa.

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## 1. Introduction

In South America, the history of vertebrates is especially well documented in Argentina. Most of the records of Pleistocene mammals of the southern tip of South America come from deposits located in Argentina, and more precisely in the Pampean areas of Buenos Aires province (Tonni and Scillato-Yané, 1997; Cione et al., 1999; Tonni et al., 1999). During the last decades, several authors have revealed extra-Pampean Pleistocene paleofaunal assemblages, particularly in the provinces of Corrientes, Entre Ríos, Chaco, Formosa, and Santa Fe (Zurita et al., 2007 and references therein). In this context, the knowledge of the Pleistocene fauna of Córdoba province remains relatively scarce and based on several works dating back to more than sixty years ago (e.g., Ameghino, 1889; Frenguelli, 1921; Castellanos, 1925, 1944; see Tauber, 2014). Notable exceptions are the taxonomic, systematic, chronostratigraphic or biostratigraphic contributions of Tauber (1997, 1999, 2000a, 2000b), Tauber and Di Ronco (2000, 2003), Cruz and Bargo (2003), Tauber and Goya (2006), Krapovickas and Tauber (2010,

2012a, 2012b), Luna and Krapovickas (2011), Martínez et al. (2012), Cruz et al. (2012), Cruz (2013), Tauber et al. (2014), and Luna and Cruz (2014). The Pleistocene and Holocene sedimentary deposits and fossil assemblages of Córdoba Mountains are still poorly explored from the paleontological point of view, compared with its piedmont (Ameghino, 1885, 1889; Doering, 1907, 1918; Outes, 1911; Castellanos, 1943, 1944; Cioccale et al., 1997; Tauber, 1999, 2000a, 2000b).

The mountainous region of Córdoba is part of southeastern end of the Pampeanas mountain system of Argentina; it comprises four main meridian cords: Sierra Norte, Sierra Chica-Las Peñas, Sierra Grande-Sierra Comechingones, and Sierra de Pocho-Guasapampa. These areas are composed by metamorphic rocks of Precambrian and Paleozoic age and Paleozoic granitoids of batholithic dimensions, and Mesozoic sedimentary rocks (Gordillo and Lencinas, 1979; Martino and Guerreschi, 2014). These mountain ranges are at the same time separated by inter-mountain Cenozoic sediments (Beltromone, 2007; Astini et al., 2014; Kröhling and Carignano, 2014). One of the main morphological characteristics of the Sierras Pampeanas of Córdoba is the existence of flattened surfaces of erosional origin located at different altitudes (Carignano et al., 1999). These areas called high pampas are located on the eastern slopes of the tilted blocks of the Córdoba Mountains (Capitanelli, 1979). These “high plains” are defined as remains of erosion

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surfaces, which retain the structural and morphometric style of an ancient plain (Manzur, 1995). The gently undulating morphology has allowed the accumulation of post-Pliocene fluvial/wind-generated sediments and with them the remains of past life forming the basis of the present work (Carignano et al., 1999).

The study of Quaternary stratigraphy and paleontological sites of the Sierras Pampeanas are of particular interest because biological (e.g., endemism and insular distribution, mass extinction, and biodiversity), climatic and environmental (global climate changes, high diversity of microclimates, and microhabitats), archaeological and anthropological (arrival of early human populations of hunters-gatherers) processes can be analyzed together. These processes find an appropriate framework in the Pampean Sierras of Córdoba since all of them are concurrent in time and space. In addition, Ringuet (1961) and Polop (1989) indicate that the Pampa de Achala, the higher area of the hills of Córdoba, would be a biogeographical “island” with elements mainly Andean, Patagonian and Guianan-Brazilian, presenting in this sense a discontinuity with the rest of the province of Córdoba. Indeed, in the Sierras Pampeanas of Córdoba is observed a marked endemism in some groups of invertebrates and vertebrates – such as *Urofonius achalensis* (Scorpiones, Bothriuridae), *Melanophryniscus stelzneri* (Anura, Bufonidae), *Odontophrynus achalensis* (Anura, Leptodactylidae), and *Pristidactylus achalensis* (Squamata, Polychrotidae) – and an insular distribution of many elements of the fauna and flora (Nores, 1995, 1996; Acosta y Rosso de Ferradas, 1996; Di Tada et al., 1996; Cantero et al., 2011). In addition, several genera of grasses as *Stipa* and *Bromus* are present in the high pampas of the mountains of Córdoba and also in other regions of semi-arid climates like the Puna (Tauber, 1999). Both phenomena (distribution on islands and endemic fauna) are also observed in other areas of similar topography (e.g., Sierra de la Ventana; Kristensen and Frangi, 1995).

Within this general framework, a comprehensive analysis of the paleontological and biostratigraphic record from the mountain region of Córdoba was undertaken, using modern techniques and concepts, to allow us to interpret their geochronological and paleobiogeographical significance, and to compare the results obtained from previous interpretations of the high plains of the Sierras de Córdoba with the deposits of the Pampeana Region of the provinces of Córdoba and Buenos Aires.

## 2. Material and methods

Eastern Sierras Pampeanas of Argentina constitute the study area for this work, extending between 30°45' and 33°10' S and between 64°20' and 65° 25' W, and covering an area of 21,136 km<sup>2</sup> (Abril et al., 2003). Although the primary study area was the high pampas of the Sierra of Córdoba, exploration was extended also to the Interserrana area of Punilla, Los Reartes, Calamuchita, and San Alberto.

This contribution reviews the information previously reported in works of Leonardi (1961), Álvarez and Tauber (1999), Tauber and Goya (2006), Córdoba et al. (2005), Tauber et al. (2008), and Krapovickas and Tauber (2010, 2012b). The fossiliferous sites are located in Vaca Corral (31°9'–31°11' S, 64°51'–64°52' W, 1600 m a.s.l.), Pampa de Olaen (31°00'–31°15' S, 64°30'–64°40' W, 1100 m a.s.l.), Huerta Grande (31°3'55.6" S, 64°30'33.3" W, 1003 m a.s.l.), San Clemente (31°37'1.3" S, 65°4'1.9" W, 985 m a.s.l.), Bosque Alegre (31°39'59.8" S, 64°35'6.27" W, 930 m a.s.l.), Los Morteritos (31°34'57.7" S, 65°4'21.5" W, 1026 m a.s.l.), Rio Panaholma (31°37'1.3" S, 65°4'1.9" W, 985 m a.s.l.), Atos Pampa (31°56'4.1" S, 64°34'35.56" W, 1100 m a.s.l.) and Atum Pampa (32°7'26.4" S, 64°44'32.3" W, 1152 m a.s.l.), Villa del Dique (32°9'59" S, 64°30'4" W, 534 m a.s.l.), and Amboy (32°10'18.5" S, 64°33'41.38" W, 603 m

a.s.l.) (Fig. 1). Macrofossils have not been found in the Pampa de Achala and San Luis (located at 2000 m a.s.l.).

Taxonomic identification of fossil vertebrates was performed by reading specialized literature and comparing fossils of the major museums in the province of Córdoba. The systematic study is based on Zamorano (2012) for *Panochthus*; Miño-Boilini (2012, 2016) and Pujos et al. (2012) for scelidotheriine ground sloths; Duarte (1997) and Zurita et al. (2011a) for Glyptodontidae; Alberdi and Prado (2004) for *Hippidion* and *Equus*; Vizcaíno and Bargo (1993), Squarcia et al. (2006) and Krmpotic et al. (2008) for Dasypodidae; Pujos and Salas (2004) and Pujos (2006) for *Megatherium*; Cope (1891) and Guérin and Faure (2004) for *Macrauchenia patachonica*; Flynn et al. (2005) for Mesotheriidae; Miño-Boilini et al. (2006) for Toxodontidae; Morando and Polop (1997) for *Oncifelis geoffroyi*; Alberdi and Prado (2008) and Mothé et al. (2012) for *Notiomastodon*; Lucero et al. (2008) for *Ctenomys*; and Jackson et al. (1996) for *Lagostomus maximus*.

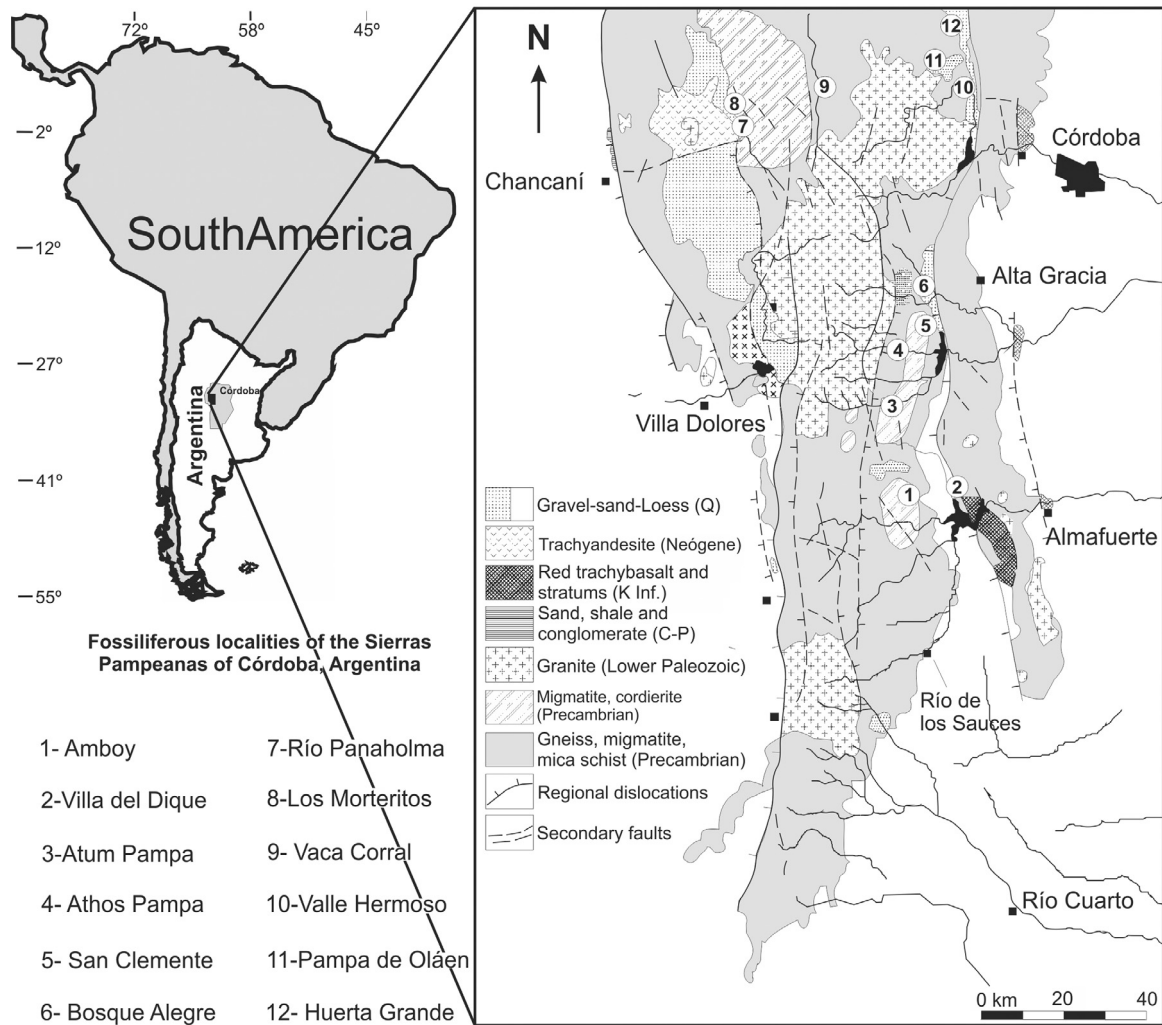
For the biostratigraphical analysis, we followed Cruz et al. (2012) and Cruz (2013): taxa were listed on the profile of each locality with their respective stratigraphic origin, listing the correlated fossiliferous levels (FL). The records were established based on several taxa and the mammal associations were documented with the description and correlation of sedimentary strata where they were discovered. Biostratigraphic units proposed follow the Argentine Code of Stratigraphy (Comité Argentino de Estratigrafía, 1992).

**Abbreviations:** CORD-PZ: Museo de Paleontología de la Universidad Nacional de Córdoba, Argentina; MCNC-PV: Museo Provincial de Córdoba, Argentina; MPAM: Museo Provincial Aníbal Montes, Río Segundo city, Argentina; MDVS-PV: Museo Dalmasio Vélez Sarsfield, Amboy town, Argentina; MRFA: Museo Regional Florentino Ameghino, Río Tercero city, Argentina.

## 3. Stratigraphical and geochronological framework

The stratigraphy of the high areas of mountain of Córdoba shows marked sedimentological discontinuities hindering regional correlations (Krapovickas and Tauber, 2012b). However, a common pattern was observed mainly in the high pampas, which can be of predictive value for geochronology of new areas that will be studied soon. In these high plains, we delimited three sedimentary sections. The two basalmost stratigraphic sections are reddish to yellowish and contain representatives of Pleistocene fossil taxa, while the upper section of dark tones yields only representatives of living species. These three sedimentary sections were grouped in the Vaca Corral Fm. of Lujanian age (Fig. 2; Krapovickas, 2014; Krapovickas and Tauber, 2016).

The first section is referred to a set of sediments consisting mainly of fine to coarse sands, yellowish to reddish, with remains of extinct taxa and evidence of bioerosion (e.g., crotonines, as registered in Huerta Grande, Panaholma, Pampa Vaca Corral, Los Molinos, and Atos Pampa; Goya, 2003; Tauber, 2006a, 2006b; Bárcena Esquivel, 2013; Krapovickas, 2014), bioaccumulation (e.g., coprolites and *Coprinisphaera* sp., as registered in Pampa Vaca Corral, Pampa de Olaen, and Panaholma; Krapovickas, 2014), bioturbation (mainly rhizoliths of up to 10 cm in transverse diameter, as found in Panaholma; Krapovickas, 2014), and evidence of pedogenesis manifested macroscopically by prism or granular peds, cutans, nodules, and calcareous septa. Among pedofeatures are found iron and manganese nodules (e.g., in Atos Pampa, Pampa de Olaen, and Pampa Vaca Corral), poral coatings of micritic carbonate (e.g., in Atos Pampa) or of clay (e.g., in Pampa de Olaen), large voids formed by cameras connected by canals (e.g., in Pampa de Olaen and Pampa Vaca Corral) or small voids not connected, and the existence of feces (e.g., in Vaca Corral). This set



**Fig. 1.** Location map of the eastern Sierras Pampeanas of Argentina and geological map of the mountains of Córdoba, with the position of all fossiliferous localities studied in this work.

would have been deposited during the late Pleistocene (OSL datings:  $37,095 \pm 2020$  and  $14,040 \pm 785$  years BP). This section is synchronous with the deposition of the Tezanos Pinto Fm. (between ca. 36 and 8 ka BP; Iriondo and Kröhling, 1995; Kröhling, 1999), General Paz Fm. (Santa Cruz, 1972), and La Invernada Fm. (Cantú, 1992; age: between  $63.9 \pm 6.4$  and  $16.2 \pm 1.1$  ka years BP; Kröhling and Carignano, 2014, and references therein). In this group, FL 1 (Vaca Corral), 3 (Pampa de Olaen), 12 (Atos Pampa), and 14 (Atum Pampa) were identified (Fig. 3).

The second stratigraphic section includes silty-sandy sediments, yellowish, friable, and massive, interpreted as loess-like sediments (e.g., Pampa de Olaen). It contains remnants of extinct taxa and would have been deposited between the latest Pleistocene and the early Holocene (temporal range estimated by OSL and AMS datings:  $14,040 \pm 785$  and  $9,181$  cal. years BP, respectively). In this group, the FL 4 (Pampa de Olaen) and 15 (Atum Pampa) were recognized (Fig. 3).

The third and last stratigraphic section is characterized by dark gray thick sands with more organic matter in their matrix and a greater number of paleosols (Krapovickas, 2014; Krapovickas and Tauber, 2016). Extinct species are not recorded in this section but representatives of modern taxa are present. It shows strong evidence of vegetable bioturbation. The basal paleosol was formed in the early Holocene; it has an estimated age between 9,181 and 7,206 cal. years BP (Sanabria et al., 2014). This paleosol can be correlated with the “suelo fósil I” (Montes, 1955, 1956) and

“Geosuelo El Ranchito” (Carignano, 1997); it has a regional distribution and is found also in San Luis, Santa Fe, and Buenos Aires provinces (Krapovickas, 2014; Krapovickas and Tauber, 2016). In this stratigraphic section are registered the FL 2 (Vaca Corral), 5 (Pampa de Olaen), and 13 (Atos Pampa) (Fig. 3).

The localities of Huerta Grande (matrix-supported conglomerate; FL 6), Valle Hermoso and Los Morteritos (friable coarse-middle sands; FL 7 and 8, respectively), Río Panaholma (sandy clay; FL 9), and Bosque Alegre, San Clemente and Amboy (fanglomerate; FL 10, 11 and 16, respectively) all exhibit extinct faunas (Fig. 3).

#### 4. Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Cingulata Illiger, 1811

Family Dasypodidae Bonaparte, 1838

Subfamily Euphractinae Pocock, 1924

Genus *Chaetophractus* Fitzinger, 1871

*Chaetophractus* sp.

