Early Pliocene continental vertebrate Fauna at Puerto de la Cadena (SE Spain) and its bearing on the marine-continental correlation of the Late Neogene of Eastern Betics

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ABSTRACT

In this paper, we synthesize sedimentological, magnetostratigraphic and paleontological data from the continental vertebrate site of Puerto de la Cadena (Murcia, SE Spain), in order to clarify its age. The study site is located on the northern edge of the Carrascoy mountain range, in the upper part of the Cigarrón Unit. The end-Messinian discontinuity has been detected at the base of this unit, which indicates it has an early Pliocene age. Abundant remains of small and large vertebrates, including rodents, lagomorphs, primates, carnivorans, perissodactyls, artiodactyls, proboscideans, testudines, squamats, and crocodiles, have been found in this area. Some of these elements are of African origin, such as *Debruijnimys* sp., *Macaca* sp., and *Sivatherium* cf. *hendeyi*, and their presence is related to the Messinian Salinity Crisis. In addition, remains found at this site verify the persistence of Crocodylia in the European record beyond the late Miocene. The association includes typical elements of the early Ruscinian terrestrial record (MN14), like *Apocricetus* cf. *barrierei*, *Sivatherium*, *Gazella* aff. *baturra*, and *Hipparion fissurae*. The Puerto de la Cadena site is located in a reversed geomagnetic chron that has been correlated with C3n.3r (from 4.997 to 4.896 Ma). According to this correlation, the MN13/MN14 boundary has a minimum age of 4.9 Ma.

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1. Introduction

The importance of the newly discovered site of Puerto de la Cadena lies in its great abundance and diversity of fossil vertebrate remains, as the large mammal association is novel for the Spanish fossil record of the Miocene/Pliocene boundary. In fact, contemporary large-vertebrate sites are scarce in the Iberian Peninsula, which makes Puerto de la Cadena a reference locality.

The area of Puerto de la Cadena has a rich paleontological record, known since the early 1970s (Montenat and Crusafont, 1970; Montenat, 1973; Mein et al., 1973). The sites of La Alberca and La Paloma stand out among the sites with continental vertebrate remains as they were identified during the first geological study in the area (Montenat and Crusafont, 1970). Aguirre et al. (1974) and de Bruijn et al. (1975) established a late Miocene age for these localities by correlating them to the site of El Arquillo (Teruel, Spain). La Alberca yielded an important fossil assemblage, being Montenat (1973) the first to report its faunal list, which has been subsequently revised and updated (Morales, 1984; López Martínez, 1989; Freudenthal et al., 1998; Pérez-García et al., 2011): *Cricetus kormosi* (=*Apocricetus alberti*), *Stephanomys medius* (=*Stephanomys dubari*, *Stephanomys cordii*), *Ruscinomys lasallei*, *Paraethomys miocaenicus* (=*Paraethomys meini*), *Castillomys* sp., *Eliomys* sp., *Hispanolagus crusafonti* (=*Trischizolagus crusafonti*), *Prolagus michauxi*, *Percrocuta minor*, *Plioviverrops guerini*, *Hipparion concudense*, *Dicerorhinus schleiermacheri*, *Birgerbohlinia* sp., Cervidae indet., Bovidae indet., *Titanochelon* cf. *bolivari*, and Trionychinae indet. The La Paloma site has only yielded two taxa (Montenat and Crusafont, 1970): Cervidae indet., and *Decennatherium pachecoi*. Based on the faunal assemblage, these localities were correlated with the MN13 unit (Aguirre et al., 1976; Morales, 1984), and more recently with the Ventian land mammal age (latest Miocene/earliest Pliocene; Morales et al., 2013).

Besides the giant tortoise shell from the locality of La Alberca (here reassigned to *Titanochelon* sp.), additional specimens have been recovered from the vicinity of Puerto de la Cadena. This is the case of the unpublished, more-incomplete shell remains found at the Autovía site (Murelaga et al., 2007), which could belong to the same taxon. Another example is the carapace of an adult specimen from Barranco del Cigarrón (located to the west of the Puerto de la Cadena site), which Mancheño et al. (2001) reported and preliminary assigned to '*Testudo*' *bolivari*. This taxonomic ascription is not supported here, thus we consider the presence of a second synchronous testudinid from Barranco del Cigarrón (see Supplementary information).

From the stratigraphical and sedimentological points of view, the fossil remains recovered from the Puerto de la Cadena area come from roughly equivalent levels to those of Autovía and Barranco del Cigarrón, and were deposited under similar depositional environments (Murelaga et al., 2007; Romero and Fierro, 2010). Even though the area of Puerto de la Cadena is very rich in continental vertebrate remains, none of these outcrops has been hitherto accurately dated. The aim of the present paper is to provide taxonomic attributions for the vertebrate fauna recovered from Puerto de la Cadena, as well as to accurately date this site based on a synthesis of geological, magnetostratigraphic and paleontological data.

2. Geological setting

The Neogene outcrop of Puerto de la Cadena (Murcia Region, SE Spain) is located 8 km SSW of the town of Murcia, and 2.5 km south of El Palmar, on the northern flank of the Carrascoy range mountain (Fig. 1). The location coordinates are 37° 55′ 9″ N, 1° 9′ 41″ W, with an altitude of 160 m AMSL. This site was discovered in 2008 as a result of the construction of the MU-31 motorway in the vicinity of Puerto de la Cadena, which is an open natural pass between the mountains of Carrascoy and Cresta del Gallo, connecting the cities of Murcia and Cartagena.

Some geological units with great lateral continuity are located in Puerto de la Cadena area, and their position is influenced by the neotectonic activity. In 2008, the construction works of the MU-31 motorway began to affect some of these units, which led to the recovery of large vertebrate remains.

2.1. Regional context

One of the best sites for describing the Neogene stratigraphic record on the northern side of the Carrascoy mountain range is Barranco del Cigarrón, where we have documented a stratigraphic succession that includes at least five lithostratigraphic units (Figs. 1–2). The lower three units are clearly recognizable and equivalent to those described in the Bajo Segura Basin: Columbares Formation, Torremendo Formation and La Virgen Formation (Montenat, 1990; Soria et al., 2008). The two uppermost units, identified here as Cigarrón Unit and La Paloma Unit, have not been previously described.

The fossiliferous outcrop of Puerto de la Cadena is located on the upper part of the Cigarrón Unit, which might be the lateral equivalent to the Rojales and Variegated Marl formations of Montenat (1977), both early Pliocene in age (Soria et al., 2008). On the north side of the Carrascoy range, Montenat (1977) described these units as composed of marls and gray calcareous sands, with conglomeratic levels, cross stratification and reactivation surfaces. He further reported the presence of bone debris in yellow sandy outcrops (such as at the La Alberca and La Paloma paleontological sites).

The lower stratigraphic boundary of the Cigarrón Unit, which hosts the Puerto de la Cadena site in the upper part, corresponds to a surface of marked erosion. This surface is present in both the La Virgen Fm. and Torremendo Fm. (see geological map in Fig. 1). This stratigraphic discontinuity is immediately overlain with sands and sandy marls, which include large-sized clasts bored by lithobiont bivalves and abundant shells of small ostreids similar to those of the genus *Pycnodonte*. The marls are finely laminated and contain a diversified microfossil assemblage, represented by foraminiferans, ostracodes bryozoans, bivalves, carbonate sponge spicules, and sea urchin spicules. All the macro and micropaleontological data indicate that sedimentation of the Cigarrón Unit began under normal salinity marine conditions in a shallow water depositional environment, and a subsequent transgressive event can be recognized at the top of La Virgen Fm. This transgressive event is recorded in the same way in numerous places in the Bajo Segura Basin, coinciding with the beginning of the Pliocene (Corbí and Soria, 2016). This implies that the erosive surface documented at the base of the Cigarrón Unit corresponds to the end-Messinian discontinuity (Soria et al., 2005, 2008).

2.2. Sedimentary record at the fossil site

The Cigarrón Unit at the Puerto de la Cadena site is represented by a sand and lutite alternating succession (Fig. 2). The sandy facies association is characterized by coarse sediments (mainly sands, but also microconglomerates and conglomerates), that are mainly organized in sets of trough and planar cross-stratification. These sets have a thickness of between a few centimeters and a meter, and most of them have an erosive base that exhibits a basal lag with intraformational mud clasts, fragmentary bones and plant fossil remains. They fine upwards, with frequent reactivation surfaces.

The macrovertebrate fossil remains are mainly located in the conglomeratic layers of the sands or in the basal lag of the sedimentary sets. The sand components are medium-sized to coarse siliciclastic grains with very little matrix and no cement. Cross-bedding in the sedimentary sets exhibits internal lamina that are variably inclined, from quasi-horizontal to 30°, and in most cases points towards N55°E.

The lutitic intercalations display different features. Some of them are thick lutitic intercalations (metric scale) with a concave base and a planar top. Bioturbation frequently occurs at the top of these bodies,
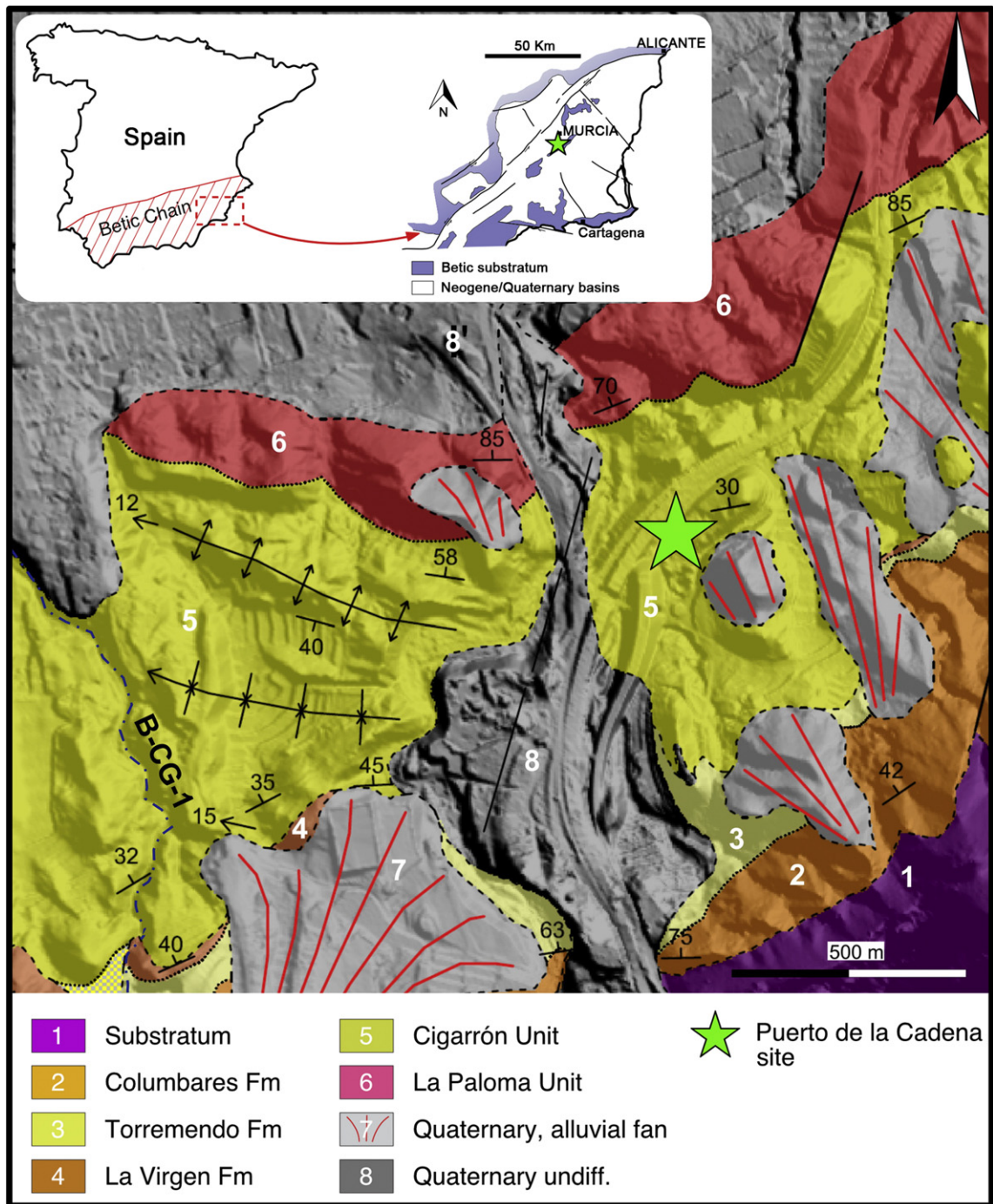
Fig. 1. Geographical and geological setting of the Puerto de la Cadena site.

consisting of 5–7 cm long (vertical development) traces with a characteristic U-shape and circular cross-section of about 0.5 cm (*Arenicolites* isp.; Simo and Olsavsky, 2007). In contrast, other thinner (centimetric to metric) lutitic intercalations have an irregular morphology. Most of the micromammal remains (about 5% of the total fossil remains) were obtained from the latter lutitic levels.

2.3. Geological interpretation

Mancheño et al. (2001) provided an interpretation of the depositional context for a tortoise carapace found in geological units similar to those described above, and concluded that fluvial transport would have brought the carapace to the sea. However, stratigraphical and sedimentological information from the different subunits at the top of the Cigarrón Unit leads us to favor a continental depositional context related to fluvial systems near the coast.