Fig. 4(A, B)

**Material and provenance:** CORD-PZ 4472: isolated mobile osteoderm found at a reddish fanglomerate in the profile of “Camino a San Clemente” in the locality of Copina-San Bernardo (FL 11;  $31^{\circ}36'39.9''$  S,  $64^{\circ}34'9.57''$  W, 982 m a.s.l.); CORD-PZ 4473: 9 non-articulated mobile osteoderms found in a reddish sandy-clay, at the base of the “Río Panaholma 1” profile in the Pampa of



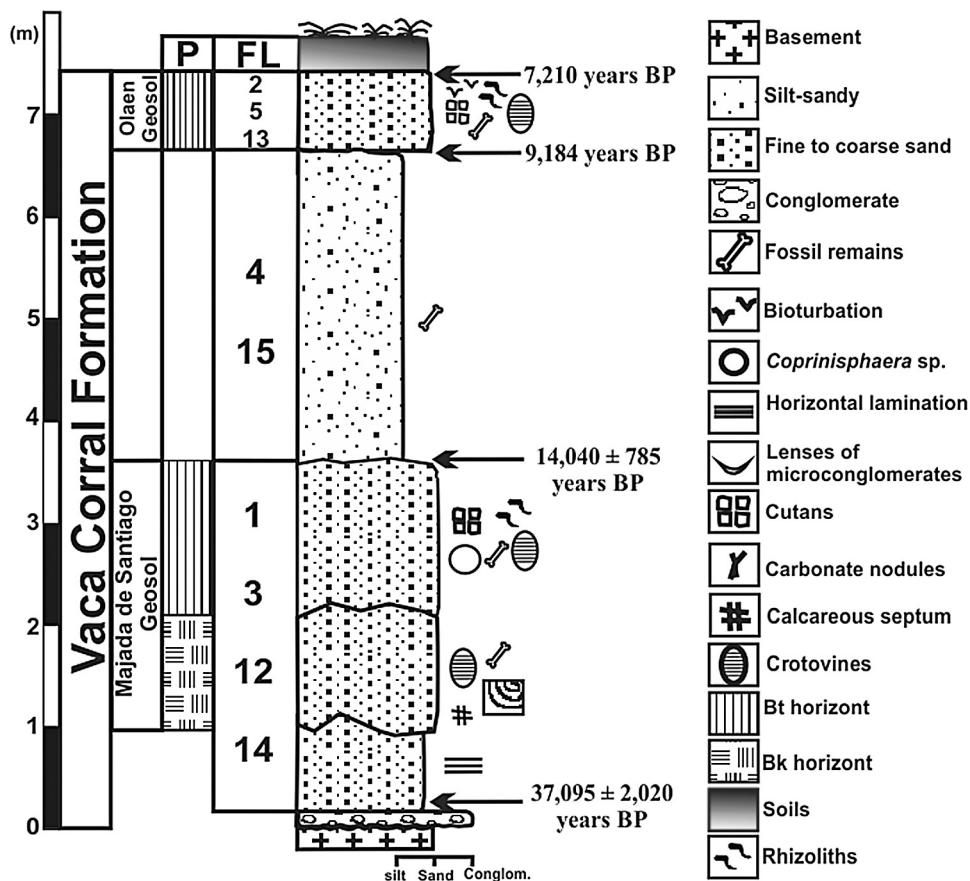


Fig. 2. Generalized stratigraphic column of the Vaca Corral Formation (modified from Krapovickas and Tauber, 2016). P: pedogenic horizons inferred; FL: fossiliferous levels.

Pocho-Panaholma locality (FL 9; 31°37'13.3" S, 65°3'45.4" W, 974 m a.s.l.).

**Biostratigraphical and geographical distribution:** The genus *Chaetophractus* is represented, at least, by the species *C. villosus* recorded from the "Huayquerian" of the Province of Buenos Aires (Tauber, 2005; Brandoni et al., 2012). It ranges from the Paraguayan Chaco and southern Bolivia to Argentinian Tierra del Fuego and along the southeastern border of Chile (Squarcia et al., 2006; Krmpotic et al., 2008).

**Description:** The studied material consists of mobile osteoderms rectangular in shape and always three to four times longer than wide. The cranial parts of the osteoderms are smooth in their external surface, raised relative to the rest of the osteoderm (e.g., CORD-PZ 4473; Fig. 4(A, B)). The transverse depression is mesiodistally larger and more rough (Fig. 4(B)), owing to the presence of longitudinal sulci that give it a more striated aspect compared to *Zaedyus* (Vizcaíno and Bargo, 1993; Krmpotic et al., 2008). The caudal part of the osteoderms present three figures extended longitudinally. The central figure is not subdivided (Fig. 4(A)). Both lateral figures are divided into four figures that are better defined than in *Zaedyus*. These lateral figures do not connect at the distal border of the osteoderms. All these characteristics, cranial portion of the smooth and elevated osteoderm, striated aspect of transverse depression, and the configuration of the longitudinal figures allow assigning this material to *Chaetophractus* (Krmpotic et al., 2008).

Genus *Eutatus* Gervais, 1867

*Eutatus cf. seguini*

Fig. 4(C)

**Material and provenance:** CORD-PZ 4483: mandibular fragment extracted from a crotovine located in the reddish pedogenetic sandy silt from the layer B<sub>t</sub> in Atum Pampa (FL 14; 32°7'26.5" S, 64°44'34" W, 1152 m a.s.l.).

**Biostratigraphical and geographical distribution:** The oldest record of the genus is Chapadmalalan (early Pliocene) in age; the species distributes along the Bonaerian, Lujanian, and Platan ages (middle Pleistocene–early Holocene) in Argentina (Buenos Aires, Córdoba, Entre Ríos, Santa Fe, Santiago del Estero, and Tucumán provinces) and Uruguay (Krmpotic et al., 2009).

**Description:** The proximal part of the left dentary presents the distalmost six teeth. These are all of circular section, with smooth occlusal surface, without crests or cusps (Fig. 4(C)), contrasting with the condition present in *Chaetophractus villosus*, in which the mandibular teeth always present serially beveled occlusal surfaces that are worn at a considerable degree (Squarcia et al., 2006). In *Eutatus*, the distal teeth tend to be flat in occlusal view. The dentine is arranged in three parts: a dense external layer that resembles enamel (the durodentine), as is also the nucleus of the tooth. Between both parts a low density layer is present, which is worn out faster, allowing the harder layers to rise above it (Vizcaíno and Bargo, 1998).

**Remarks:** Although there is no dental evidence to separate the two valid *Eutatus* species, *E. seguini* distributes in the Bonaerian, Lujanian and Platan ages (middle Pleistocene–early Holocene) whereas *E. pascuali* would be present in the Marplatan (Vorohuan; late Pliocene) to Ensenadan (early Pleistocene) ages (Krmpotic et al., 2009). Taking into account the time distribution of these two species, CORD-PZ 4483 probably relates to *Eutatus seguini*.

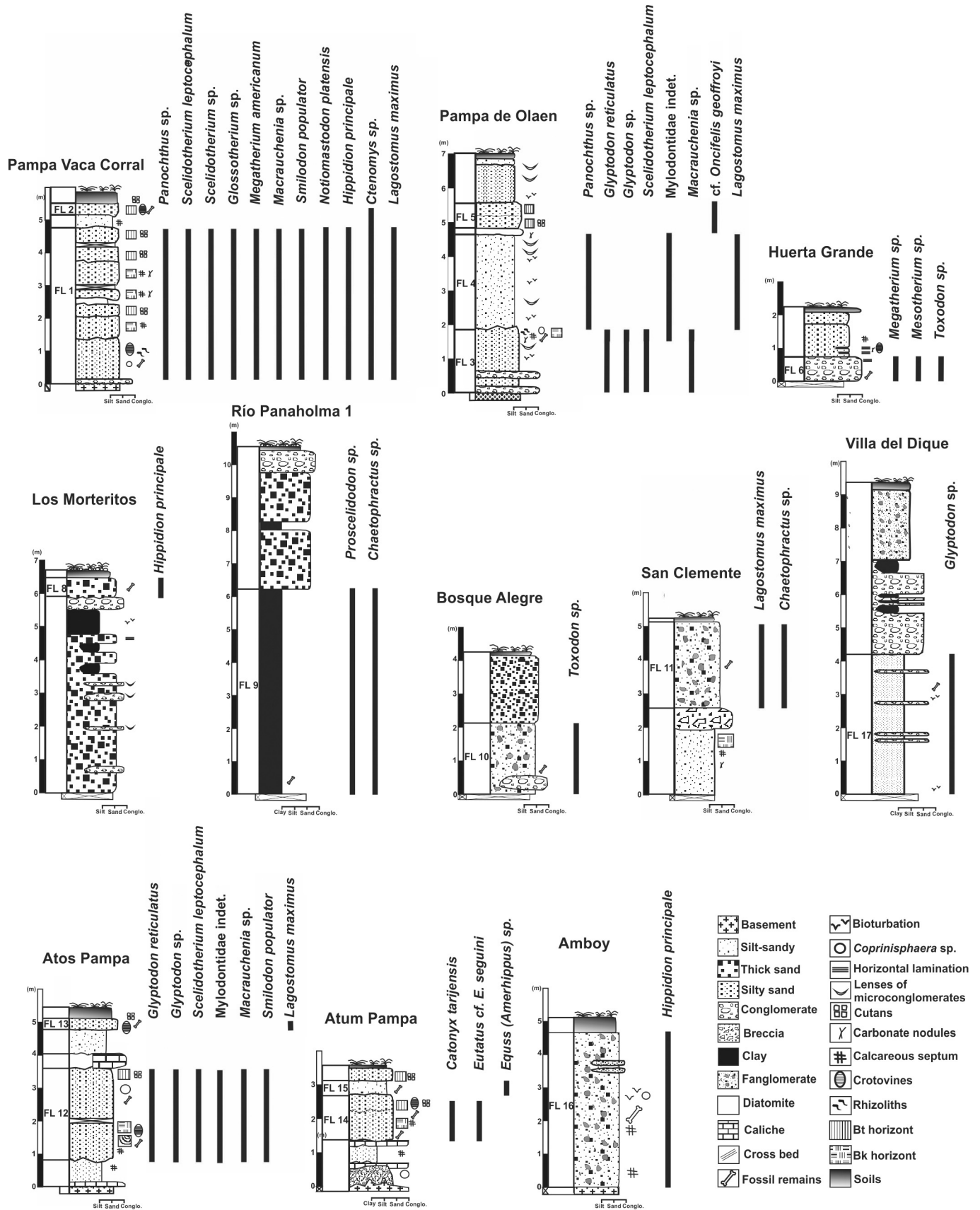
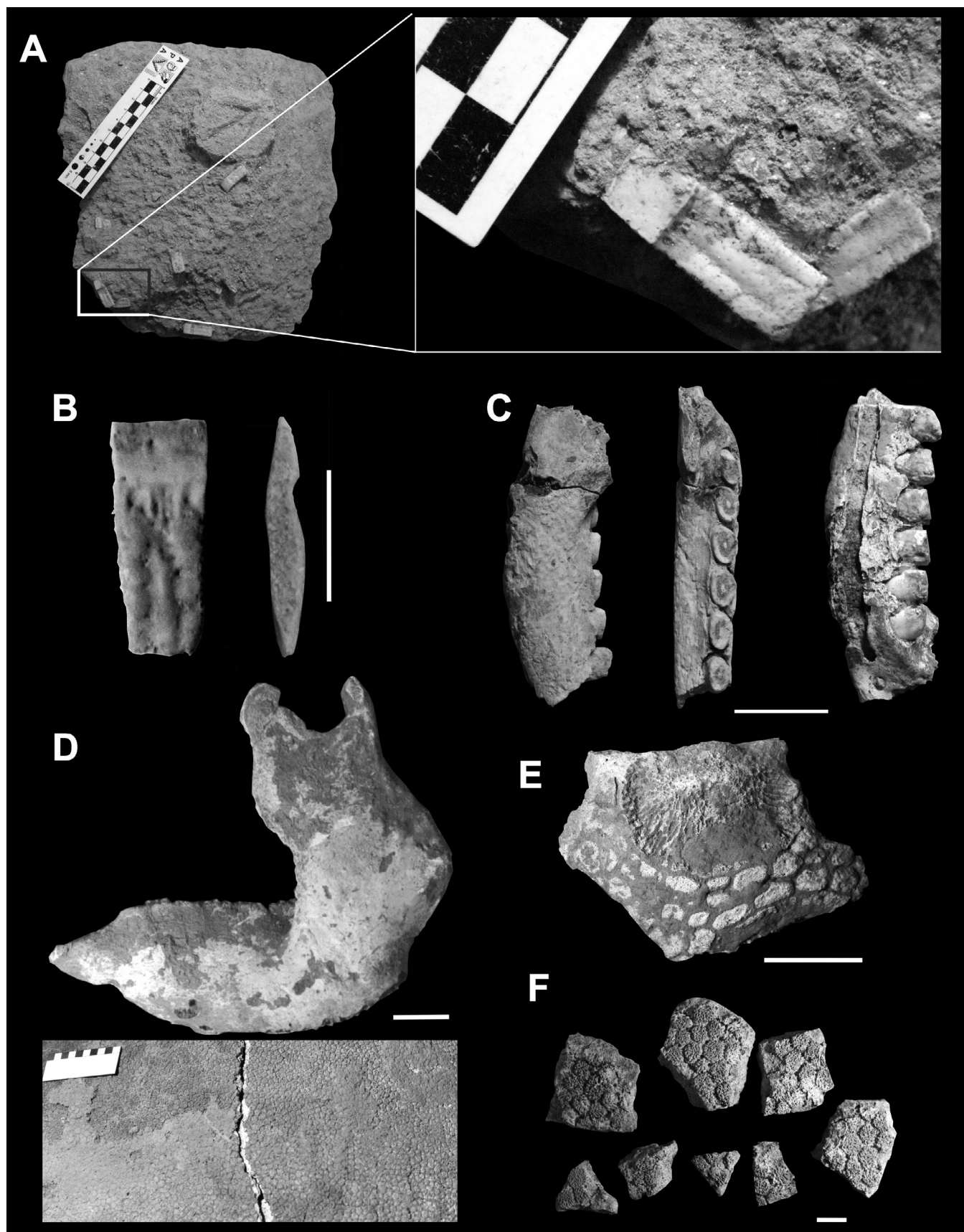


Fig. 3. Stratigraphic profiles and distribution of taxa found in the different fossiliferous localities of the mountains of the province of Córdoba.



**Fig. 4.** **A, B.** *Chaetophractus* sp. Non-articulated mobile osteoderms. **A.** CORD-PZ 4473, osteoderms found in a reddish sandy-clay in Panaholma location; **B.** CORD-PZ 4472, in dorsal (left) and lateral (right) views. **C.** *Eutatus* cf. *E. seguini* (CORD-PZ 4483): mandibular fragment in labial (left), occlusal (middle), and lingual (right) views. **D, E.** *Panochthus* sp. **D.** CC-PZ 100 and CC-PZ 101: large carapace fragments and left mandibular ramus, respectively; **E.** Caudal tube fragments (CORD-PZ 4462). **F.** *Glyptodon reticulatus*: eight osteoderm fragments found in Atos Pampa (CORD-PZ 4463). Scale bars: 1 cm (B), 2 cm (C), 3 cm (E, F), and 5 cm (D).

Family Glyptodontidae Burmeister, 1879

Genus *Panochthus* Burmeister, 1866

*Panochthus* sp.

Fig. 4(D, E)

**Material and provenance:** CC–PZ 100 and CC–PZ 101: large carapace fragments and a left mandibular ramus with complete dentition, respectively, proceeding from the reddish pedogenetic sandy silt of Pampa Vaca Corral (FL 1; Goya, 2003). CORD–PZ 4462: two caudal tube fragments found in the yellowish sandy silt of Pampa de Oláen (FL 4; 31°7′58.1″ S, 64°34′45.4″ W, 1131 m a.s.l.).

**Biostratigraphical and geographical distribution:** This is the only recorded genus of the tribe Panochthini during the Pleistocene (Ensenadan to Lujanian; ca. 2.588 to 0.007 My?). This Pleistocene taxon seems to be restricted to the southern and northeastern regions of South America, including the Chaco-Pampean Plains, Mesopotamian, SubAndean, and northern Patagonian Regions of Argentina (southernmost records come from the localities of Fitz Roy and Puerto Deseado, Santa Cruz Province; Tauber and Palacios, 2007; A.T., pers. obs.), Tarija (Southern Bolivia), Paraguay, western Uruguay, and southern and northeastern Brazil (Zamorano, 2012).

**Description:** The carapace fragments (CC–PZ 100) consist of thick osteoderms that form a mosaic designed with uniform, finely punctuated figures arranged in two rows (Fig. 4(D)). The dorsal cuirass is compressed and cranially raised, with polygonal-shaped osteoderms showing small, similar-sized polygonal figures (tubercles) which present a flat surface. These tubercles are arranged in a reticular pattern distributed all over the cuirass, without central figure (except in the osteoderms closer to the lateral margins; Zurita et al., 2011a; Zamorano, 2012), unlike those of *Glyptodon*, *Doedicurus*, and *Neosclerocalyptus*. The dorsal cuirass osteoderms present a large number of small figures, which in some cases may bear a distinct central figure. The mandible (CC–PZ 101) resembles that of other species of the genus (Fig. 4(D)). It is robust, similar to those of the largest *Glyptodon* species (e.g., *G. munizi* and *G. reticulatus*; Zamorano, 2012).

The caudal tube fragment (CORD–PZ 4462; Fig. 4(E)) bears the attachment scars of the caudal spines. The fragment would belong to the right dorsal margin close to the distal end of the tube judging from the condition of the caudal tubes of comparative material (e.g., CORD–PZ 4587 or MDVS–PV 0008).