We agree with Mancheño et al. (2001) about the fluvial context for the upper part of the Cigarron Unit, where the Puerto de la Cadena site is located. Sand and gravel beds with unidirectional cross-stratification correspond to channels through which dunes and megaripples migrate. The fluctuating flow regime causes the frequent reactivation of surfaces that separate the sets of cross-stratification. The lutitic interbeds between sandy bodies represent floodplain deposits of the fluvial system, dominated by channel overbank processes. The presence of micromammal fossils in the lutites indicates that there were episodes of vegetation development. The inferred depositional context for the
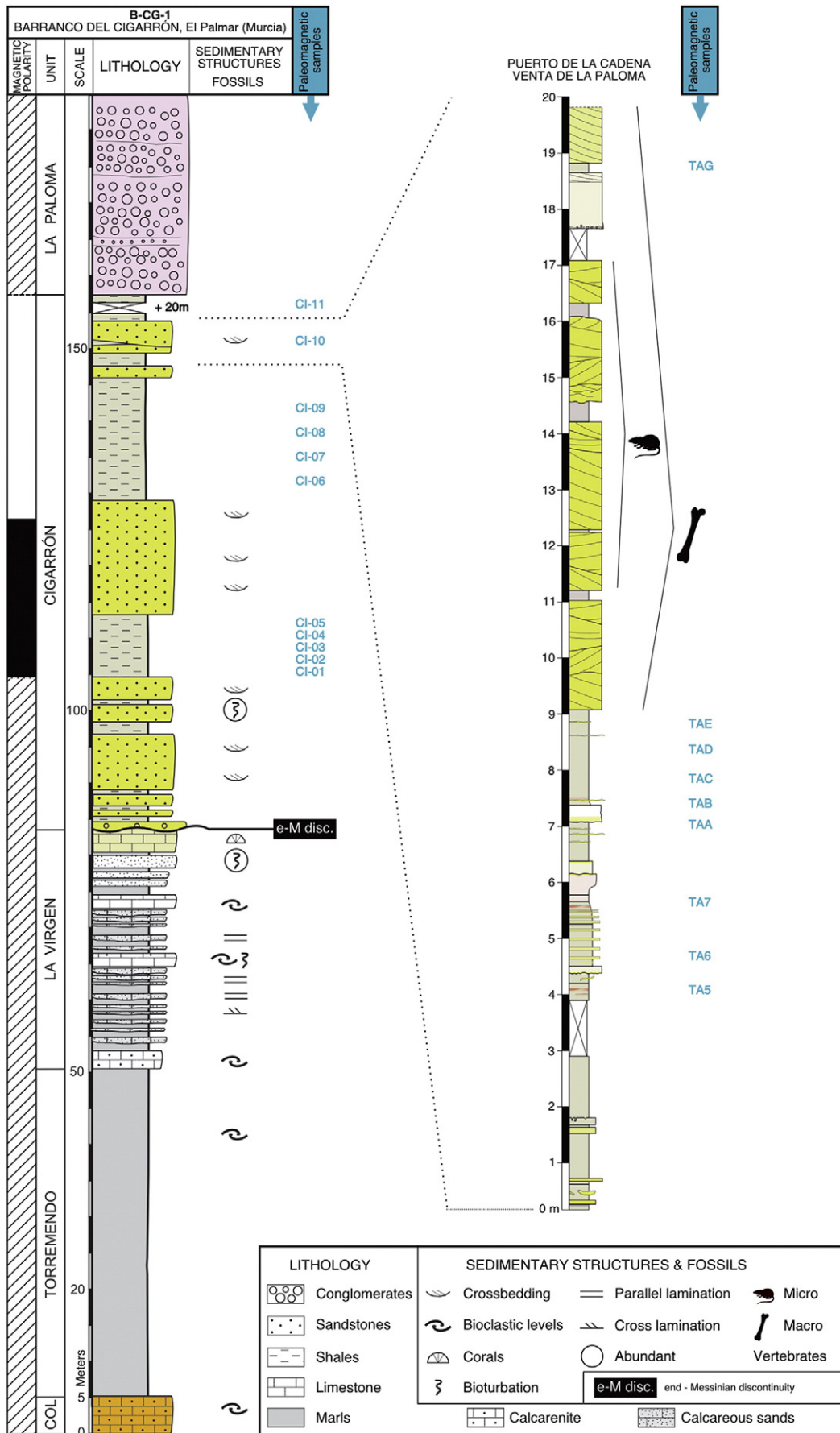
Fig. 2. Stratigraphic log on Barranco del Cigarrón with detailed of the Puerto de la Cadena paleontological site.

Puerto de la Cadena site shows certain similarities to the fluvial system described for the Rojales micromammal site (early Pliocene) located in the Bajo Segura Basin (Soria et al., 1996). In this case, as in the Puerto de la Cadena, microfossils are concentrated in vegetated areas of the floodplain.

2.4. The age of the Cigarrón Unit

The basal marine sediments of the Cigarrón Unit contain a varied assemblage of foraminifera in which benthic forms dominate (ca. 80%) over planktonic forms. The benthic foraminifera association includes the genera *Ammonia*, *Amphicoryna*, *Biasterigerina*, *Bigenerina*, *Bolivina*, *Bulimina*, *Cibicides*, *Elphidium*, *Fursenkoina*, *Globulina*, *Nonion*, *Pullenia*, *Reussella*, *Siphonina*, *Textularia*, and *Trifarina*. The dominant planktonic association includes *Globigerinoides extremus*, *Globigerinoides obliquus*, *Globigerinoides trilobus*, *Neogloboquadrina* spp., *Globorotalia scitula*, *Globigerina bulloides*, *Globoturborotalita* spp., and *Orbulina universa*. This marine microfossil biofacies is similar to that of the transgressive deposits at the base of the Pliocene Unit (P Unit; Soria et al., 2005) in the Bajo Segura Basin. This implies that the two units are correlative and that the underlying erosive surface corresponds to the end-Messinian discontinuity described by Soria et al. (2005). More specifically, there are four significant features at the beginning of the Pliocene Unit from the Bajo Segura Basin that coincide with those in the Cigarrón Unit: (a) abundant ostreids (*Pycnodonte* sp.) and clasts bored by lithobionts (Montenat, 1990; Soria et al., 2005; Caracuel et al., 2011); (b) prevalence of benthic foraminiferans (70–90%) over planktonic ones (Corbí, 2010); (c) abundant and diversified content of benthic foraminiferans, most of them represented by the genera *Ammonia*, *Bolivina*, *Bulimina*, *Cibicides*, *Elphidium*, *Nonion*, and *Textularia* (Corbí et al., 2016); and (d) an association of normal-sized planktonic foraminiferans, typical of oligotrophic warm water, dominated by *Globigerinoides* (mainly *G. trilobus* and *G. obliquus/extremus*; Corbí et al., 2016).

Assigning the Cigarrón Unit to the Pliocene implies a post-MSC (Messinian Salinity Crisis) sedimentation, i.e., it occurred after the Mediterranean flooded with normal marine water from the Atlantic Ocean. In this basin, under high-level sea conditions, the Mediterranean margins were progressively filled with sediments, leading to regressive or shallowing sequences (Caracuel et al., 2004, 2009; Soria et al., 2005). The Cigarrón Unit represents one of these sequences, and displays an evolution from shallow marine to continental environments over time. The latter are represented by fluvial systems with channels and floodplain development, which is the depositional context in which the sediments of the Puerto de la Cadena site were accumulated.

3. Material and methods

Systematic excavations were carried out at the Puerto de la Cadena site in 2009, 2010 and 2011. They yielded about 2000 well-preserved fossil remains of a diverse fauna of continental vertebrates (Figs. 5–9). Large amounts of sediment were also screen-washed using superimposed 4.0, 1.0 and 0.5 mm mesh screens. The recovered fossils represent at least 26 species and are currently housed at the Museo Arqueológico de Murcia (MAM; Murcia, Spain).

In this work, we update the systematic of the vertebrate taxa found so far in the early Pliocene levels of the Puerto de la Cadena area. We both review previously found remains and analyze and discuss recently found material (see Supplementary information and Table 1).

Measurements of the small mammal teeth were taken on the occlusal plane of the molars with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. Micromammal teeth are illustrated by means of micrographs taken with Environmental Scanning Electron Microscopy (ESEM) at the Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili (Tarragona). Upper and lower teeth are denoted by capital letters ('P' for premolars and 'M' for molars) followed by superscripts and subscripts

Table 1
Vertebrate faunal list of the site of Puerto de la Cadena.

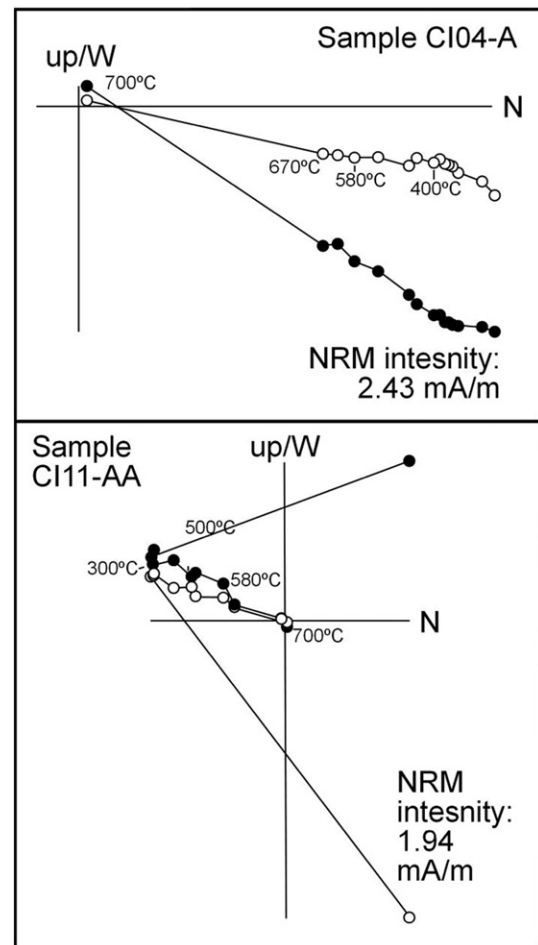| Order	Family	Species
Rodentia	Muridae	*Stephanomys* cf. *dubari*
		Paraethomys cf. *meini*
		Debruijnimys sp.
	Cricetidae	*Apocricetus* cf. *barrierei*
		Ruscinomys lasallei
Lagomorpha	Leporidae	*Trischizolagus maritsae*
	Prolagidae	*Prolagus* cf. *michauxi*
Primates	Cercopithecidae	*Macaca* sp.
Carnivora	Canidae	*Eucyon monticinensis*
Proboscidea	Gomphotheriidae	*Anancus arvernensis*
Perissodactyla	Equidae	*Hipparion* aff. *fissurae*
	Rhinocerotidae	*Dihoplus schleiermacheri* vel *Dihoplus megarhinus*
Artiodactyla	Cervidae	Cervidae indet.
	Giraffidae	*Sivatherium* cf. *hendeyi*
	Bovidae	*Gazella* aff. *baturra*
		Gazella aff. *lydekkeri*
		Bovidae indet. sp. 1
		Bovidae indet. sp. 2
		Bovidae indet. sp. 3
		Parabos sp.
Crocodilya		Crocodilya indet.
Testudines	Testudinidae	*Titanochelon* sp.
		Testudinidae indet.
	Trionychidae	Trionychidae indet.
Squamata	Viperidae	*Vipera* sp.
	Colubridae	*Malpolon* gr. *monspessulanus-mlynarski*

Fig. 3. Demagnetization plots of the Barranco del Cigarrón section. Top: sample with normal polarity zone from the La Virgen formation. Bottom: sample with reversed polarity from the Cigarrón Unit.

respectively, whereas deciduous premolars are denoted with the letter 'D'.

The descriptions and measurements of murid molars follow van de Weerd (1976) and Martín Suárez and Freudenthal (1993) respectively. The terminology used to describe gerbillid teeth is that of Wood and Wilson (1936), and length and width were measured as defined by Minwer-Barakat (2005). Mein and Freudenthal (1971) were followed when we described and measured cricetid teeth. The term "prelophid" is taken from Freudenthal (1985). The terms used to describe prolagid teeth follow Angelone and Sesé (2009). The descriptions and

measurements of leporid remains follow the nomenclature and methods proposed by López-Martínez et al. (2007) and Angelone and Sesé (2009) respectively.