**Remarks:** The species of the genus *Panochthus* currently accepted are *P. tuberculatus* (Owen, 1845), *P. frenzelianus* Ameghino, 1889, *P. intermedius* Lydekker, 1895, *P. subintermedius* Castellanos, 1937, *P. greslebini* Castellanos, 1942, and *P. jaguaribensis* Moreira, 1965 (Zamorano, 2012). These species are principally distinguished by skull characters, postcranial characters of the humerus, dorsal armour (osteoderms without central figures, except for *P. intermedius* and *P. jaguaribensis*; Zamorano, 2012) and caudal tube (distal region of the dorsal surface of the tube with two large, rugose, subelliptical depressions, one in each side, and behind these two smaller, subcircular depressions – contrasting with the single one of *P. subintermedius* and *P. greslebini* – which are not symmetrical, contrasting with *P. jaguaribensis*; Zamorano, 2012). None of the different characters mentioned above can be assessed in the material studied here, so only the genus-level assignment is supported here.

Genus *Glyptodon* Owen, 1838

*Glyptodon reticulatus* Owen, 1845

Figs. 4(F), 5(A)

**Material and provenance:** CORD–PZ 4463: eight osteoderm fragments found in the sandy silt with blocks and intraclasts of Atos Pampa (FL 12; 31°59′31.3″ S, 64°41′20.5″ W, 1078 m a.s.l.). CORD–PZ 15400: cuirass fragment reported in Leonardi (1961) above the reddish pedogenetic sandy silt on the Los Talas stream, 500 m N to confluence with El Pungo stream, Pampa de Oláen (FL 3; Córdoba, 2005).

**Biostratigraphical and geographical distribution:** The first record of this species occurs at the Bonaerian (0.78 to ca. 0.5 Ma) and the last record occurs at the Lujanian (~130–7 ka BP) (Cione and Tonni, 2005; Cione et al., 2009).

**Description:** The osteoderms of the carapace fragment are formed by a hexagonal central figure somewhat larger than the peripheral ones (e.g., Figs. 4(F) and 5(A)). The latter vary in number between six and eight, which are shared with neighboring osteoderms. The central and peripheral figures are always located in the same level, forming a reticular pattern which makes difficult individualization of the osteoderms (Fig. 5(A)). No piliferous foramina were found; the sulci are deep and narrow and the surface of all osteoderms is strongly punctuated, which makes their aspect rough. This fragment belongs to the mediolateral region of the carapace, as recognized by Duarte (1997), although some differences are found, including the number of peripheral little figures which surround the central figures, corresponding to individual variability.

The osteoderm fragments found at Atos Pampa (CORD–PZ 4463) present a central figure of the same size of the peripheral figures. The contour of the central figure is hexagonal, which bears a piliferous perforation at each of its corners. The osteoderm surface is finely punctuated, giving it a rough appearance compared to the former case. The peripheral figure number varies from six to seven. These features locate this set of osteoderms in the middle region of the cuirass, as defined by Duarte (1997); the much-roughened aspect of the material may indicate incomplete ossification and a relatively young ontogenetic age.

**Remarks:** The records of this species in the region of the Sierras Pampeanas are known and well documented by findings of exceptionally preserved specimens, which are completely articulated and preserving the ventral osteoderms, an extremely scarce situation in the fossiliferous record (Tauber and Di Ronco, 2000).

*Glyptodon* sp.

Fig. 5(B–E)

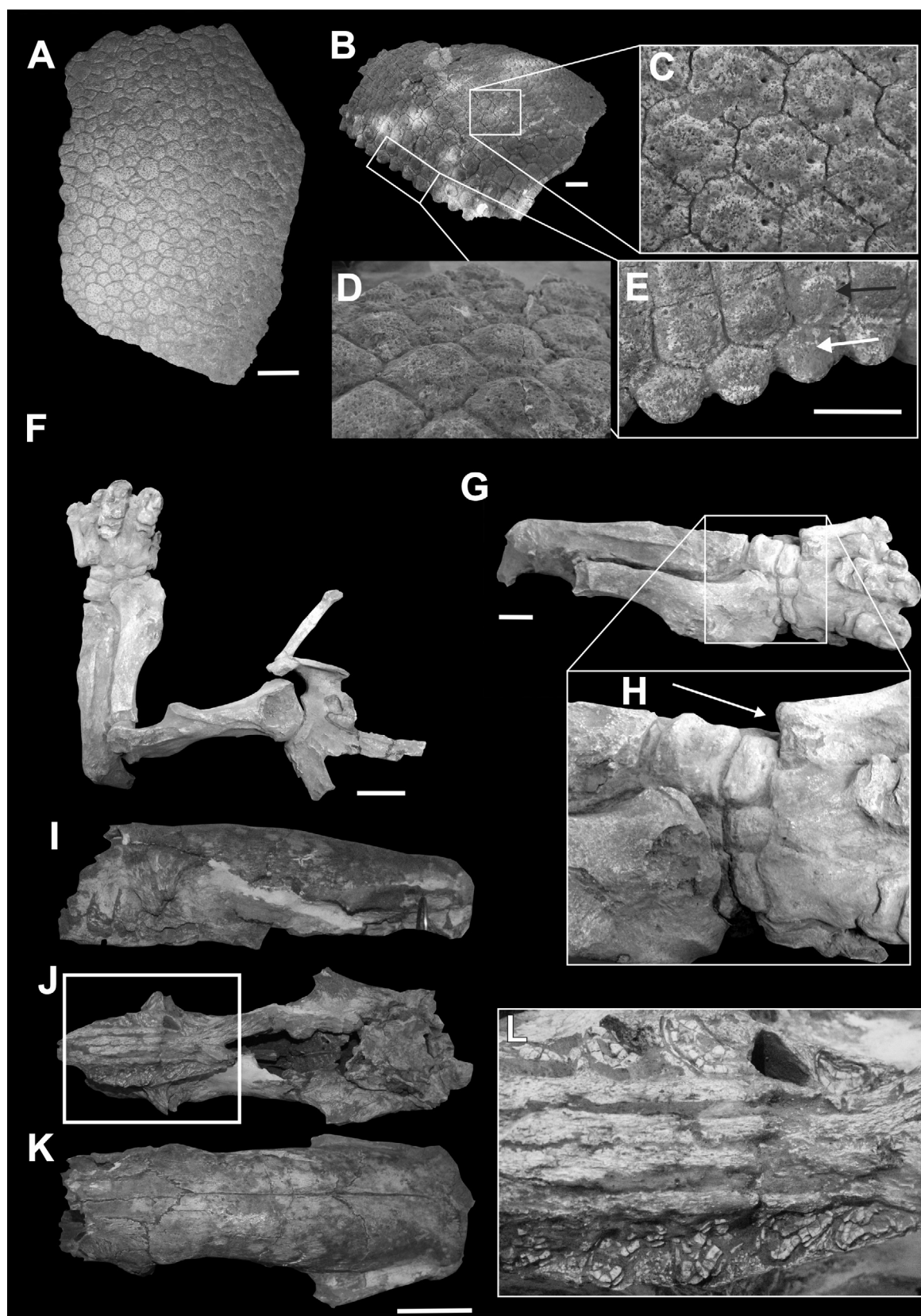
**Material and provenance:** CORD–PZ 15420: isolated osteoderm found in reddish pedogenetic sandy silt (FL 4) by Leonardi (1961). CORD–PZ 4291: fragment of splanchno- and neurocranium including both maxillae and zygomatics, of which the left one is the more complete. The left temporal region with part of the zygomatic apophysis, as well as teeth fragments are also preserved. The material proceeds from the basal level (brown-reddish sandy silt) of Pampa de Oláen (FL 4; 31°06′4.8″ S, 64°36′0.7″ W). MCNC–PV 246: 90 osteoderms of the dorsal cuirass, 19 of the caudal rings, right tibial, and fibular diaphyses, a vertebra, right ilium, and part of the right ischium of a young specimen. The material proceeds from a sandy silt package with conglomerate lenses at the margins of the Río Tercero dam, west of Villa del Dique (FL 17; 32°09′59″ S, 64°30′04″ W). MDVS–PV 0064: dorsal armour fragment of a young specimen, in sandy silt outcrops with blocks and intraclasts at Atos Pampa (FL 12; 31°59′35″ S, 64°41′21.8″ W).

**Biostratigraphical and geographical distribution:** *Glyptodon* has been recorded from the early-middle Ensenadan (“Toscas” of Río de La Plata; ca. 1.7–0.98 Ma), up to the Lujanian (late Pleistocene–early Holocene) (Soibelzon et al., 2006).

**Description:** CORD–PZ 15420 morphologically coincides with the osteoderms of the third caudal ring of the *Glyptodon* sp. (Duarte, 1997). The osteoderm is thick, with a very rough external surface, without figures (either central or peripheral), sulcus, nor perforations.

CORD–PZ 4291 is similar in size to the species *Glyptodon reticulatus* and smaller than *Panochthus* and *Doedicurus*. The lateral walls of both maxillae converge forward, suggesting a narrow face and relatively narrow narial openings compared to *Neosclerocalyptus*, *Doedicurus*, and *Panochthus*. The





**Fig. 5.** **A.** *Glyptodon reticulatus*: cuirass fragment reported by [Leonardi \(1961\)](#) from the Pampa de Oláen (CORD-PZ 15400). **B–E.** *Glyptodon* sp.: dorsal armour fragment of a young specimen found in Atos Pampa (MDVS-PV 0064). **C, D.** Morphotype 1 osteoderms described by [Luna and Krapovickas \(2011\)](#); **E.** New morphotypes described for a juvenile *Glyptodon*: morphotype 11: pentagonal osteoderms (black arrow); morphotype 12: robust osteoderms with a wider apex (white arrow). **F–L.** *Scelidotherium leptocephalum*. **F.** Left thoracic member with complete clavicle and distal part of scapula (CORD-PZ 4464); **G.** Detail of forearm and hand articulated; **H.** Detail of the wrist in dorsal view, showing the lack of articulation between digit V and the unciform (white arrow); **I–K.** Skull in lateral (top), occlusal (middle) and dorsal (bottom) views (MDVS-PV 0043); **L.** Detail of the semi-elliptic molariform and the palate with two lines parallel to tooth series. Scale bars: 5 cm (A, B, E, G, I–K), 10 cm (F); not to scale (C, D, H, L).



infraorbital foramen is large and oval in contour. Above the zygomatic, on the rostrorodorsal border of the orbit, a globular area presents a rough surface similar to the one observed in *Glyptodon reticulatus* specimens (e.g., CORD-PZ 16879). On the right rostral part, one of the first teeth bears two shallow apicobasal sulci on the lingual surface. The labial surface bears a wide and shallow apicobasal sulcus (Córdoba, 2005).

The specimen MCNC-PV 246 has been previously studied by Luna and Krapovickas (2011), who identified up to ten osteoderm morphotypes, divided in two sets. The first set of osteoderms (morphotypes 1 to 8) belongs to the dorsal cuirass, whereas the other (morphotypes 9 to 10) belongs to the caudal rings.

MDVS-PV 0064 provides additional information on the relationships between osteoderm morphotypes in young specimen of *Glyptodon*. The fragment comes from the dorso-lateral region of the dorsal cuirass, formed mainly by morphotype 1 osteoderms as described by Luna and Krapovickas (2011) (Fig. 5(B–D)). However new morphotypes are distributed in two rows at the lateral border of the cuirass, and do not fully adjust with the description of those near the caudal part of the lateral border of the cuirass. The first row (morphotype 11; Fig. 5(E), black arrow) is composed by pentagonal osteoderms bearing two or three perforations only on the dorsal border, without annular sulcus or defined peripheral figures. The central figure is raised and lacks a central depression. The second row (morphotype 12; Fig. 5(E), white arrow) consists of osteoderms very similar in shape (and function) to those of morphotype 8, but more robust and with a wider apex. These two morphotypes probably belong to the more cranial region of the dorsal cuirass of the juvenile *Glyptodon*, taking into account the anatomical distribution proposed for morphotypes 1 to 10 (Luna and Krapovickas, 2011).

**Remarks:** The genus *Glyptodon* includes four well-recognized species (*G. munizi*, *G. reticulatus*, *G. elongatus*, and *G. clavipes*; Zurita et al., 2011a). The exposed surface of the dorsal cuirass in MCNC-PV 246 and MDVS-PV 0064 presents a relatively elevated central figure in comparison with the peripheral region, as previously highlighted by Lydekker (1894), Rinderknecht (2000), and Zurita et al. (2009a), and attributed to juvenile specimens of *Glyptodon* (Luna and Krapovickas, 2011).

The juvenile *Glyptodon* material also presents most osteoderms with a central figure, a shallow depression, especially well marked in morphotype 5, or almost undetectable, as in the morphotypes 3 and 4. This character was considered by Ameghino (1889) as a diagnostic feature of the genus *Glyptodon*. The aspect is decisive in the diagnosis of species as *G. munizi* (Ensenadan; Ameghino, 1889; Soibelzon et al., 2006) and *G. clavipes*, which proceeds from the Bonaerian-Lujanian of the Pampean Region (Ameghino, 1889; Duarte, 1997). This character has also been noted in the juvenile specimen illustrated by Lydekker (1894), which has been referred to the species *G. clavipes*, and by Rinderknecht (2000) who suggested the depression allowed a tentative assignment of the fossils studied therein to the same species. Although this depression is also present in juvenile specimens of other glyptodontid groups, as in some genera of the subfamily Sclerocalyptinae (e.g., *Eosclerocalyptus*, *Neosclerocalyptus*; Zurita, 2007; Zurita et al., 2005), in the context of association with other characters it allows a clear assignment to the genus *Glyptodon*. These descriptions allowed recognition of material previously referred to the genera *Neothoracophorus* and *Pseudothoracophorus* as belonging to juvenile *Glyptodon* specimens (Zurita et al., 2011a).

Order Folivora Delsuc, Catzefflis, Stanhope & Douzery, 2001  
Family Mylodontidae Ameghino, 1889  
Subfamily Scelidothieriinae Ameghino, 1904  
Genus *Scelidothierium* Owen, 1839

*Scelidothierium leptocephalum* Owen, 1840

Fig. 5(F–L)

**Material and provenance:** CC–PZ 102: femur, tibia, fibula, patella, cuboid, astragalus, metatarsals, and several sesamoids, belonging to an articulated hindlimb, and a tooth fragment. All this material was found in the reddish pedogenetic sandy silt from Pampa Vaca Corral (FL 1; Tauber and Goya, 2006; Krapovickas and Tauber, 2016). CORD-PZ 4464: left complete forelimb with complete clavicle and distal part of scapula, found in the pedogenetic sandy silt from Pampa de Oláen (FL 3; 31°9'11.2" S, 64°35'31.3" W, 1138 m a.s.l.). MDVS-PV 0043: incomplete skull, without teeth crowns, basicranium, and zygomatic arches, from the reddish pedogenetic sandy silt from Atos Pampa, in the Bt layer from this paleosol (FL 12; 31°58'37.8" S, 64°41'51.6" W, 1110 m a.s.l.).

**Biostratigraphical and geographical distribution:** This species first appears during the Bonaerian (0.78–ca. 0.5 Ma) and the last record occurs in the Lujanian (~130–7 ka BP) (Cione and Tonni, 2005; Cione et al., 2009; Miño-Boilini, 2012), reaching 7550 ± 60 years BP at the eastern piedmont of Sierra de las Peñas, in the province of Córdoba (Cruz et al., 2010). In Argentina, it is recorded in the Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Salta, San Luis, and Santa Fe provinces. However, the best records in both number and preservation come from the Pampean Region (Miño-Boilini, 2012).

**Description:** The material of CORD-PZ 4464 (Fig. 5(F–H)) was assigned to this species on the basis of three features: absence of ungual phalanx in digit I of the manus (Fig. 5(G); McDonald, 1987; Miño-Boilini, 2012), absence of articulation between the unciform and metacarpal V (Fig. 5(H)), and entepicondylar foramen in the humerus undivided (Esteban et al., 1992).

MDVS-PV 0043 is an elongate and tubular skull (Fig. 5(I–K)). In palatal view, the dental series are almost parallel, as in *Catonyx tarijensis*, *C. chiliensis*, and *Scelidothierium bravardi* (Fig. 5(L)). In addition, two longitudinal sulci are found in the palate, parallel to the dental series. Miño-Boilini (2012) postulated that *C. tarijensis* and *C. chiliensis* present a sulcus parallel to the upper tooth rows, unlike *Scelidothierium leptocephalum*. In MDVS-PV 0043 these sulci are present (Fig. 5(L)). The palate is almost flat in lateral view, as in *Scelidothierium*, whereas in *Valgipes* and *Catonyx* it is uniformly convex (Miño-Boilini, 2012). The Mf1–3 sections are subelliptical and Mf4–5 sections are subtriangular, as in *Scelidothierium*. In frontal view, the external nares are dorsally wide and ventrally narrow, giving the skull a triangular aspect, as in *Scelidothierium*, and contrasting with the subcircular shape of the skull of *Catonyx*. The frontals are elongated and form most of the cranial vault. The postorbital constriction is more marked in *Scelidothierium* and *Catonyx*, and less marked in *Valgipes*. In MDVS-PV 0043, two separate temporal crests are seen, as in *Scelidothierium*. These crests are slightly marked in the studied material. In *Catonyx*, these two temporal crests are fused with the sagittal crest. Most of the cranial features described here (except for the palatal sulci parallel to the maxillary dental series) allow the assignment of MDVS-PV 0043 to *Scelidothierium leptocephalum*.

The left well-complete hindlimb (CC–PZ 102) was found articulated, with almost all bones present, except for the calcaneum and some metatarsals, and in a very good state of preservation. The tooth was found united to the fibula by means of carbonatic material. It is oval in section, with a longitudinal crest in the convex surface which extends along the entire tooth.

**Remarks:** The genus *Scelidothierium* and, especially, the species *S. leptocephalum* has been considered associated to digging ability and to the production of crotonines in the sedimentary record (Vizcaíno et al., 2001). These filled paleocaves are very profuse in the area in which the fossil remains of this species were found.

*Scelidotherium* sp.