A magnetostratigraphic study was performed based on 22 paleomagnetism stations distributed along a 60 m-thick composite series of the Puerto de la Cadena. Rock samples were extracted both with a portable drilling machine and by hand shaping of oriented blocs. Analytics were carried out at the Paleomagnetism Laboratory of SCT-Universitat de Barcelona-CSIC. A minimum of one sample per paleomagnetism station underwent a stepwise thermal demagnetization. The
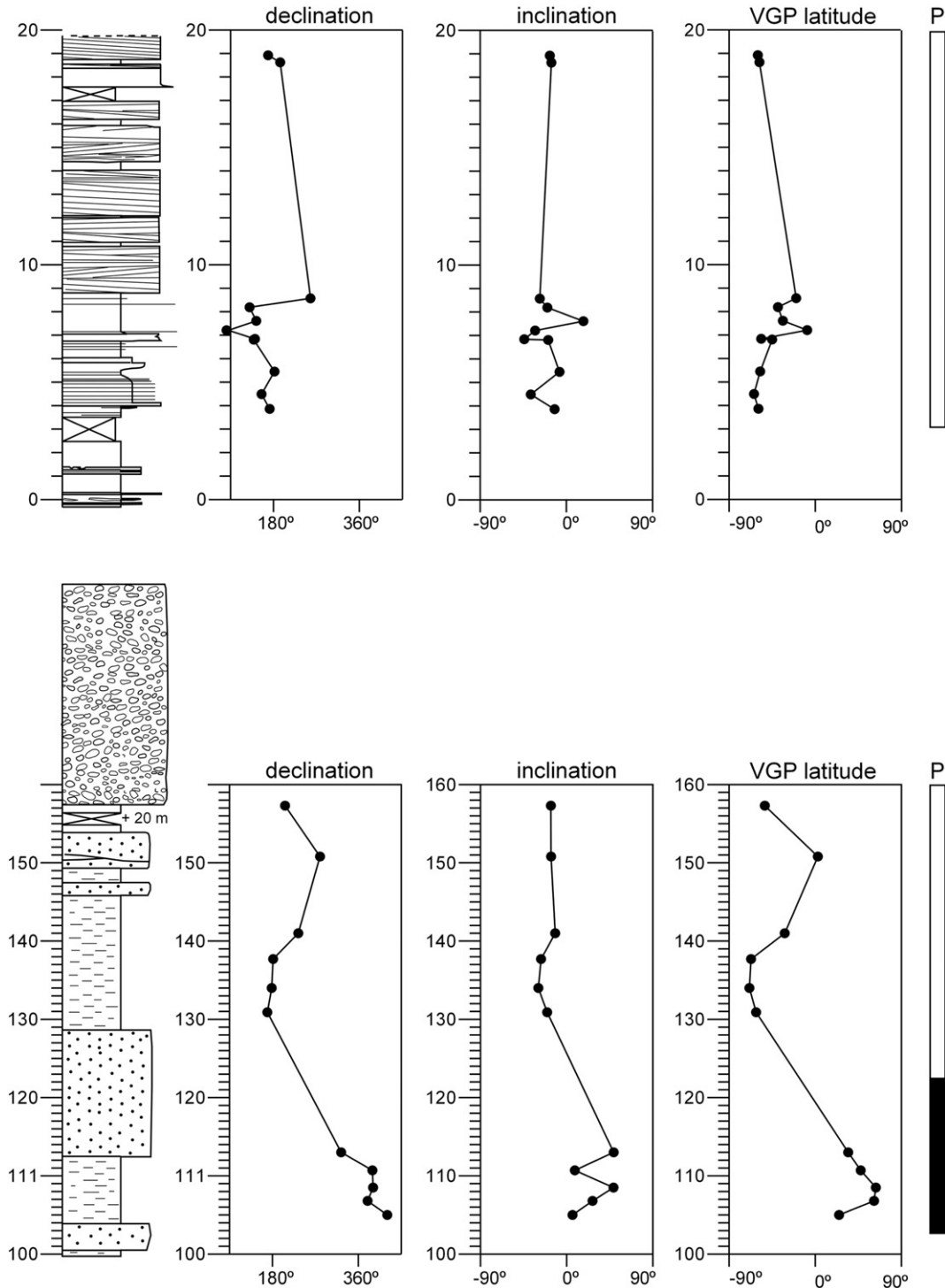

Fig. 4. Magnetostratigraphic results from the studied sections. Top: Isleta section, encompassing the Puerto de la Cadena site. Bottom: Upper part of Barranco del Cigarrón section. P indicates polarity (normal in black and reversed in white).

demagnetization included up to 15 steps, from room temperature to 700 °C. A few alternating field demagnetizations were also carried out, and bulk susceptibility was measured during the whole process to detect any mineralogical changes. The results were correlated to the latest Astronomical Tuned Neogene Time Scale (ATNTS; Hilgen et al., 2012).

4. Magnetostratigraphy

A magnetostratigraphic survey was carried out in order to date the Puerto de la Cadena site based on the correlation with both the magnetostratigraphy-calibrated mammal scale for the Iberian Peninsula (Agustí et al., 2001) and the magnetostratigraphically dated successions of nearby sections with the same age and stratigraphic units (Krijgsman et al., 2006; Soria et al., 2008). The limited stratigraphic context of the Puerto de la Cadena site (relatively thin Isleta section) made it necessary to also include the thicker Barranco del Cigarrón section in the magnetostratigraphic study. Thus, a first sampling was focused on the Cigarrón Unit in the two sections, and a second sampling was focused on the uppermost part of the La Virgen Units.

Thermally demagnetized samples displayed a stable demagnetization plot (see examples in Fig. 3) with high magnetization intensity values. A high temperature interval from around 300 °C to full demagnetization was considered to calculate a primary component. At lower temperatures, a normal polarity component was observed, and is considered to be a recent overprint of the geomagnetic field. The high temperature component provided both normal and reversed polarities (Fig. 4). In the Cigarrón Unit, normal polarities are recorded from meter 100 to 120, while in the upper remaining section only reversed polarities have been found. In the Isleta section only reversed polarities are observed. Samples from the La Virgen Unit provided unreliable results due to the low intensities and the instability of the magnetization.

5. Biostratigraphic correlations

5.1. Small mammals

The micromammal list of Puerto de la Cadena includes *Stephanomys* cf. *dubari*, *Paraethomys* cf. *meini*, *Apocricetus* cf. *barrierei*, *Ruscinomys lasallei*, *Debruijnimys* sp., *Prolagus* cf. *michauxi*, and *Trischizolagus*

Fig. 5. Rodent teeth collection from Puerto de la Cadena. *Stephanomys* cf. *dubari*: A. partial right M^1, MAM/DA/2012-0019/A5-2; B. right M_1, MAM/DA/2012-0019/A5-1. *Paraethomys* cf. *meini*: C. right M_2, MAM/DA/2012-0019/A27′06-9; D. right M_1, MAM/DA/2012-0019/A26-2; *Debruijnimys* sp.: E. right M^1, MAM/DA/2012-0019/A5′06-1. *Apocricetus* cf. *barrierei*: F. left M_3, MAM/DA/2012-0019/VLP2-831a; G. left M_2, MAM/DA/2012-0019/VLP2-831b; H. left M_1, MAM/DA/2012-0019/VLP2-831c. *Ruscinomys lasallei*: I) right M^1, MAM/DA/2012-0019/VLP2-799; J. left M_2, MAM/DA/2012-0019/A5′06-4; K. right M_2, MAM/DA/2012-0019/VLP2-869b; L. right M_1, MAM/DA/2012-0019/VLP2-869a; M. left M_3, MAM/DA/2012-0019/Puerto-de-la-Cadena. Scale bar equals 1 mm.

maritsae (see Figs. 5–6, Table 1, and Supplementary information), and can be assigned to the base of MN14 (earliest Ruscinian).