Fig. 6(A)

**Material and provenance:** CORD-PZ 4466: humerus found at the highest part of Unit A by Tauber and Goya (2006), in the Northern lateral profile of Pampa de Vaca Corral (FL 1; 31°10'54.8" S, 64°52'8.8" W, 1593 m a.s.l.).

**Description:** This humerus is much eroded, precluding recognition of most features. Few muscular insertion crests are preserved. The deltoid tuberosity is not preserved. The humeral diaphysis is elongated and slender, contrasting with the condition of *Catonyx*, in which it is very robust and short. However, the diaphysis of CORD-PZ 4466 is more massive than those of *Catonyx cuvieri* and *Valgipes bucklandi*. The entepicondylar foramen is present (Fig. 6(A), white arrow), indicating that the specimen does not belong to *Catonyx cuvieri*.

Genus *Catonyx* (Ameghino, 1881)

*Catonyx tarijensis* (Gervais and Ameghino, 1880)

Fig. 6(B–D)

**Material and provenance:** CORD-PZ 4465: incomplete mandible with disjointed rami, coming from the layer B<sub>k</sub> of the basal paleosol of Atum Pampa (FL 14; 32°7'25.5" S; 64°44'34.1" W, 1149 m a.s.l.).

**Biostratigraphical and geographical distribution:** *Catonyx tarijensis* is recorded in the Ensenadan of the “Toscas” of the Río de La Plata and Miramar, the Bonaerian of the Mar del Plata City, the Lujanian of the Provinces of Buenos Aires and Corrientes, and in the Pleistocene of Córdoba (Miño-Boilini, 2012).

**Description:** In lateral view, the mandible is more robust than in *Scelidotherium*; the tooth-bearing and symphyseal region are complete and present a strongly convex and dorsally inclined ventral border, in contrast with the condition in *Scelidotherium*, *Catonyx cuvieri*, and *Valgipes* (Fig. 6(B); Miño-Boilini, 2016). No mandibular keel is observed at the symphysis (Fig. 6(C)).

The teeth are worn out. All dental pieces, except for the third molariform, are subtriangular in section, in contrast with *Scelidotherium* and *Catonyx chiliensis*, in which the mandibular series present a subelliptical contour in section. The three-mesialmost teeth possess wide and deep vertical lingual apicobasal sulci, unlike *Catonyx chiliensis* (Fig. 6(D)).

**Remarks:** In the last decades, a debate emerged on the nomenclatural validity of the genus name “*Scelidodon*”. Ameghino (1881) coins this genus on the basis of a maxillary fragment in which Mf1 is complete, Mf2 broken, and the other teeth lacking, although their alveoli are present (Miño-Boilini, 2012). Ameghino (1881) selected this specimen as the holotype of *Scelidodon copei*, this species representing the type species of the genus *Scelidodon*. Latter on, the species *S. tarijensis* (Gervais and Ameghino, 1880) and *S. chiliensis* (Lydekker, 1886) were also referred to the genus. Lydekker (1894) and McDonald (1987) claimed that the type specimen is very fragmentary, precluding any precise taxonomic assignment. McDonald (1987) proposed that *S. copei* is a junior synonym of *Scelidotherium*, and so *S. copei* is a *nomen dubium*; Miño-Boilini (2012) considers it a *nomen vanum*. On the other hand, McDonald and Perea (2002) proposed that, as *Catonyx* is a junior synonym of *Scelidotherium* and as *S. tarijensis* and *S. chiliensis* are recovered as near relatives of *Catonyx cuvieri* in their phylogenetic analysis, *Catonyx* is the most appropriate name to include the species traditionally assigned to *Scelidodon* (Corona et al., 2013).

Genus *Proscelidodon* Bordas, 1935

*Proscelidodon* sp.

Fig. 6(E)

**Material and provenance:** CORD-PZ 4471: isolated tooth found in a reddish sandy-clay stratum, at the base of the profile in the Panaholma town (FL 9; 31°37'1.3" S; 65°4'1.9" W, 985 m a.s.l.).

**Biostratigraphical and geographical distribution:** Its distribution ranges from the Huayquerian (middle to late Miocene) to the Chapadmalalan (late Pliocene) in Argentina, and from the Montehermosan (late Miocene or early Pliocene; Reguero and Candela, 2011; Esteban et al., 2014) to the Chapadmalalan in Bolivia (Pujos et al., 2012).

**Description:** The studied material is a tooth crown formed by two lobes, which are limited by two deep and wide sulci extended along the tooth. One of the sulci is wider than the other. The tooth is high, somewhat curved; the base of the root is not exposed, but the occlusal surface is present (Fig. 6(E)). In occlusal view, the lobes are located in the corners of an isosceles triangle. The assignment of the material is partially based on this feature, because the species of *Proscelidodon* have maxillary teeth with the most perfectly triangular section among all of the *Scelidotheriinae* (i.e., *Scelidotherium* and *Catonyx*; Miño-Boilini, 2012). In addition, comparison with the material of *P. patrius* published by Pujos et al. (2012) and the reduced size of the dental piece (50 mm in partial height, 14.2 mm in medio-distal diameter, and 11.4 mm in labio-lingual diameter) excludes its referral to large-sized sloths within the subfamily. Among the previously described sulci, the widest is labially directed, and the narrowest is directed medio-lingually (Pujos et al., 2012), so this tooth probably corresponds to a right M2–M4 (this one is subelliptical in section).

Subfamily Mylodontinae Gill, 1872

Genus *Glossotherium* Owen, 1839

*Glossotherium* sp.

Fig. 6(F–H)

**Material and provenance:** MCNC-PV 290: partially complete mandible extracted from the pedogenetic sandy silt (layer B<sub>12</sub>) of the base of the Pampa Vaca Corral (FL 1; 31°10'57.2" S, 64°52'9.9" W, 1554 m a.s.l.).

**Biostratigraphical and geographical distribution:** Its biostratigraphical distribution ranges from the Middle Marplatian (Vorohuan, late Pliocene) to the Bonaerian (middle-late Pleistocene) (Cione and Tonni, 2005), Pliocene of Argentina, and Pleistocene of South America (Brandoni et al., 2010).

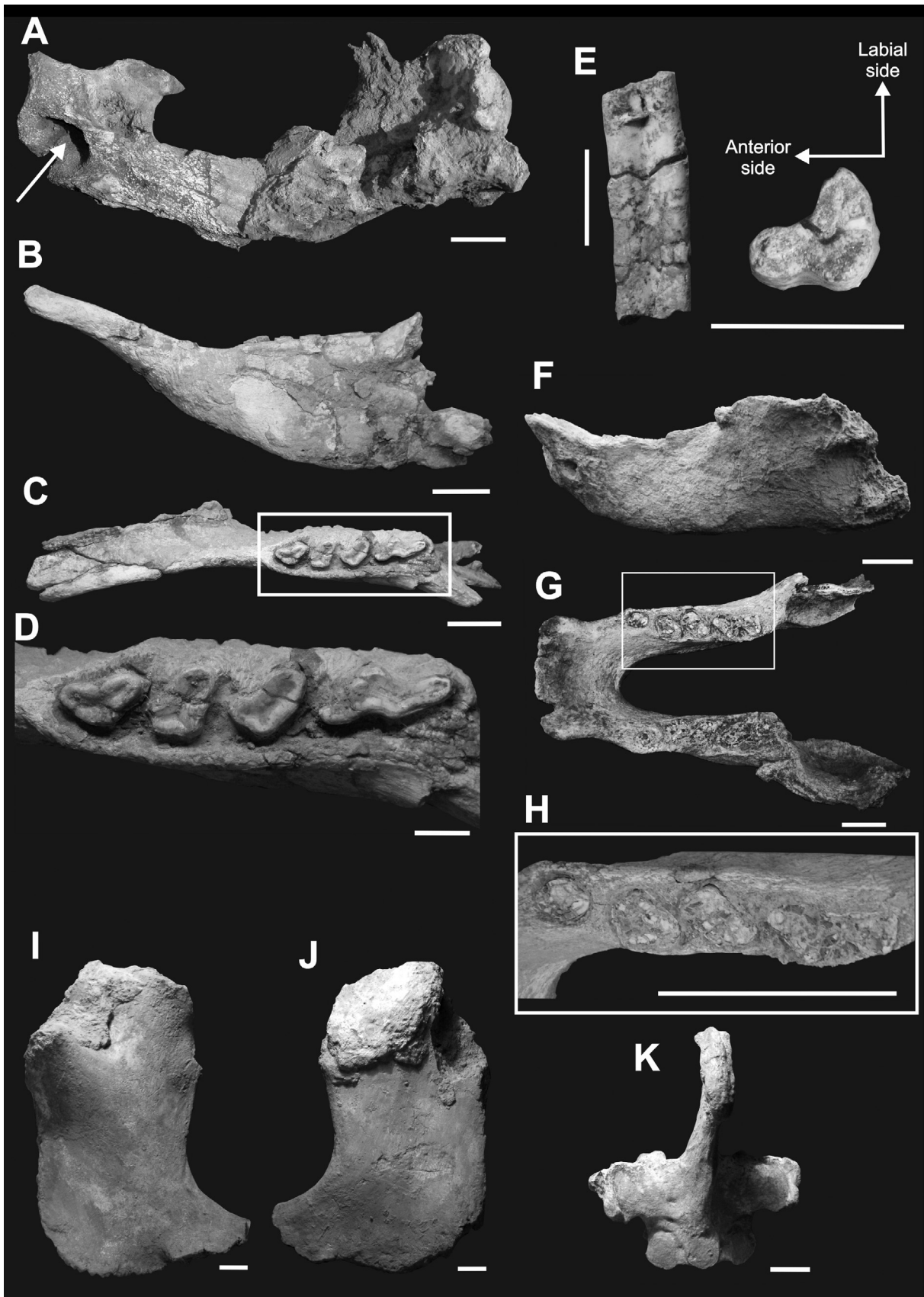
**Description:** The referred material is a robust mandible; the horizontal ramus is short (Fig. 6(F)), in contrast with *Myloodon darwini*, in which the mandible is relatively elongated and gracile (Owen, 1842; Brandoni et al., 2010). The ventral margin of the mandible is almost straight, deflecting dorsalward to the symphysis, in contrast with *Myloodon darwini* in which the symphysis forms a lower angle relative to the tooth-bearing region. The symphyseal region is flat, shovel-shaped, toothless, concave in dorsal view, convex in its ventral limit, and much wider than in *Myloodon*. The small mandibular keel is blunt in lateral view, whereas in *Myloodon* it is larger and pointed (Brandoni et al., 2010).

The dental series consists of four badly preserved molariforms (mf1–mf4; Fig. 6(G)). These teeth lean somewhat towards the oral cavity, although to a lower degree than in *Myloodon*. The mf1 are circular in section (Fig. 6(H)), in contrast with *Lestodon*, in which they are triangular (Hoffstetter, 1958). They are separated from the rest of the dental series by a large diastema, whereas the feature is absent in *Myloodon* (Brandoni et al., 2010). The mf2 are rhomboidal in section, as in *Myloodon*.

Myloodontidae indet.

Fig. 6(I–K)

**Material and provenance:** CORD-PZ 4475: femoral diaphysis found in Atos Pampa, in the basal paleosol (FL 12; 31°58'52.7" S, 64°42'24.1" W, 1135 m a.s.l.). CORD-PZ 4288: two thoracic vertebrae found by Córdoba (2005) in Pampa de Oláen, approximately 150 m from the section of Arroyo Los Talas, on a brown-yellowish massive sandy silt (FL 4; 31°7'41.6" S, 64°36'22.7" W).



**Fig. 6.** **A.** *Scelidotherium* sp. (CORD-PZ 4466): humerus with entepicondilar foramen (white arrow). **B–D.** *Catonyx tarijensis* (CORD-PZ 4465). **B, C.** Left mandibular ramus in labial (top) and occlusal (bottom) views; **D.** Detail of caniniform and molariforms. **E.** *Proscelidodon* sp. (CORD-PZ 4471): left upper molariform in labial (left) and occlusal (right) views. **F–H.** *Glossotherium* sp. (MCNC-PV 290). **F, G.** Partially complete mandible in lateral and occlusal views, respectively; **H.** Detail of the molariforms in occlusal view. **I, J.** Mylodontidae indet. (CORD-PZ 4475): femoral diaphysis in anterior and posterior views, respectively. **K.** Mylodontidae indet. (CORD-PZ 4467): thoracic vertebrae in dorsal view. Scale bars: 2 cm (D, E), 3 cm (I–K), and 5 cm (A–C, F–H).



CORD-PZ 4467: incomplete thoracic vertebra found in the basal paleosol of Atos Pampa (FL 12; 31°59'33.8" S, 64°41'20.4" W, 1074 m a.s.l.). CORD-PZ 4468: 71 bone remains found in the basal paleosol from Atos Pampa (FL 12; 31°58'57" S, 64°42'29.9" W, 1117 m a.s.l.).

**Biostratigraphical and geographical distribution:** This family ranges from the late Oligocene of the Argentinian Patagonia (Hoffstetter, 1954) and Bolivia (Pujos and De Iuliis, 2007) to the late Pleistocene of South and North America (Brandoni et al., 2010), and early Holocene of Argentina (Cruz et al., 2010).

**Description:** CORD-PZ 4475: the femoral diaphysis is medio-laterally expanded, with a subelliptical transverse section. The epiphyses were not preserved (Fig. 6(I, J)), and the unfused joining surfaces for the latter are exposed, suggesting the bone belongs to a juvenile or sub-adult individual. The diaphyseal surface does not present crests or sulci for muscular attachment, which are common in the femora of *Megatherium*. In *Glossotherium*, the femoral diaphyses are mediolaterally expanded, with scarcely raised crests (Owen, 1842), as in the present material.

Most of the rest of the material corresponds principally to thoracic vertebrae (e.g., CORD-PZ 4288, 4467, and 4468). These have a centrum similar in size to the medullar canal, a raised and robust neural spine, wide transverse processes and parapophyses for the capitula of the ribs. An interesting feature found in these material is the presence of an accessory midline articulation between the neural arches (Fig. 6(K)). This configuration is common in many different sloth taxa: *Megatherium americanum* (Owen, 1861), *Paramylodon harlani* (Stock, 1925), *Scelidotheriinae*, and many other extant xenarthrans (Gaudin, 1999). CORD-PZ 4468 presents a fragment of ungual phalanx of circular section and smaller in size than that of an adult *Scelidotherium*.

Family Megatheriidae Owen, 1843

Subfamily Megatheriinae Gill, 1872

Genus *Megatherium* Cuvier, 1796

*Megatherium americanum* Cuvier, 1796

Fig. 7(A–E)

**Material and provenance:** MCNC-PV 00189: skull, mandible, and atlas found in the B<sub>12</sub> and B<sub>12</sub> from the paleosol of Vaca Corral (FL 1; 31°10'55.9" S, 64°52'9.1" W, 1550 m a.s.l.).

**Biostratigraphical and geographical distribution:** Ranges from the Bonaerian (middle Pleistocene, 0.78–ca. 0.5 Ma; Cione and Tonni, 2005) up to the Lujanian (late Pleistocene–early Holocene, ~130–6.7 ka BP; Politis and Messinio, 2008). It is the only megatheriine species recorded in Argentina for this time span, ranging approximately from Patagonia to southern Bolivia (Pujos et al., 2017).

**Description:** The skull is very different from that of other Quaternary sloths from Argentina; its general shape is cylindrical, with relatively short, narrow and high face (Fig. 7(A)). The size is bigger and more robust than all species of *Megatherium* (i.e., *M. altiplanicum*, *M. medinae*, *M. celendinense*, *M. sundti*, *M. tarijense*, and *M. gallardoi*; Saint-André and De Iuliis, 2001; Iuliis et al., 2009).

The incomplete premaxilla is elongate and quadrangular in shape (Fig. 7(A)). In *Eremotherium*, the premaxillae are approximately triangular, showing V-shaped plates with an anterior apex, and lack elongated anterior processes (Iuliis et al., 2009). The maxilla, which possesses all the teeth, is trapezoidal and its ventral border is straight. The anterior portion of the maxilla is short as in all *Megatherium* species and not elongated as in *Eremotherium* (Pujos, 2006). The premaxillae are fused to each other and with the maxillae (Fig. 7(B)), unlike *Megatherium medinae*, *M. celendinense*, *M. sundti*, *M. tarijense*, and *M. gallardoi* (Pujos, 2006; Brandoni et al., 2008). However, one review postulates that *M. tarijensis* presents the same condition as *M. americanum* in the fusion degree of

premaxillary and maxillary (Iuliis et al., 2009). The zygomatic arch is elongated and robust; the descending process is dorsoventrally elongate and rostrocaudally wide, almost reaching the ventral border of the mandible if the latter is articulated to the skull in closed mouth position.

The upper dental series is complete and consists of five teeth, which are beveled and quadrangular in section (Fig. 7(C)). In *M. americanum*, normally the last one is more triangular in section (F.P., comm. pers.). The first four molar teeth are approximately similar in size, and the most distal one is far smaller. The palate is narrow and shows numerous nutritive foramina.

The mandible is robust, with the ventral border very convex, and “U”-shaped in lateral view at the middle part, reflecting the increased hypsodonty in this species (Fig. 7 (A, D); Bargo, 2001). The Hypsodonty Index (HI) is 98 in MCNC-PV 00189, following McDonald (1995). This value lies within the variation of *M. americanum* (HI = 92–112; Brandoni et al., 2008). The mandibular dental series is parallel to the long axis of the mandible (Fig. 7(D, E)), without leaning towards the oral cavity, contrasting with the condition in Quaternary mylodontids (e.g., *Scelidotherium*, *Catonyx*, *Glossotherium*, etc.). The series is formed by four quadrangular teeth of approximately the same size, and similar in shape to those in the maxillary series. The ascending ramus of the mandible is robust and tall, with the long axis leaning caudally. The angular and coronoid processes are large and bear strong crests for muscular attachment. The articular process is elongated in the medio-lateral direction. The mandibular canal is dorsally open, as in all Megatheriinae (Fig. 7(E); Pujos, 2006). The position of the posterior extremity of the symphysis of the mandible is posterior with respect to m1 (Fig. 7 (E)), like in all Megatheriinae except for *Megathericulus patagonicus* and *Plesiomegatherium halmyronomus* (Pujos, 2006).

In the ear region of the skull, the ectotympanic bone is approximately smooth, unlike in *Eremotherium* (Pujos, 2006). The atlas is complete and not fused with the axis, unlike in *Eremotherium* (Pujos, 2006).

*Megatherium* sp.

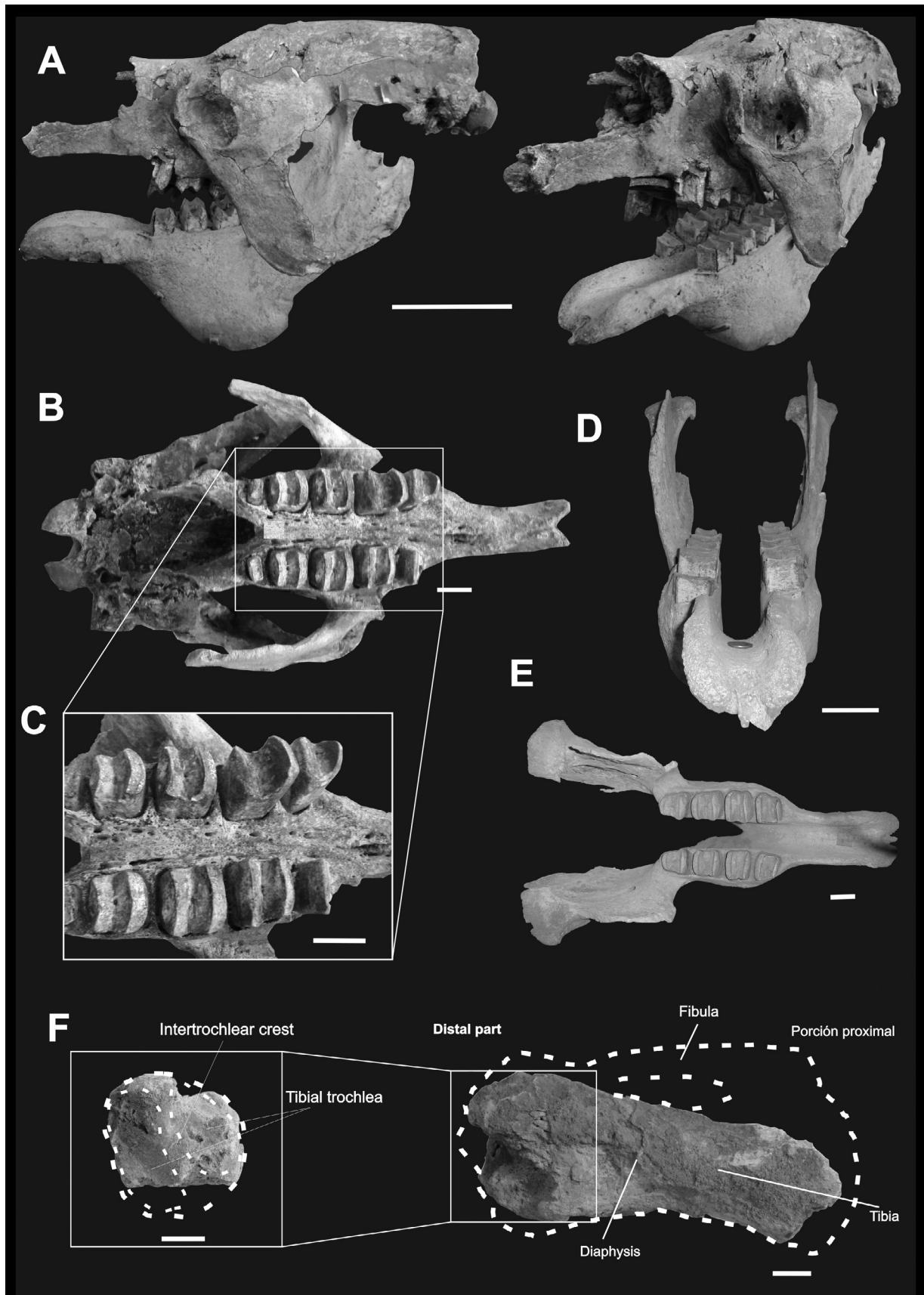
Fig. 7(F)

**Material and provenance:** CORD-PZ 4470: highly eroded tibia found in clast-supported conglomerate from Huerta Grande (FL 6; 31°3'55.6" S, 64°30'33.3" W, 1003 m a.s.l.).

**Biostratigraphical and geographical distribution:** The genus ranges from the Montehermosan (early Pliocene, *Megatherium altiplanicum* from Bolivia; De Iuliis and St-André, 2001) to the Lujanian (late Pleistocene–early Holocene, *M. americanum*, ~130 to 7 ka BP, probably 6.7 ka BP; Politis and Messinio, 2008).

**Description:** Only parts of the diaphysis and distal articular end are preserved. Its dimensions are large (> 495.6 mm long and > 196.4 mm wide at the distal end). The referral was performed comparing to MPAM 855 (tibia of *Notiomastodon platensis*, compared because of its size) and CORD-PZ 4588 (complete skeleton of *Megatherium americanum*).

In the present material, the distal articular surface (for articulation with the tarsal bones) is subdivided in two shallow smaller facets (the tibial trochleas; Fig. 7(F)) by a blunt longitudinal intertrochlear crest. In *Notiomastodon*, comparable in size with the tibia of CORD-PZ 4470, this crest is not very evident and in MPAM 855 it is absent, resulting in a single, strongly concave articular facet. The paired trochlear configuration is typical of Argentinian Quaternary ground sloths. However, in mylodontids as *Glossotherium*, both facets for articulation with the astragalus are very deep (Owen, 1842). In *Megatherium* the tibio-astragalar articulation is much laxer (Owen, 1851).



**Fig. 7. A–E.** *Megatherium americanum* (MCNC-PV 00189). A. Articulated skull and jaw in lateral (left) and antero-lateral (right) views; B, C. Skull in occlusal view; D, E. Jaw in frontal and occlusal views, respectively. **F.** *Megatherium* sp. (CORD-PZ 4470): very eroded tibia in distal (left) and lateral (right) views. Scale bars: 5 cm (B–F), and 10 cm (A).

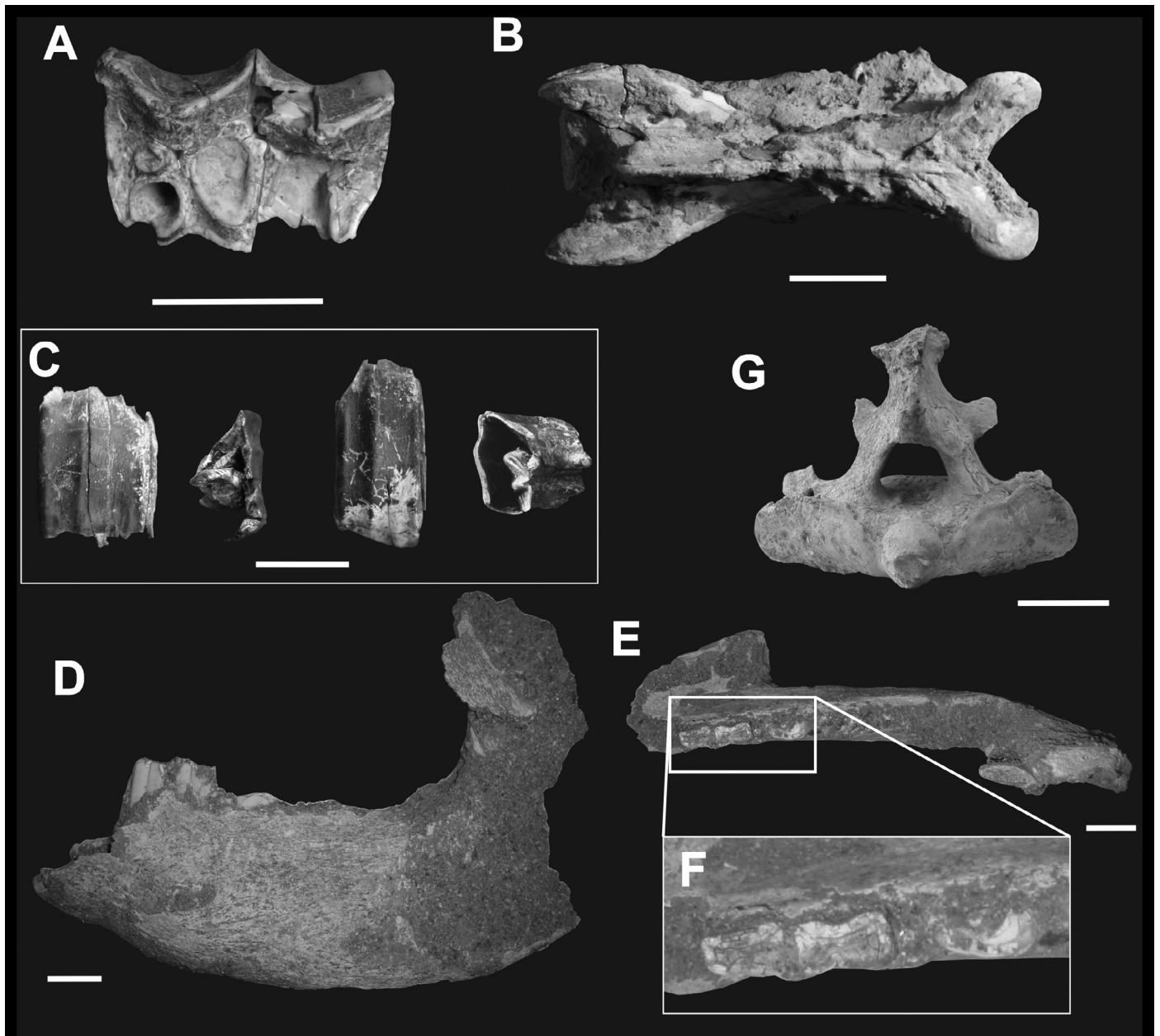
Order Litopterna [Ameghino, 1889](#)  
 Family Macraucheniidae Gill, 1872  
 Genus *Macrauchenia* Owen, 1838  
*Macrauchenia* sp.

[Fig. 8\(A, B\)](#)

**Material and provenance:** CORD-PZ 4292: fragment of a p4 extracted from Unit A (reddish pedogenetic sandy silt, FL 1), collected in the fossil bed of Vaca Corral by [Goya \(2003\)](#). CORD-PZ 15416: left M2 from the origin of the Los Talas stream in the area of Pampa de Olaen, in a level which seems to correlate to the basal pedogenetic sandy silt (FL 3), collected by [Leonardi \(1961\)](#). CORD-PZ 4474: complete cervical vertebra, and fragment of another found at the highest part of the reddish carbonatic sandy silt stratum (layer B<sub>k</sub>) in the locality of Atos Pampa (FL 12; 31°58'52.7" S, 64°42'24.1" W, 1135 m a.s.l.).

**Biostratigraphical and geographical distribution:** The genus presents a widespread distribution, ranging from Pernambuco, Brazil, in the Atlantic slope, to the Última Esperanza Inlet caves, in southern Chile. The oldest record of the species *Macrauchenia patachonica* is Bonaerian ([Cione and Tonni, 2005](#)), and the youngest is early Holocene, with a record associated with human beings dated as  $8390 \pm 140$  years BP ([Goya, 2003](#)).

**Description:** CORD-PZ 15416: This M2 is worn out. In labial view, the ectoloph is smooth, deeply curved and divided along the crown by a blunt crest, which forms the very noticeable mesostyle. Paracone and metacone are selenodont; the protoloph presents three fossettes, two mesial and one lingual. A distal fossette was figured by [Leonardi \(1961\)](#) which, owing to wear, opens relative to the hypocone, creating a deep sulcus which extends along the height of the crown in lingual view ([Fig. 8\(A\)](#)). However, this



**Fig. 8. A, B.** *Macrauchenia* sp. A. Fragment of a p4 (CORD-PZ 15416) in occlusal view; B. Cervical vertebra (CORD-PZ 4474). C. *Mesotherium* sp. (from left to right): fragment of M2 in labial and occlusal views, and fragment of M3 in labial and occlusal views, respectively. D–G. *Toxodon* sp. D. Left mandibular ramus in lateral view (CORD-PZ 4476); E. Mandibular ramus in occlusal view; F. Detail of p1, p2 (with trigonid and talonid), and p3; G. Axis (CORD-PZ 4477) in proximal view. Scale bars: 2 cm (C), 3 cm (A, B), 4 cm (D, E), and 5 cm (G).



fossette is not conserved in this specimen. These features agree with those figured for *Macrauchenia patachonica* by Cope (1891) and Guérin and Faure (2004).

CORD-PZ 4292: the lingual surface of the p4 crown is concave and presents a vertical crest at its middle portion, which becomes narrower towards the occlusal border. The labial surface is convex and more curved than the lingual one. The occlusal surface is not worn, and the contour of the crown preserves a serrated edge. The greatest width exceeds 22 mm, whereas the height exceeds 26 mm. The thickness at the level of the middle process is 9 mm, narrowing towards the occlusal border to 2 mm.

The cervical vertebra CORD-PZ 4474 is compact and elongate (approximately twice as long as wide); the pre- and post-zygapophyses are short, robust, and aligned in the plane of the vertebral body, which presents a low but continuous keel along its extension (Fig. 8(B)). Over the dorsal border, the vertebrae are very decayed, precluding adequate description. This material was referred to the genus *Macrauchenia* because of its elongate proportions.

**Remarks:** Remains of this species collected by Ameghino were reported by Castellanos (1944) for the “upper Bonaerian”, and by Cruz et al. (2012), coming from the “Cava de Carobolante” in the locality of San Francisco, considered as Bonaerian in age *sensu* Cione and Tonni (2005).

Order Notoungulata Roth, 1903  
Family Mesotheriidae Alston, 1876  
Genus *Mesotherium* Serres, 1867  
*Mesotherium* sp.

Fig. 8(C)

**Material and provenance:** CORD-PZ 15568: enamel fragments of at least three upper molars found in the clast-supported basal conglomerate from Huerta Grande (FL 6; 31°4'8.62" S, 64°30'14.52" W, 1003 m a.s.l.).

**Biostratigraphical and geographical distribution:** The only Pleistocene *Mesotherium* species of biostratigraphical use is *M. cristatum*, and its distribution is limited to the Ensenadan (early Pleistocene; Cione and Tonni, 2005).

**Description:** The teeth are small, rectangular, high-crowned, with smooth ectoloph, except for a crest extending along its height at the labial surface (Fig. 8(C)). The teeth are curved towards the oral cavity, with mesio-distal diameter greater than the labio-lingual one, and with two shallow sulci (in occlusal view, they do not surpass the tooth moiety) that delimitate three lobes on the lingual surface which constitute the anterior, medial, and posterior fossettes (Fig. 8(C); Flynn et al., 2005). We identified at least three teeth, interpreted as the left M1–M3.

These features point to Mesotheriidae notoungulates. Members of the family Hegetotheriidae do not present lingual sulci in upper molars (e.g., *Hegetotherium* and *Pachyrucos*; Sinclair, 1909) and those belonging to the family Interatheriidae present a single sulcus (e.g., *Protypotherium* and *Interatherium*; Krapovickas et al., 2008; Krapovickas, 2009). In Toxodontidae, the molars are larger, subtriangular and bear two lobes towards the lingual surface (Miño-Boilini et al., 2006). *Mesotherium cristatum* is very common in Pleistocene deposits from the Pampean Region of Argentina. In addition, *Mesotherium* is the youngest representative of this family. For these reasons, we identified these remains as belonging to the genus *Mesotherium*.

Family Toxodontidae Gervais, 1847  
Genus *Toxodon* Owen, 1837  
*Toxodon* sp.

Fig. 8(D–G)

**Material and provenance:** CORD-PZ 4476: left mandibular ramus with p1, p2, and part of p3, found in the clast-supported conglomerate from Huerta Grande (FL 6; 31°3'55.6" S, 64°30'33.3"

W, 1003 m a.s.l.). CORD-PZ 4477: axis found in the basal fanglomerate from the eastern coast of Arroyo Bosque Alegre in the Copina-Bosque Alegre area (FL 10; 31°39'59.8" S, 64°35'6.27" W, 930 m a.s.l.).

**Biostratigraphical and geographical distribution:** The oldest record of the genus *Toxodon* dates back to the Chapadmalalan (Pliocene, ca. 4.8–4.2 Ma) and is frequent in the Lujanian (middle Pleistocene–early Holocene) of Argentina and Uruguay. This genus has also been found in Bolivia, Brazil, Paraguay, and Northern Venezuela (Miño-Boilini et al., 2006).

**Description:** CORD-PZ 4476: the mandibular ramus is robust, proportionally taller and shorter than in *Mixotoxodon*. The wear of the tooth elements is high (Fig. 8(D, E)). The p1 is elliptical (mesio-distal diameter: 25.4 mm; labio-lingual diameter: 14.2 mm); p2 (mesio-distal diameter: 29 mm) is typical of members of *Toxodon*, with a well-formed trigonid (labio-lingual diameter: 16.6 mm) and talonid (labio-lingual diameter: 17 mm); p3 only preserves the lingual surface of the ectoloph, in which the enamel layer is found, but not the cement (Fig. 8(F)).