Mein et al. (1990) defined the base of MN14 in the Teruel Basin as the entry of *Celadensia*. However, Agustí et al. (2001) considered the base of MN14 to be the first appearance of the arvicolid *Promimomys* due to the occurrence of *Celadensia* in Baccinello (Italy), a MN13 locality (Rook and Torre, 1995). The range of *Promimomys* within the Iberian Peninsula is limited to the Teruel region (Mein et al., 1990), so correlations with southern Iberian basins are difficult to establish. In the absence of arvicolids, Agustí et al. (2001) proposed differentiating MN13 and MN14 based on the evolutionary stages of *Apodemus, Stephanomys, Paraethomys, Ruscinomys* and *Apocricetus*. In agreement with Morales et al. (2013), the appearance of a large-sized *Paraethomys* (*P.* aff. *abaigari, P. abaigari*) with a smaller one (*P. meini*) marks the beginning of the subzone N2. Mansino et al. (in press) considered this subzone to be early Ruscinian (MN14). The remains of *Stephanomys* from Puerto de la Cadena display a more derived evolutionary stage than those of *S. ramblensis*, the most characteristic late Turolian taxon in Spanish basins (Agustí and Llenas, 1996). In contrast, its descendant, *Stephanomys dubari*, is common in latest Turolian and earliest Ruscinian assemblages (García-Alix et al., 2008; Mansino et al., 2015). *Apocricetus barrierei* is a typical taxon of early Rusinian or MN14 unit (Mein, 1975; Mein et al., 1990; Freudenthal et al., 1998; Kälin, 1999; García-Alix et al., 2008). Therefore, the joint occurrence of *Apocricetus* cf. *barrierei* and *Stephanomys* cf. *dubari*, leads us to assign Puerto de la Cadena to the base of the MN14 unit.

We can compare the small mammal record of Puerto de la Cadena with that of some nearby late Turolian localities. Librilla 1, Molina de Segura 9, Sifón 61, and Sifón 79, located in the Fortuna Basin (Agustí et al., 1983, 2006), and Crevillente 6, situated in the Crevillente Basin (Martín Suárez and Freudenthal, 1998), share with Puerto de la Cadena the presence of *Paraethomys meini* as well as a Cricetodontinae like *Ruscinomys* sp. In addition, *Prolagus michauxi* is present in the Fortuna Basin levels. However, these localities differ from Puerto de la Cadena

due to the presence of *Stephanomys ramblensis* and *Apocricetus alberti*, suggesting that they have an older age. In spite of the great faunal similarity, the absence of the gerbil *Debruijnimys* in Molina de Segura 9, Sifón 61, Sifón 79, and Crevillente 6 has a biostratigraphic interest. Following Agustí et al. (2006), the so named "Gerbil Event" (third Messinian Mammalian Event, MME 3) took place between 5.96 and 5.33 Ma, when rodents of African affinities came into the Western Mediterranean, such as members of the genera *Myocricetodon* and *Debruijnimys*. This dispersal event clearly occurred after the arrival of *Paraethomys*, and is directly related to the MSC. Therefore, all the cited localities were deposited before the onset of MME 3, as they have a lower stratigraphical position than Puerto de la Cadena. In contrast, the studied small mammal assemblage is very similar to that of the Sifón 413 locality (Agustí et al., 2006). Similar taxa have been recognized in this level: *Debruijnimys* sp., *Paraethomys miocaenicus* (=*P. meini*), *Stephanomys medius* (=*S. dubari, S. cordii*), *Ruscinomys lasallei* and *Prolagus michauxi*.

The nearby site of La Alberca has also yielded a similar small mammal association, with the occurrence of *Stephanomys medius* (=*S. dubari, S. cordii*), *Ruscinomys lasallei, Paraethomys meini, Prolagus michauxi*, and the genus *Trischizolagus* (Montenat, 1973; López Martínez, 1989; Freudenthal et al., 1998). Following de Bruijn et al. (1975), the La Alberca site is late Miocene in age. They based their dating on the association of planktonic foraminiferan association found in higher and lower marine sediments, between which the continental site is intercalated. If this dating is correct, then La Alberca would be older than Puerto de la Cadena. This is consistent with the absence of gerbils in La Alberca and the presence of *Apocricetus alberti*.

The joint presence of *Stephanomys* cf. *dubari, Paraethomys* cf. *meini, Ruscinomys lasallei, Apocricetus* cf. *barrierei* and *Debruijnimys* sp. leads us to correlate the Puerto de la Cadena site with the subzone N1 of the Ventian proposed by Morales et al. (2013), in further agreement with the large-mammal association.
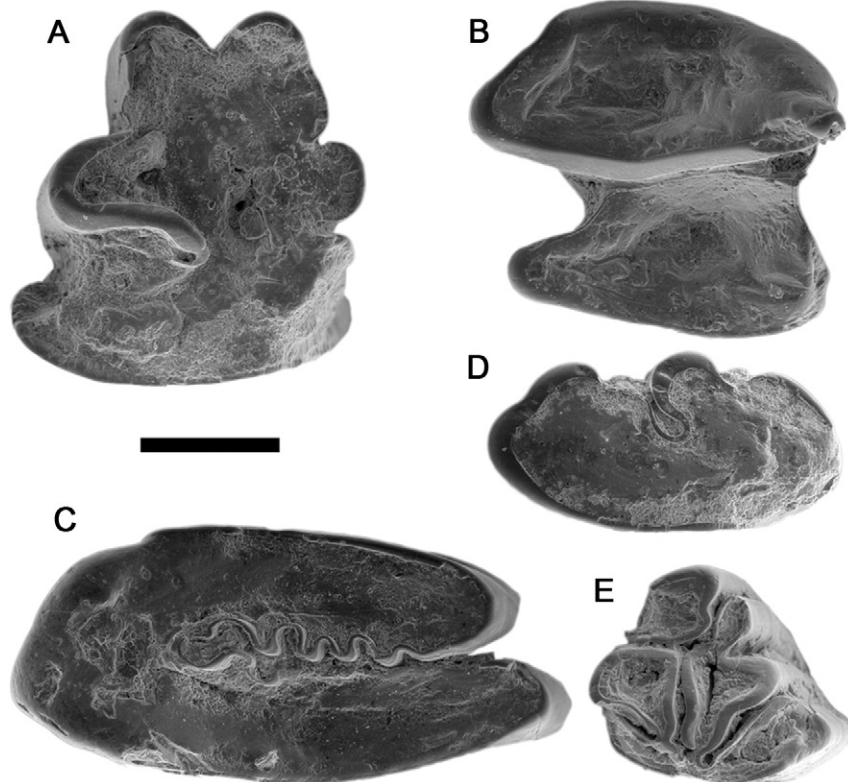

Fig. 6. Lagomorph teeth from Puerto de la Cadena. *Trischizolagus maritsae*: A. left P$_3$, MAM/DA/2012-0019/VLP2-593; B. left lower molariform, MAM/DA/2012-0019/VLP2-626; C. left P^2, MAM/DA/2012-0019/A-27; D. right upper molariform, MAM/DA/2012-0019/VLP2-656. *Prolagus* cf. *michauxi*: E. left P$_3$, MAM/DA/2012-0019/A-26. Scale bar equals 1 mm.