CORD-PZ 4477 is a large-sized axis. The maximal transverse diameter of the vertebra is of 248.6 mm. The spinal apophysis is incomplete, wide, and triangular in section. The odontoid process exceeds the vertebral body; it is elongate, robust, and blunt at the apex (Fig. 8(G)). The dorsal articular surfaces for the atlas are widely extended on both sides, equal in length to the transverse processes, in contrast with the condition present in other coeval large mammals such as *Notiomastodon*, *Megatherium*, and *Glossotherium*, in which the surfaces are subcircular, small, and laterally surpassed by far by the transverse processes (Owen, 1842, 1861; Cabrera, 1929). The articular surface for the atlas and the transverse processes form a birrameous structure. In *Megatherium*, the transverse processes are independent from the dorsal articular surfaces and present two processes. In *Glossotherium*, the transverse processes present a single process, as in CORD-PZ 4477. The postzygapophyses can be seen in dorsal view and direct towards the sides, caudally and ventrally. In cranial view, both dorsal articular facets are marked, subelliptical in shape, with the mediolateral diameter being 68 mm and the height 42.6 mm. These surfaces are somewhat concave, contrasting with the condition of *Megatherium*, in which they are clearly convex (Owen, 1861). In caudal view, the size of the vertebral body is similar to that of the neural canal, and the postzygapophyses are subelliptical in section. In *Notiomastodon*, the vertebral body is proportionally larger than the neural canal. Ventrally, the vertebral keel is absent, but a concave surface is present, which is limited by the dorsal articular surfaces and the odontoid process.

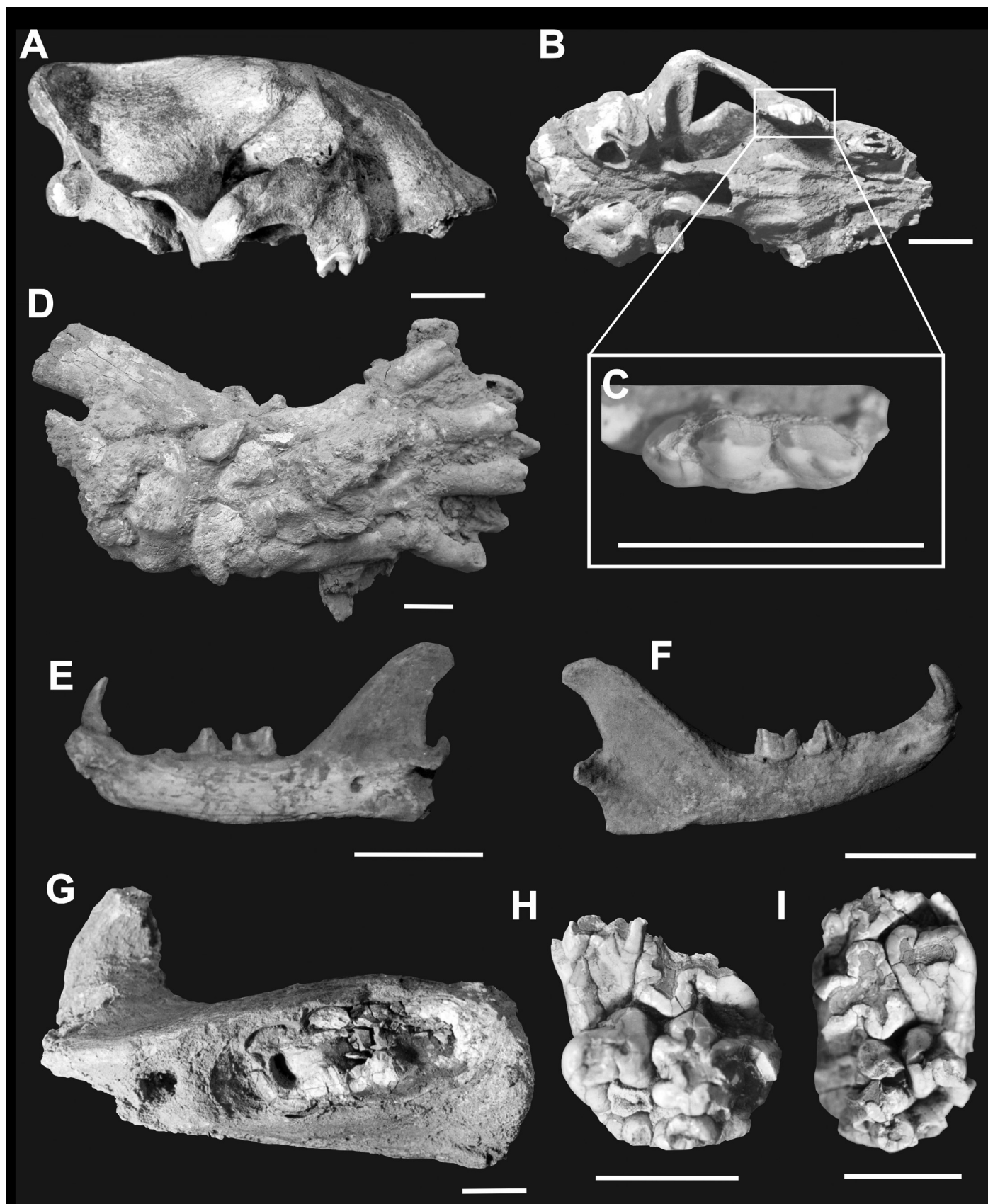
**Remarks:** The axis is referred to the genus *Toxodon* owing to its large size and its morphological differences with megatheriines, mylodontids, and gomphotheriids. So far, only two species of *Toxodon* are known for the Quaternary of Argentina: *T. platensis* and *T. gracilis*.

Order Carnivora Bowdich, 1821  
Family Felidae Gray, 1821  
Genus *Smilodon* Lund, 1842  
*Smilodon populator*

Fig. 9(A–D)

**Material and provenance:** CC-PZ 103: subcomplete skull of an adult individual found in the pedogenetic sandy silt (FL 1; equivalent to Unit A in Goya, 2003; Tauber and Goya, 2006) in the fossiliferous beds from Vaca Corral. CORD-PZ 4478: two thoracic member autopodia, of which the left one is complete, coming from the reddish carbonatic sandy silt (B<sub>K</sub> layer) from Atos Pampa (FL 12; 31°58'53.6" S, 64°42'25.4" W, 1130 m a.s.l.).

**Biostratigraphical and geographical distribution:** This species extends along the Ensenadan–Lujanian time span (Cruz et al.,



**Fig. 9.** **A–D.** *Smilodon populator*. **A, B.** Skull (CC–PZ 103) in lateral and occlusal views, respectively; **C.** Detail of the well-preserved P4; **D.** Left thoracic member autopodia (CORD–PZ 4478/1). **E, F.** *Oncifelis* sp. (CORD–PZ 4480): left mandibular ramus in lingual and labial views, respectively. **G–I.** *Notiomastodon platensis* (CC–PZ 106; modified from Goya, 2003). **G.** Left mandibular ramus with the root of a molar in occlusal view; **H, I.** Fragments of lower molariforms in occlusal view. Scale bars: 2 cm (E, F), 3 cm (D), and 5 cm (A–C, G–I).

2012). In Córdoba Province, a nearly complete skeleton was recovered in San Francisco (Zurita et al., 2007).

**Description:** CC-PZ 103: subcomplete skull, lacking the left zygomatic bone and part of the ipsilateral squamosal (Fig. 9(A)). The right P4 is very well preserved. From the right P3 and the canines, only the roots are preserved. The latter are approximately aligned parallel to the longitudinal axis of the skull (Fig. 9 (B, C)). For M1 only the root is available, forming a nearly straight angle to the long axis of P4. Only the intra-alveolar parts of the incisors are preserved (Fig. 9(B); Goya, 2003).

Kurten and Werdelin, 1990 concluded that *Smilodon populator* is distinguished from *S. fatalis* by the following derived characters:

- especially large size in Lujanian times;
- skull elongated and narrow;
- cranial part of skull lengthened in comparison with facial part;
- high nasals and straight upper profile of skull;
- proximal limb segments long, distal segments shortened;
- metapodials very broad and massive;
- forelimb somewhat elongated relative to hind limb.

In CC-PZ 103, the second, third and fourth characters mentioned above are presents (Fig. 9(A)). Also, the skull is much more robust than in *Homotherium* (Rawn-Schatzinger, 1992). The morphology of CC-PZ 103 coincides with the material previously assigned to *S. populator* (e.g., CORD-PZ 1739).

CORD-PZ 4478 is a left manus with seven carpals preserved, arranged in two rows: from medial to lateral side, the proximal row consists of the scapholunar, cuneiform, and pisiform, and the distal row consists of the trapezium, trapezoid, magnum, and unciform (Fig. 9(D)). The scapholunar is a large and massive bone, contrasting with *Homotherium* in which it is small and gracile. It is irregular in shape, approximately “S”-shaped in lateral view, whereas in *Homotherium* it is rectangular. Another diagnostic feature is the articulation between the cuneiform and metacarpal V (Rawn-Schatzinger, 1992). On the right manus, several carpals and the entire digit V are lacking. Metacarpal II presents a prolongation surrounding the proximal part of metacarpal III. This lateral process is much larger in CORD-PZ 4478 than in *S. fatalis* and *Homotherium*. The manus is more robust than in *Homotherium*. The ungual phalanges are robust, in contrast with *Homotherium*, but proportionally less developed than in *S. fatalis*.

Genus *Oncifelis* Severtzov, 1858

*Oncifelis* sp.

Fig. 9(E, F)

**Material and provenance:** CORD-PZ 4480: complete left mandibular ramus (the crown of the p3 is missing), from a bioturbated dark sandy silt in Pampa de Olaen (FL 5; 31°8'4" S, 64°34'38.9" W, 1122 m a.s.l.).

**Biostratigraphical and geographical distribution:** the fossil record of this genus spans from the late Pleistocene (Seymour, 1999; Prevosti, 2006) to Present days (Soibelzon and Prevosti, 2007). Species of this genus are distributed from Southeastern Bolivia, Southern and Western Paraguay, Southern Brasil, Uruguay and most of the Argentinian territory (Seymour, 1999).

**Description:** The small size, proportionally larger c1 (Fig. 9(E)), and upwardly curved jaw near the symphysis (Fig. 9(F)) identify this specimen as a Neotropical cat (Prevosti, 2006; Christiansen, 2008). The small mandibular ramus is nearly complete, only lacking the caudal border of the angular process. The lower canine is large, distally curved, leans labialwards, and without lingual cavity, unlike *Lynchaillurus colocolo* (Prevosti, 2006). At the base of this tooth, a mental foramen is present. The mandible is gracile, and its ventral border is straight. The ascending ramus is high, ending in a coronoid process at the tip, which is caudally curved.

The coronoid fossa is wide and deep, occupying all of the ascending process to the ventral border of the mandible. The articular process is small, approximately cylindrical in caudal view.

The p4 is formed by a tall protoconid and two small, barely visible accessory cusps on each side (paraconid and first posterior accessory cusp). The m1 is present, indicating that CORD-PZ 4480 corresponds to an adult individual (Salles, 1992). This tooth is bicuspidate, with the distal cusp (i.e., the paraconid) taller than the mesial one (i.e., the protoconid) and than the protoconid of p4.

**Remarks:** The fossil record of this genus is very scarce (Soibelzon and Prevosti, 2007), and the available diagnoses and descriptions for species of this genus are based on soft tissue characters (Seymour, 1999) and upper teeth (Salles, 1992; Mattern and McLennan, 2000).

Order Proboscidea Illiger, 1811

Family Gomphotheriidae Cabrera, 1929

Subfamily Anancinae Hay, 1922

Genus *Notiomastodon* Cabrera, 1929

*Notiomastodon platensis*

Fig. 9(G–I)

**Material and provenance:** CC-PZ 106: occipital fragment of skull including the condyles, fragment of left maxilla with rests of a molar, left mandibular ramus with the root of a molar and two other molar fragments, collected in the reddish pedogenetic sandy silt (FL 1; Goya, 2003).

**Biostratigraphical and geographical distribution:** Ensenadan and Lujanian stages (middle and late Pleistocene). It is the typical gomphothere of the South American lowlands, and distributes through Brazil, Ecuador, Venezuela, Colombia, Peru, Paraguay, Chile, Argentina, and Uruguay (Alberdi and Prado, 2008; Mothé et al., 2012).

**Description:** The mandibular ramus fragment preserves the roots of a large molar (Fig. 9(G)). The molar crown wear produced simple pairs of clover-like figures (trefoils) on the enamel (Fig. 9(H, I)). The alveolus of the lacking premolar is found at the frontal part of the mandible. Three characters, namely the big size of the mandible (> 40 cm), jaw with bunolophodont and trilophodont intermediate teeth (Prado et al., 2005), and worn molar accessory conelets showing a single trefoil pattern (Mothé et al., 2012), in addition to comparative study with the comparative material (e.g., CORD-PZ 11487, MCNC-PV 289, and MPAM-PV 20) allows the assignment of this specimen to *Notiomastodon platensis*.

**Remarks:** *Notiomastodon* seems to be adapted to plains with hot and wet to temperate climates. *Notiomastodon platensis* shows an evolution of food habits through time, with middle Pleistocene individuals presenting a mixed diet of C3–C4 plants, whereas the late Pleistocene specimens exclusively ate C3 plants (Prado et al., 2005).

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Subfamily Equinae Gray, 1821

Genus *Hippidion* Owen, 1869

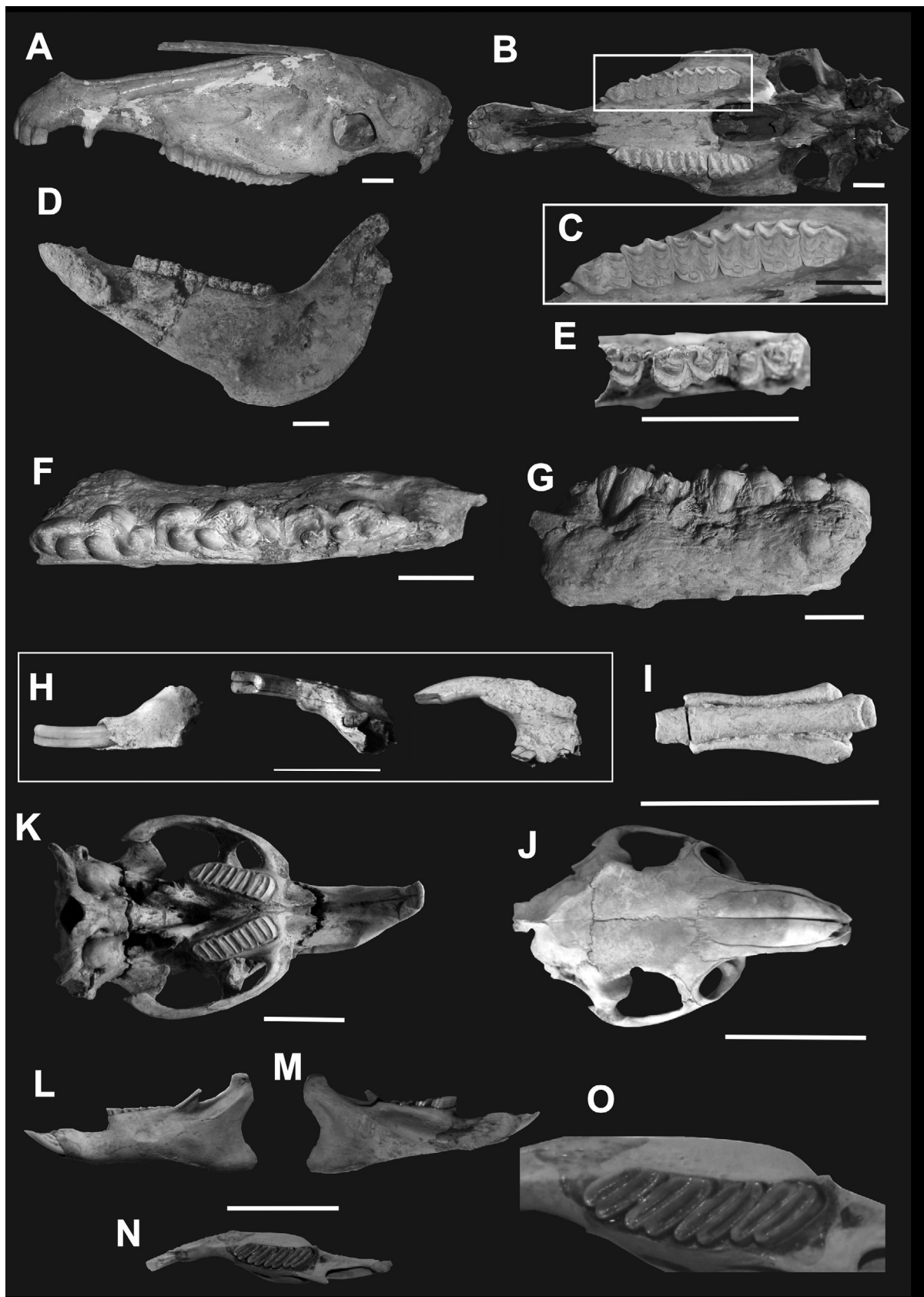
*Hippidion principale*

Fig. 10 (A–E)

**Material and provenance:** CC-PZ 107: right mandibular ramus fragment with two complete molars and half of a third, extracted from the pedogenetic sandy silt (FL 1; Goya, 2003) from the fossiliferous beds at Vaca Corral. CORD-PZ 4481: complete right mandibular ramus and ascending process of right mandible, unearthed in the Panaholma's area (FL 8; 31°34'57.7" S, 65°4'21.5" W, 1026 m a.s.l.). MDVS-PV 0012: nearly complete skull found at the base of the fanglomerate from Amboy (FL 16; 32°10'18" S, 64°33'41.3" W, 603 m a.s.l.).

**Biostratigraphical and geographical distribution:** Marplatense (late Pliocene; Cione and Tonni, 2005) to Lujanian (late Pleistocene





**Fig. 10.** A–E. *Hippidion principale*. A, B. Complete skull (MDVS-PV 0012) in lateral and occlusal views, respectively; C. Detail of the left upper tooth row (P1–M3), where it is observed a subcircular protocone and well-developed mesial and distal hypoconal sulci; D. Right mandibular ramus in lingual view (CORD-PZ 4481); E. Right mandibular ramus in occlusal view (CC–PZ 107). F, G. *Equus (Amerhippus)* sp. (CORD-PZ 4482): left mandibular fragment in occlusal and lateral views, respectively. H. *Ctenomys* sp. (CORD-PZ 4486): distal fragment of left mandibular ramus in frontal (left), occlusal (middle), and lingual (right) views. I–O. *Lagostomus maximus*. I. Metatarsals II–IV (CORD-PZ 4284); J, K. Complete skull in dorsal (CORD-PZ 4284) and occlusal (CORD-PZ 4485) views, respectively; L–N. Left mandibular ramus (CORD-PZ 4484) in labial, lingual, and occlusal views, respectively; O. Detail of bilophodont lower premolars and molars. Scale bars: 2 cm (F–H), 3 cm (K–N), 4 cm (A–C), and 5 cm (D, E, I).

to early Holocene). Its geographical range includes the Province of Buenos Aires (Argentina), Tarija (Bolivia), Artigas (Uruguay), Taguatagua (Chile), and several localities in Brazil (Alberdi et al., 2006).

**Description:** MDVS-PV 0012 is a complete skull with both dental series I1–M3. In lateral view, several diagnostic features of the species can be observed (Alberdi and Prado, 1993; Álvarez and Tauber, 1999):

- the dorsal profile shows an anterior convexity followed by a frontal-nasal inflection (unlike *H. devillei*; Alberdi and Prado, 2004), which in occipital-dorsal view is narrow;
- the upper cheek teeth are relatively curved in the linguo-ventral side;
- an inflection in the dorsal profile of the fronto-nasal region;
- retraction of the nasal bones to reach the level of the M2–M3 (unlike *Equus (Amerhippus)* sp.; Alberdi and Prado, 2004);
- stiletto-shaped nasals (Fig. 10 (A)).

The incisors are approximately equal in mesio-distal length; the canine is present and stiletto-shaped, as does the reduced P1 (Fig. 10(B, C)). The space between the incisors and the canine is smaller than the space formed between C and P1 (Fig. 10(B)). In occlusal view, the P2 is rectangular in shape, whereas the other premolars and molars are square. The P4–M1 are mesio-distally and labio-lingually longer than all the other teeth in the maxillary series. All the dental elements present a high degree of wear. The premolars and molars show a subcircular protocone and well-developed mesial and distal hypoconal sulci (Fig. 10(C)).

CORD-PZ 4481 is a complete mandibular ramus stouter than in *Equus* (Fig. 10(D)). The incisors are equal in mesio-distal diameter; a small canine is present, so the material may belong to a female according to Alberdi et al. (2006). The p1 cannot be observed, and the m3 is just emerged. The other premolars present an intermediate degree of wear. The p2–m2 are about the same size and rectangular in shape. In these dental elements, the linguoflexid is barely developed within the double knot and the ectoflexid surpasses half of the tooth (especially in m1).

CC–PZ 107 is a mandibular fragment with three teeth presenting a moderate degree of wear. The ectoflexid is well-developed, surpassing half of the molar, and almost reaches the linguoflexid (Fig. 10(E)), unlike *Equus (Amerhippus)* sp., which forms the double knot typical of this species (Alberdi and Prado, 2004).

**Remarks:** Among the South American fossil horses, two genera have been recognized: *Hippidion* Owen, 1869, and *Equus (Amerhippus)* Hoffstetter, 1950. Alberdi et al. (2006) recognized three valid species within the genus *Hippidion*: *H. principale* (Lund, 1846), *H. devillei* (Gervais, 1855), and *H. saldiasi* (Roth, 1899). *H. devillei* is known by its moderate size, being more gracile than *H. principale*, having less retracted nasal bones (which only reach the mesial part of the M2), and lacking inflection on the dorsal profile at the naso-frontal region, being completely convex. *H. saldiasi* is mainly distinguished by its postcranial bones (because dental elements are poorly known) and is restricted to Southern Patagonia (Alberdi and Prado, 2004). *H. principale* is less adapted to open prairie environments than other equiids. Its simpler tooth morphology indicates a diet of soft plants lacking silica. The narrower nasomaxilar region and the caudally retracted nasal slit indicates adaptation to relatively close environments such as arboreal steppes (Goya, 2003).

Genus *Equus* Linnaeus, 1758

Subgenus *Equus (Amerhippus)* Hoffstetter, 1950

*Equus (Amerhippus)* sp.

Fig. 10(F, G)

**Material and provenance:** CORD-PZ 4482: left mandibular fragment bearing three molars, extracted from the yellowish sandy silt from the highest part of the profile at Atum Pampa (FL 15; 32°5'50" S, 64°40'51" W, 1003 m a.s.l.).

**Biostratigraphical and geographical distribution:** This taxon is exclusively Lujanian in age (Cione and Tonni, 2005). *Equus (A.) neogeus* is the only species currently recorded in Argentina and Brazil, whereas the other species are reported for Andean environments in Bolivia, Chile, Colombia, Ecuador, Peru and Venezuela (Cruz et al., 2012).

**Description:** The mandible in CORD-PZ 4482 is much more gracile than in *Hippidion*, both in height and width. The molar cusps are not worn out (Fig. 10(F, G)), so this specimen may be a juvenile. The ectoflexid does not surpass the mesio-distal half of the tooth (unlike *Hippidion* sp.; Alberdi and Prado, 2004).

Order Rodentia Bowdich, 1821

Family Octodontinae Waterhouse, 1839

Genus *Ctenomys* Blainville, 1826

*Ctenomys* sp.

Fig. 10(H)

**Material and provenance:** CC–PZ 104: Skull with visible incisors and mandible, unearthed from Unit A (FL 1) from the fossiliferous bed at Vaca Corral (Goya, 2003). CORD-PZ 4486: distal fragment of left mandibular ramus found in the Holocene paleosol at the highest part of the northern profile of Pampa Vaca Corral (FL 2; 31°10'54.8" S, 64°52'8.8" W, 1593 m a.s.l.).

**Biostratigraphical and geographical distribution:** The oldest remains of *Ctenomys* are Marplatian in age (Sanandresan; late Pliocene or early Pleistocene). The genus *Ctenomys* currently includes more than 16 species of fossorial rodents distributed throughout Southern South America, from the central-western part of Peru to the Tierra del Fuego province in south Argentina (Lucero et al., 2008).

**Description:** CC–PZ 104: The skull and mandible are articulated in a carbonatic concretion, so this specimen remains largely unexposed. The apex of the incisor crowns is beveled, and these teeth present a thick enamel layer with strong orange pigmentation, which is observed in *Ctenomys*.

In CORD-PZ 4486 the pattern is present, with a tall, curved, and wide incisor (relative to more basal ctenomyines such as *Actenomys* or *Eucelophorus*) with orange enamel on the labial surface and a strongly beveled apex. The p4 is present, with a great degree of wear. It is bilobate, as a result of two smooth sulci (lingual and labial) opposite to each other, which produce a reniform shape (Fig. 10(H); Lucero et al., 2008).

**Remarks:** The Octodontidae are fossorial rodents which use the incisors and forelimbs for burrow construction. In addition to their use for burrow construction (especially where the substrate is hard), the incisors of some species of *Ctenomys* are used for fast chopping of woody stems and gnawing the most resistant plant structures (De Santis et al., 2001).

Family Chinchillidae Bennet, 1833

Genus *Lagostomus* Brookes, 1828

*Lagostomus maximus*

Fig. 10(I–O)

**Material and provenance:** CC–PZ 105: right mandibular ramus bearing the incisor and four complete molars, extracted from Unit A (FL 1) at Vaca Corral (Goya, 2003). CORD-PZ 4284: incomplete skull and metatarsals II–IV, proximal phalanx of digit II, and indeterminate intermediate and distal phalanges, found in Pampa de Oláen (FL 4; 31°07'03.2" S, 64°36'18.4" W; 31°7'12.3" S, 64°36'23.4" W; Córdoba, 2005). CORD-PZ 4484: left mandibular ramus with teeth found in the locality of Copina-Bosque Alegre (FL 11; 31°36'39.9" S, 64°34'9.57" W, 982 m a.s.l.). CORD-PZ 4485: complete skull extracted from a crotonine in the Holocene paleosol

at the highest part of the profile from Atos Pampa (FL 13; 64°42'26" S, 31°58'52" W, 1126 m a.s.l.).

**Biostratigraphical and geographical distribution:** The oldest record of this genus is Marplatan in age; however, the species occurs principally in the Platan (middle Holocene to Present days; Cione and Tonni, 2005).

**Description:** The skulls are medium to large in size. The cranial sutures are not completely fused, in spite of a great dental wear pointing towards adult individuals. The more diagnostic characters allowing determination of this material and distinguishing *Lagostomus maximus* from other members of the family Chinchillidae are: the bilophodont molars (Fig. 10(K, N, O)), the strong occipital crest (Fig. 10(J)), and the presence of three digits in the pelvic member bones (Fig. 10(I); Jackson et al., 1996).

The tooth series converge rostrally (Fig. 10(K)). The upper teeth present a thick enamel layer covering all their periphery. The P4 is undifferentiated from M1 and M2. The M3 presents three prisms, among which the more distal one shows a mesiodistal diameter larger than those of the mesialmost prisms. The oblique arrangement of these prisms relative to the sagittal plane is the same in all the teeth, lacking recognizable differences with those of the extant members of the species. The premaxillae present a caudally directed ramus, which exceeds the caudal border of the nasals. The caudal border of the zygomatic apophysis of the maxilla locates at the level of the junction between both laminae of the P4. The incisor is subtriangular in section and presents a thick enamel layer on its labial surface.

From the i1 extends a thick, smooth-edged crest formed on the lingual surface of the mandibular ramus up to the level of the m3, as in *Lagostomus maximus* and contrasting with the condition found in *Chinchilla* and *Lagidium*, in which the crest only reaches m1 and m2, respectively (Fig. 10(L–N); Kerber et al., 2011). The ascending process is thin and low, and does not include the coronoid process. The latter is represented by an independent small branch arising from the level of the distal extremity of m3. In *Chinchilla* and *Lagidium*, the location of the coronoid process is more caudal, and the process is more vertically oriented. The incisor presents a beveled occlusal surface, with the cutting edge facing labially. The upper and lower premolars and molars are bilophodont, with two oblique crests, which form an angle of 70° in

relation with the main anteroposterior axes of the maxillae and mandibles, respectively.

The foot involves three digits (Fig. 10(I)). Metatarsal IV is the shortest and thinnest, followed in length by metatarsal II, whereas the metatarsal III is the longest, being more robust and straighter. Metatarsal IV is curved (Córdoba, 2005).

**Remarks:** Chinchillidae includes two subfamilies, Chinchillinae and Lagostominae. Chinchillines have cheek teeth with two flexi/flexids and three lophi/lophids, whereas lagostomines have two lophi/lophids separated by only one flexus/flexid. Within Lagostominae, two genera are recognized, only differentiated by size: *Lagostomopsis* and *Lagostomus* – the reason why some authors consider *Lagostomus* as the only valid genus (Kerber et al., 2011). In the past, especially through the Pliocene, the diversity of this genus was very high (Rasia and Candela, 2013). Since the Pleistocene, it is only represented by a single species, *L. maximus*, which is very common in the study area. Its fossorial abilities are well known: the species produces intricate burrows that may occupy several square meters below the ground surface (Jackson et al., 1996). The habitat of the species ranges from wet subtropical grasslands to dry spiny scrublands (Jackson et al., 1996).

## 5. Discussion

### 5.1. Biostratigraphic analysis

The present study is based on fossil mammal assemblages (Table 1) collected from 12 sections in 11 distinct localities in the mountainous area of Córdoba (Fig. 3). Zones with abundant taxa are the high pampas, especially the Vaca Corral, Pampa de Olaen, and Atos Pampa sections. The fossil association recorded for each area is represented in Fig. 11.

Absolute datings obtained for the FL 1 (between 37,095 ± 2020 and 14,040 ± 785 years BP, from the type locality and section of Majada de Santiago Geosol and Vaca Corral Formation; Krapovickas and Tauber, 2016) enable the confirmation of a Lujanian age for that level (~130–7 ka BP; Cione and Tonni, 2005; Cione et al., 2009). This interpretation is supported by the mammal association recorded for that level, including *Scelidotherium leptocephalum*,

**Table 1**

Quaternary faunal composition of the high plains in the Sierras Pampeanas of Córdoba, Argentina, with their respective fossiliferous and stratigraphic levels. References for the stratigraphic units: 1, Krapovickas (2014); 2, Krapovickas and Tauber (2016).

Order	Family	Species	FL	Stratigraphic unit
Cingulata	Dasypodidae	<i>Chaetophractus</i> sp.	9, 11	Reddish sandy-clay, fanglomerate <sup>1</sup>
		<i>Eutatus</i> cf. <i>E. seguini</i>	14	Majada de Santiago Geosol <sup>2</sup>
	Glyptodontidae	<i>Panochthus</i> sp.	1, 4	Majada de Santiago Geosol and Loessoid <sup>2</sup>
		<i>Glyptodon reticulatus</i>	3, 12	Majada de Santiago Geosol <sup>2</sup>
Folivora	Mylodontidae/Scelidotheriinae	<i>Glyptodon</i> sp.	4, 12, 17	Majada de Santiago Geosol <sup>2</sup> , fanglomerate <sup>1</sup>
		<i>Scelidotherium leptocephalum</i>	1, 3, 12	Majada de Santiago Geosol <sup>2</sup>
		<i>Scelidotherium</i> sp.	1	Majada de Santiago Geosol <sup>2</sup>
		<i>Catonyx tarijensis</i>	14	Majada de Santiago Geosol <sup>2</sup>
		<i>Proscelidodon</i> sp.	9	Fanglomerate <sup>1</sup>
	Mylodontidae/Mylodontinae	<i>Glossotherium</i> sp.	1	Majada de Santiago Geosol <sup>2</sup>
	Mylodontidae	<i>Mylodontidae</i> indet.	4, 12	Loessoid and Majada de Santiago Geosol <sup>2</sup>
	Megatheriidae	<i>Megatherium americanum</i>	1	Majada de Santiago Geosol <sup>2</sup>
		<i>Megatherium</i> sp.	6	Clast-supported conglomerate <sup>1</sup>
	Macraucheniiidae	<i>Macrauchenia</i> sp.	1, 3, 12	Majada de Santiago Geosol <sup>2</sup>
Litopterna	Mesotheriidae	<i>Mesotherium</i> sp.	6	Clast-supported conglomerate <sup>1</sup>
Notoungulata		<i>Toxodon</i> sp.	6, 10	Clast-supported conglomerate, fanglomerate <sup>1</sup>
Carnivora	Felidae	<i>Smilodon populator</i>	1, 12	Majada de Santiago Geosol <sup>2</sup>
		<i>Oncifelis</i> sp.	3	Olaen Geosol <sup>2</sup>
Proboscidea	Gomphotheriidae	<i>Notiomastodon platensis</i>	1	Majada de Santiago Geosol <sup>2</sup>
Perissodactyla	Equidae	<i>Hippidion principale</i>	1, 8, 16	Majada de Santiago Geosol <sup>2</sup> , reddish sandy-clay and fanglomerate <sup>1</sup>
		<i>Equus (Amerhippus)</i> sp.	15	Loessoid <sup>2</sup>
Rodentia	Octodontidae	<i>Ctenomys</i> sp.	1, 2	Majada de Santiago and Olaen Geosols <sup>2</sup>
	Chinchillidae	<i>Lagostomus maximus</i>	1, 4, 11, 13	Majada de Santiago Geosol <sup>2</sup> , fanglomerate <sup>1</sup> , and Olaen Geosol <sup>2</sup>



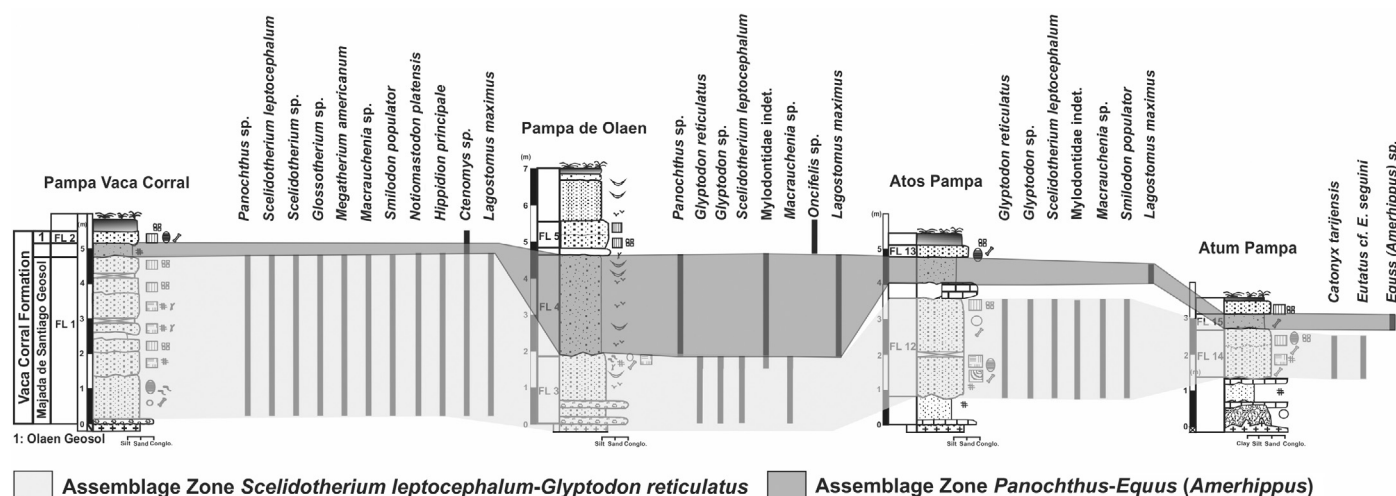


Fig. 11. Assemblage zones proposed for the main fossil localities of the Mountain region of Córdoba, Argentina.