5.2. Large mammals

The large mammal assemblage from Puerto de la Cadena (Fig. 7 and Table 1) includes taxa that, in Spain, either (a) first appear in MN13 (*Eucyon, Macaca, Parabos*); (b) are as yet only known from MN14 (*Sivatherium, Gazella* aff. *baturra, Hipparion fissurae*); (c) are recorded for the first time (*Gazella* aff. *lydekkeri*); or (d) occur in both MN13 and MN14 (see Supplementary information). Taken as a whole, the large mammal association from Puerto de la Cadena suggests an age close to the MN13–MN14 transition, which is another important novelty for the Spanish fossil record of the Miocene/Pliocene boundary. In fact, in the Iberian Peninsula there are nearly no fossil localities with ages comprised between those of Venta del Moro (Valencia; local biozone M3; Morales, 1984; Montoya et al., 2006) and La Gloria 4 (Teruel; biozone O; Alcalá, 1994). The very few localities in between have

yielded a small number of large mammal fossils: Arenas del Rey (Granada; Aguirre, 1963; Alberdi and Boné, 1978), Almenara-Casablanca M (Castellon; Agustí et al., 1989, 2011; Köhler et al., 2000), La Alberca (Murcia; Montenat and Crusafont, 1970) and Baza-1 (Granada; Piñero et al., in press; Ros-Montoya et al., in press). In contrast, the micromammal record is abundant, although it is difficult to interpret (Morales et al., 2013). Therefore, it is not surprising that Puerto de la Cadena contains so many taxa not previously recorded in this geographical area: *Eucyon monticinensis, Hipparion* aff. *fissurae, Sivatherium* cf. *hendeyi, Gazella* aff. *baturra, Gazella* aff. *lydekkeri*, and the possible presence of the caprine *Norbertia hellenica. Macaca* sp. which was already known from Almenara-M (Köhler et al., 2000), although the new record from Puerto de La Cadena confirms its presence in the early Pliocene of Spain (see Supplementary information). The remaining large mammal remains from Puerto de la Cadena either cannot be assigned to a species

Fig. 7. Large mammals from the early Pliocene locality of Puerto de la Cadena. *Dihoplus schleiermacheri/megarhinus*: A. anterior part of mandible, MAM/DA/2012/VLP3-682; E. left $D_{3/4}$, occlusal (1) and lingual (2) views, MAM/DA/2012/VLP2-507. *Hipparion* aff. *fissurae*: B. right $P_{3/4}$, occlusal view, MAM/DA/2012/VLP2-446; O. left $M^{1/2}$, occlusal view, MAM/DA/2012/VLP3-579. *Anancus arvernensis*: C. left $D^{3/4}$, occlusal (1) and buccal (2) views, MAM/DA/2012/VLP2-234; L. left D^2, lingual (1), occlusal (2) and buccal (3) views, MAM/DA/2012/VLP2-282. Bovidae indet. sp. 3: D. maxilla with D^2-M^2, occlusal view, MAM/DA/2012/VLP2-212. Bovidae indet. sp. 2: F. right M_3, lingual (1), occlusal (2) and buccal (3) views, MAM/DA/2012/VLP2-563. Cervidae indet.: G. antler fragment, MAM/DA/2012/VLP4-79. Bovidae indet. sp. 1: H. right metatarsus, anterior view, MAM/DA/2012/VLP2-272. *Sivatherium* cf. *hendeyi*: I. right lower canine, lingual (1), distal (2) and labial (3) views, MAM/DA/2012/VLP2-543. *Eucyon monticinensis*: J. left M_1, buccal (1), occlusal (2) and lingual (3) views, MAM/DA/2012/VLP2-51. *Gazella* aff. *lydekkeri*: K. right metacarpus, anterior view, MAM/DA/2012/VLP2-103. *Gazella* aff. *baturra*: M. left female horn core, anterior (1) and lateral (2) views, MAM/DA/2012/VLP2-325. *Parabos* sp.: N. right M^2, occlusal (1) and buccal (2) views, MAM/DA/2012/VLP2-464. The 1.5 cm scale bar goes with figure J, the 6 cm scale bar goes with figures H and K, and the 3 cm scale bar goes with the remaining figures.
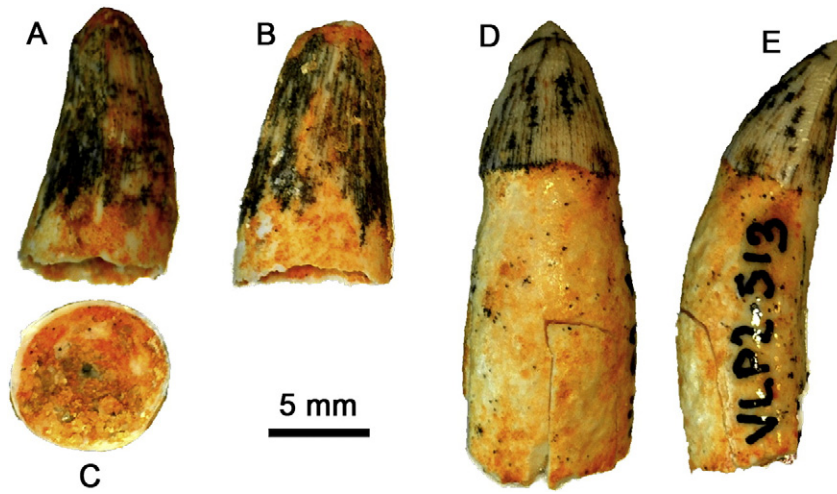
Fig. 8. Crocodylia indet. from the early Pliocene of Puerto de la Cadena. A–C. Anterior maxillary tooth (MAM/DA/2012/VLP2-63) in lateral, posterior and dorsal views; D–E. posterior maxillary tooth (MAM/DA/2012/VLP2-513) in anterior and lateral views.

(as is the case with the sole remain of a deer antler and the rhinoceros *Dihoplus*). The proboscidean *Anancus* appears in MN12 and the bovine *Parabos* at the end of MN13 (in local zone M3). These new appearances are framed within the major faunal turnover that took place at the end of the Miocene, which in part is related to the Messinian Salinity Crisis (Agustí et al., 2006; Van der Made et al., 2006; Gibert et al., 2013; Morales et al., 2013). The appearance of several of these species is also recorded in other Mediterranean localities, namely: *Eucyon monticinesis*, which was described from Brisighela, Italy (Rook, 1992); *Sivatherium*, which in Macedonia was described as *Sivatherium garevskii* (see Geraads, 2009) and in Turkish Thrace (Edirne = Adrianopolis) as *Sivatherium giganteum* (see Abel, 1904); *Gazella* aff. *lydekkeri* and likely the possible caprine dentition, which could correspond to the *Gazella* sp. and *Norbertia hellenica* from Maramena (Köhler et al., 1995).

6. Magnetobiostratigraphic correlation

The correlation of the obtained polarities with the Geomagnetic Polarity Time Scale (Fig. 10) is based on the available geological and biostratigraphic data. First, the regional geological and magnetostratigraphic context of Krijgsman et al. (2006) and Soria et al. (2008) indicates that the Cigarrón Unit is equivalent to the Pliocene Unit in Soria et al. (2005). Both units correspond to the infilling of the post end-Messinian erosion by transitional environments in which the Puerto de la Cadena paleontological remains accumulated.