*Smilodon populator*, *Macrauchenia* sp., *Glossotherium* sp., *Scelidotherium* sp., *Panochthus* sp., *Notiomastodon platensis*, *Hippidion principale*, and *Ctenomys* sp. From a biostratigraphical point of view, the co-occurrence of *Scelidotherium leptocephalum* and *Macrauchenia* sp. allows a robust correlation for the depositional units described for the high pampas (e.g., Pampa Vaca Corral-FL 1, Pampa de Oláen-FL 3, and Atos Pampa-FL 12). The species *S. populator* is present in the Vaca Corral (FL 1) and Atos Pampa (FL 12) areas, while *Glyptodon reticulatus* and *Glyptodon* sp. are shared by the Pampa de Oláen (FL 3) and Atos Pampa (FL 12) areas. Levels FL 1 from Pampa Vaca Corral and FL 4 from Pampa de Oláen share the record of *Panochthus* sp. and *Lagostomus* cf. *L. maximus*.

The presence of *Hippidion principale* enables the correlation between levels FL 1 (Pampa Vaca Corral), FL 8 (Los Morteritos–Panaholma), and FL 16 (Amboy). This long-ranging species covers the late Pliocene to early Holocene (Alberdi et al., 2006; García et al., 2008). The genus *Proscelidodon* sp. (late Miocene–middle Pliocene, according to Pujos et al., 2012), was recovered from FL 9 (assigned to the Brochero Formation on the basis of its lithological characteristics). For this formation, Cruz (2013) suggested the Assemblage Zone *Nonotherium hennigi*–*Panochthus bullifer*, defined by the common occurrence of *N. hennigi*, *P. bullifer*, *P. bonaerense*, *Phlyctaenopyga* sp., and *Plohophorus* sp. The genus *Proscelidodon* can be added to this biozone. Another common genus is *Chaetophractus* sp.; nevertheless, this taxon does not offer enough resolution as it spans the middle Pliocene to the Present (Tauber, 2005).

The presence of *Toxodon* sp. allows the correlation between levels FL 10 (Bosque Alegre) and FL 6 (Huerta Grande). This genus is recorded from the late Pliocene up to the late Pleistocene–early Holocene (Lujanian; Miño-Boilini et al., 2006). Given the geochronology and the paleofaunistic association of the Pampa Vaca Corral area, it seems more parsimonious to place levels FL 6 and FL 10 in the Lujanian age. In the Huerta Grande area, *Toxodon* sp. is recorded together with *Mesotherium* sp. and *Megatherium* sp. The latter genus ranges from the late Pliocene to the late Pleistocene–early Holocene (Pujos et al., 2017).

*Mesotherium cristatum* is a common notungulate found in deposits from the Buenos Aires Province. This species is the latest representative of Mesotheriidae with a biochron confined to the Ensenadan age (early to middle Pleistocene; Cione and Tonni, 2005; Tauber, 2008). The record of *Mesotherium* in Córdoba Province is scarce. Tauber (2008) documented this species in loessic units at the Corralito locality from the fluvio-eolian flats in

the central part of Córdoba, dated by IRSL to 115 ka BP, suggesting a Bonaerian age (middle Pleistocene; Cione et al., 2009). Nonetheless, the record of *Mesotherium* sp. in the Huerta Grande and taking into account the whole paleofaunistic ensemble of Lujanian age in this locality (i.e., *Toxodon* sp. and *Megatherium* sp.), this finding shows a retrieval of the species from east to west. This may be due to enhanced climatic conditions, or other factors, which allowed *Mesotherium cristatum* to use the mountain area as an ecological corridor towards lower latitude areas, as suggested by Tauber (2008), and as also suggested by some megatheriine ground sloths and mastodons (Pujos, 2008).

FL 17 from the Villa del Dique locality correlates with levels FL 3 (Pampa de Oláen) and FL 12 (Atos Pampa) based on the presence of *Glyptodon* sp. In Argentina, the presence of *Catonyx tarijensis* was conventionally used to indicate an Ensenadan age (Cione and Tonni, 2005; Cruz, 2013), Ensenadan–Bonaerian for the Buenos Aires Province, Pleistocene for Córdoba (Miño-Boilini and Carlini, 2009), or Ensenadan–Lujanian for Buenos Aires and Corrientes and Pleistocene for Córdoba (Miño-Boilini, 2012; Miño-Boilini, 2016). The record of a specimen of *Catonyx tarijensis* in stratigraphic level FL 17 at Atum Pampa, that correlates with Majada de Santiago Geosol ( $37,095 \pm 2020$  and  $14,040 \pm 785$  years BP; Krapovickas and Tauber, 2016; Figs. 2, 3, 11), enables us to confirm its presence during the Lujanian in the Córdoba Province. In light of this new evidence, it seems legitimate to question the designation of an older age when documenting this species in Córdoba (Krapovickas, 2014; Tauber et al., 2014).

Based on the new evidence reported herein, we propose two Assemblage Zones (based on Comité Argentino de Estratigrafía, 1992; Fig. 11) as a first approach to a biostratigraphic study for the mountain area of Córdoba province:

- ***Scelidotherium leptocephalum*–*Glyptodon reticulatus* Assemblage Zone:** this biozone is based on the co-occurrence of *Scelidotherium leptocephalum*, *Macrauchenia* sp., *Smilodon populator*, *Glyptodon reticulatus*, *Hippidion principale*, and *Toxodon* sp. Its type area and profile is Pampa Vaca (Krapovickas, 2014); it is Lujanian in age, between  $37,095 \pm 2020$  and  $14,040 \pm 785$  years BP;
- ***Panochthus* sp.–*Equus* (Amerhippus) sp. Assemblage Zone:** this biozone is based on the co-occurrence of *Panochthus* sp., *Equus* (Amerhippus) sp., and *Lagostomus maximus*. Its type area and profile is Pampa de Oláen (Krapovickas, 2014); it is Lujanian in age, between  $14,040 \pm 785$  and 9181 years BP.

These two biozones are included within the temporal range of the *Neosclerocalyptus paskoensis*-*Equus* (*Amerhippus*) Zone defined by Cruz (2013) for the Pampean region in Córdoba, correlated with the Lujanian (late Pleistocene–early Holocene;  $35,890 \pm 1030$  and  $8150 \pm 400$  years BP), for which they improve the temporal resolution for the mountain area of Córdoba province.

The presence of *Mesotherium* sp., *Catonyx tarijensis*, *Megatherium americanum*, and even *Glossotherium* sp. suggests that the mountain area in Córdoba may have served as a refuge or reservoir for the Pleistocene fauna. Indeed, this area may have offered a favorable environment for the Pleistocene fauna while the Pampas floors began to decline (Kröhling and Carignano, 2014; Krapovickas and Tauber, 2016). In agreement with this, the record of gomphotheriids in the mountains of Córdoba could indicate the survival of this group in the region. Alberdi and Prado (2008) collected the most recent radiometric dating of *Notiomastodon platensis* in Argentina:  $21,400 \pm 450$ ,  $18,280 \pm 220$  and  $17,880 \pm 60$  years BP in the Buenos Aires Province, and  $19,900 \pm 120$  years BP in the Santiago del Estero Province. The specimen of *N. platensis* found in the LF 1 level (upper part of unit A (Goya, 2003), top of Majada de Santiago Geosol (Krapovickas and Tauber, 2016)) indicate (OSL dating) a maximum age of ca. 21,400 years BP and a minimum age of ca. 14,000 years BP for that level (Krapovickas, 2014).

## 5.2. Mountain biogeography

The late Lujanian fauna recorded for the Córdoba Mountain show a wide distribution in the Argentine territory. *Glyptodon* sp., *Panochthus* sp., *S. leptocephalum*, *Megatherium americanum*, *Toxodon* sp., *Equus* (*Amerhippus*) sp., *Eutatus seguini*, *Macrauchenia* sp., *Ctenomys* sp., and *Lagostomus maximus* were recorded in different localities from the northern, center and southern parts of the Pampean flats of Córdoba (Zurita et al., 2007; Cruz et al., 2012; Cruz, 2013). Other species recorded in the mountains of Córdoba, such as *Catonyx tarijensis* and *Smilodon populator*, were recorded in plains of Córdoba, but they were assigned to older faunal assemblages (Cruz et al., 2012).

Further records from areas located in northern Córdoba province are also reported. Specimens of *Glyptodon* sp., *Catonyx* sp., *Toxodon* sp., *Megatherium* sp., *Notiomastodon platensis*, and *Equus neogeus* were collected from Corrientes, Chaco, Formosa, and Santa Fe provinces (Zurita and Lutz, 2002; Zurita et al., 2009b; Miño-Boilini et al., 2006). To the west of the Córdoba province, *Glyptodon* sp., *Panochthus* sp., *Mylodon* sp., *Hippidion* sp., *Megatherium americanum*, *Scelidotherium leptocephalum*, *Glossotherium* sp., *Macrauchenia* sp., *Toxodon* sp., *Notiomastodon platensis*, and *Equus* (*Amerhippus*) *neogeus* have been recorded in Mendoza, San Juan (García et al., 2008; Forasiepi et al., 2009), and San Luis provinces (Chiesa, 2008). On the other hand, to the northeast of the study area, paleontological records from deposits of the Yupoi Formation (ca. 36,000 years BP) that crop out in Entre Ríos and Corrientes provinces exhibited an overlap of two faunal groups. One is dominated by species of intertropical origin such as *Pteronura* sp., *Tapirus mesopotamicus*, and *Holmesia paulacoutoi*; the other one is dominated by Pampean species like *Glyptodon* sp., *Panochthus* sp., *Toxodon platensis*, *Macrauchenia patachonica*, *Antifer ensenadensis*, cf. *Mazama* sp., *Morenelaphus lujanensis*, *Stegomastodon waringi* (= *Notiomastodon platensis*; Mothé et al., 2012), and *Hippocamelus sulcatus* (Carlini et al., 2008; Alcaraz and Francia, 2013). These findings suggest that the central, west and north regions of Argentina during the Lujanian were mainly inhabited by Pampean and Patagonian taxa. The homogeneity in the species record, with its climatic and ecological implications, is contradictory with the heterogenous Brazilian and Pampean species assemblages registered in the northeast region of

Argentina, interpreted as the advances and retreats of the intertropical and Pampean faunas as a response of the late Pleistocene glacial/interglacial climate changes (Tonni et al., 1999; Carlini et al., 2004).

It is also worth noting the absence of *Neosclerocalyptus* from the Mesopotamian region, this genus being the most conspicuous one of the Pampean region (Carlini et al., 2008). This taxon has the highest record frequency from the Quaternary period (Zurita et al., 2011a). It was registered in Buenos Aires, in the Pampean flats of Córdoba, Formosa, and San Luis provinces (Alberdi et al., 1989; Zurita et al., 2007; Chiesa, 2008; Cruz et al., 2012; Cruz, 2013). This record resembles the one in the mountainous region of Córdoba. Several researchers that collected fossil material from the present study area did not mention the occurrence of this genus (e.g., Castellanos, 1944; Montes, 1955, 1956, 1958; Leonardi, 1961; Tauber and Di Ronco, 2000; Goya, 2003; Córdoba, 2005). This fact and the warm climate evidenced from the pedological data of the Majada de Santiago Geosol, suggest that the ecological and climatic conditions for this genus were not favorable in this region. Also, the probable survival of some taxa (e.g., *Mesotherium* sp., *Megatherium americanum*, *Catonyx tarijensis*, *Glossotherium* sp., and *Notiomastodon platensis*) in the Sierras Pampeanas of Córdoba province may indicate that this was a more favorable setting during the Lujanian in comparison with the Pampeana and Chaqueña flats.

The pattern of distribution of *Neosclerocalyptus* suggests that areas with constant faunal advances and retreats caused by climatic changes (e.g., Mesopotamia) can be indicative of the ecological and climatic needs for this genus. According to some morpho-functional evidences, *Neosclerocalyptus* has traditionally been associated with cold and arid climates (high degree of pneumatization of the rostral cranial area; Zurita et al., 2011b). On the other hand, Nore and D'Andrea (1997) documented fragments of carapace that belonged to *Neosclerocalyptus ornatus* with archeological elements at the Alpa Corral locality (800 m a.s.l.), south of the Sierra de Los Comechingones, suggesting that prehistoric men hunted, transported these rests to higher regions, and ate this species.

Another possibility is that the megamammals and large-sized mammals found in the mountain region of Córdoba province might have been generalist species, with a wide range of niche plasticity (except perhaps for *Neosclerocalyptus*); hence they would not allow for the identification of late Lujanian paleozoogeographical boundaries in the study area. Therefore, the vertebrate taxa that show an "island" distribution or are endemic of the Pampean highlands of Córdoba are relatively small in size (e.g., frogs and lizards; Di Tada et al., 1996; Lescano et al., 2015). Future biostratigraphical studies should focus on this type of vertebrates, especially rodents that show a faster response to paleoclimatic and paleoenvironmental changes (Martínez et al., 2012). At the moment, the Quaternary fauna recorded in the Pampean highlands is composed by the same taxa that the ones found in the Pampean flats and western and northern regions of Argentina. This zoogeographic homogeneity seems to reach the late Pleistocene of the Pampa de Pocho area based on the presence of *Hippidion principale* in the Panaholma area. No morphological differences are observed among specimens of the same species of Pleistocene mammals at both subregions.

In summary, the Sierras Pampeanas of Córdoba Province are now located in the eastern part of the Andean-Patagonian zoogeographic subregion, near the border with the Guyana-Brazilian subregion (Ringuelet, 1961; Krapovickas and Tauber, 2010). This is a dynamic boundary: sometimes the sierras Pampeanas are completely excluded from the Pampasic or subtropical subregion, and sometimes the limit is located within the longitudinal axis of the highlands, in the Pampa de Achala area. The borderline dynamics is based on the ecology of the fauna

recorded in the Pampean highland regions, with taxa adapted to the Andean-Patagonian forests and grasslands. This generates an ecotone controlled by an altitudinal, geomorphologic and climatic gradient. Finally, with the climatic improvement during the Holocene (i.e., climatic optimum evidenced by the Olaen Geosol, formed between 9181 and 7206 years cal. BP; Krapovickas, 2014; Sanabria et al., 2014; Krapovickas and Tauber, 2016), the boundary advanced towards the central region of Córdoba and stayed at approximately the same area as today. However, during the Holocene (and likely also late Pleistocene; Cabrera and Luna, 2011), paleontological evidence suggests that this boundary varied constantly, pushing the arid and cold conditions (Andean-Patagonian) to the east (evidenced by the presence of *Reithrodon auritus* in Mar Chiquita; Martínez et al., 2012) and the warm and wet conditions (Guianan-Brazilian) to the Sierras de Córdoba (evidenced by the presence of *Holochilus brasiliensis*; Teta et al., 2005).

## 6. Conclusions

The present taxonomic analysis of Quaternary mammals from the mountainous area in Córdoba reveals the presence of 20 extinct taxa: *Eutatus* cf. *E. seguini*, *Panochthus* sp., *Glyptodon reticulatus*, *Glyptodon* sp., *Scelidotherium leptocephalum*, *Scelidotherium* sp., *Catonyx tarijensis*, *Proscelidodon* sp., *Glossotherium* sp., *Myiodontidae* indet., *Megatherium americanum*, *Megatherium* sp., *Macrauchenia* sp., *Mesotherium* sp., *Toxodon* sp., *Smilodon populator*, *Notiomastodon platensis*, *Hippidion principale*, and *Equus* (*Amerhippus*) sp.; and four representatives of living species and/or genera: *Chaetophractus* sp., *Oncifelis* sp., *Ctenomys* sp., and *Lagostomus maximus*. Based on the paleontological and stratigraphical analysis achieved here, a new biostratigraphic scheme for the mountain area in Córdoba is proposed, involving two successive Lujanian assemblage zones: the *Scelidotherium leptocephalum*-*Glyptodon reticulatus* Assemblage Zone (between  $37,095 \pm 2020$  and  $14,040 \pm 785$  years BP), and the *Panochthus* sp.-*Equus* (*Amerhippus*) sp. Assemblage Zone (between  $14,040 \pm 785$  and 9181 years BP).

The presence of some Ensenadan or Bonaerian taxa in late Pleistocene deposits at the Pampean region in Argentina (i.e., *Mesotherium* sp., *Catonyx tarijensis*, *Megatherium americanum*, and *Glossotherium* sp.) suggests that the mountainous area of Córdoba may have acted as a refuge or reservoir area, providing a favorable setting for the Pleistocene fauna at times were the Pampean flats started to decline. For this reason, we suggest to proceed with certain caution when assigning an older age than the Lujanian to the taxa recorded in Córdoba Province.

Finally, the Quaternary fauna recorded in the Pampean highlands, Pampean flats, and west and north regions of Argentina do not show differences in the taxonomic richness and morphological characters. We suggest that during the late Pleistocene, the boundary between the current zoogeographic regions was located in territories of the Corrientes and Entre Ríos provinces. With the Holocene climatic optimum, this boundary would have advanced towards its current position in the Pampa de Achala area.

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