The entire Puerto de la Cadena section records a reversed polarity chron, whereas the Cigarrón Unit, whose upper part includes the Puerto de la Cadena site, records a normal-reversed polarity sequence (Fig. 4).

According to the above-mentioned end-Messinian discontinuity at the base of the Cigarrón Unit, correlation with the reversed chron C3r is discounted because it covers the Mio-Pliocene boundary. Therefore, the normal polarity interval at the base of the Cigarrón section must be correlated with chron C3n.4n (or younger).

In turn, the correlation among Iberian micromammal sites that have been magnostratigraphically dated and the Puerto de la Cadena site supports that the correlation of the latter must be older than C3.2n. This is the case of Sifón P (correlated to C3.2n by Garcés et al., 2001), a site which has a more derived *Stephanomys* than that from Puerto de la Cadena. Such constraints indicate that the reversed polarity span at Puerto de la Cadena is likely correlated to C3n.3r or C3n.2r. A correlation to C3n.3r is preferred based on the large similarity in the small mammal association with Fuente del Viso (see Supplementary information), which is correlated with that chron (Opdyke et al., 1997; Freudenthal et al., 1998). Therefore, we correlate the normal interval at the Cigarrón section with chron C3n.4n, and the upper reverse span at the upper part with C3n.3r. The Puerto de la Cadena site is therefore dated between 4.997 and 4.896 Ma (Fig. 10).

Our interpretation is consistent with other well-dated sites. The older age indicated for Venta del Moro and Sifón 79 is in line with their assignment to the normal chron C3An.1n (6.252–6.033 Ma; Garcés et al., 2001; Agustí et al., 2006; Gibert et al., 2013). Similarly, the somewhat older Purcal 3, 4, and Zorreras 3A were correlated to chron C3r, ranging from 5.235 to 6.033 Ma (Martín-Suárez et al., 1998, 2000). Finally, the Sifón 413 level was situated in the Pliocene span of chron C3r (5.330–5.235 Ma; Garcés et al., 2001), and although its small mammal association resembles that of Puerto de la Cadena,
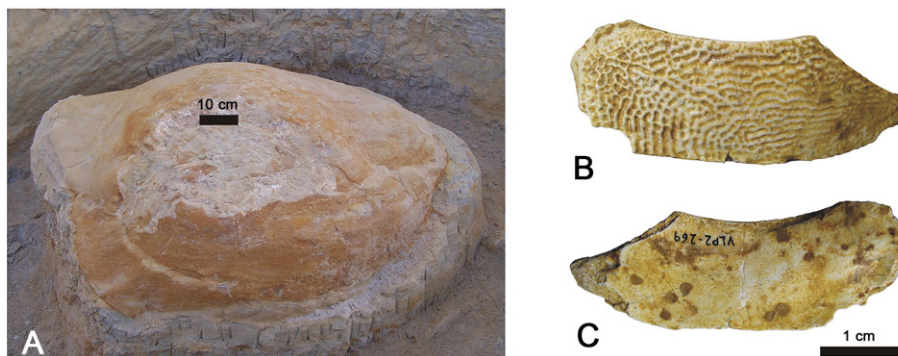

Fig. 9. The two clades of turtles identified in the early Pliocene site of Puerto de la Cadena (Murcia). A. Carapace of *Titanochelon* sp. "in situ"; B–C. VLP2-269, nuchal plate of Trionychidae indet. (Cryptodira), in dorsal (B) and ventral (C) views.
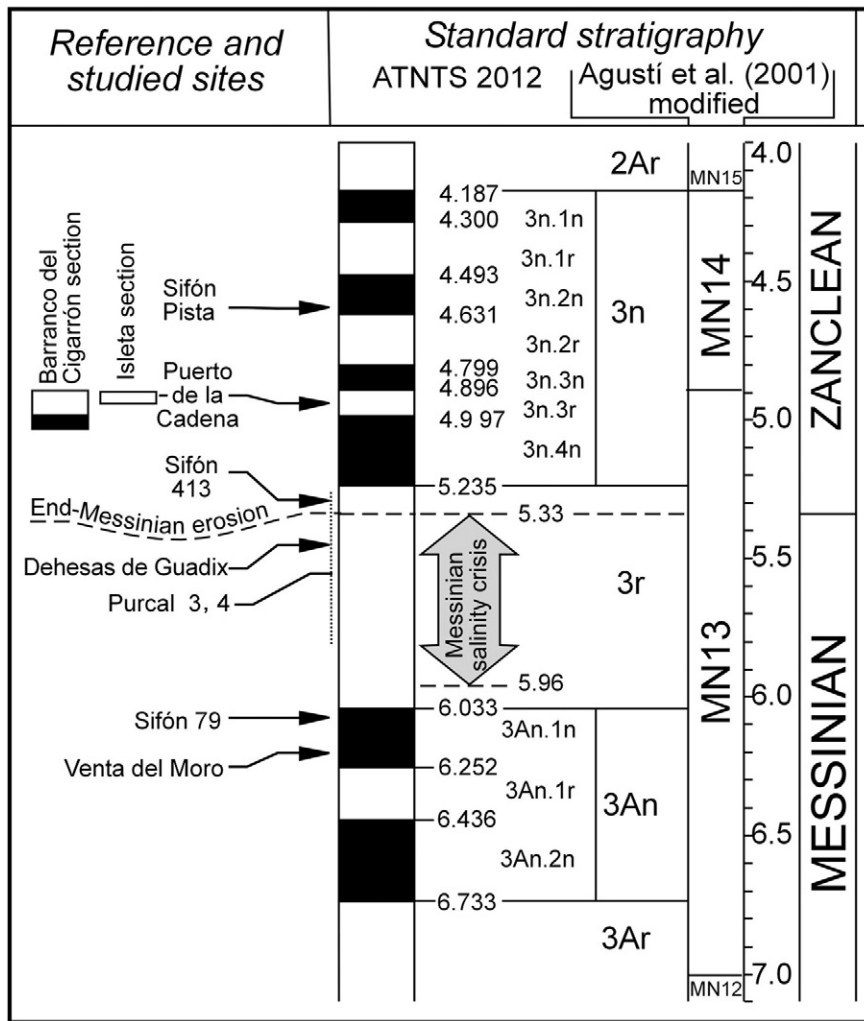
Fig. 10. Magnetobiostratigraphic correlation of the studied locality and other reference sites, with the magnetic polarity time scale.

considering the chronostratigraphic information, Sifón 413 is at least 200 kyr older.

Martín-Suárez et al. (2000) and Agustí et al. (2001) considered the Fuente del Viso faunal association as MN14, instead of latest MN13 as indicated by Opdyke et al. (1997). The faunal assemblage of Puerto de la Cadena has been interpreted in this work as earliest MN14. Considering these data, a minimum age for the base of MN14 is established within the chron C3n.3r. This permits bracketing the MN13/MN14 boundary between 4.997 and 4.896 Ma. This correlation is consistent with that of Opdyke et al. (1997) and Agustí et al. (2001), who supported an MN13/MN14 limit younger than its traditional position at the marine Miocene/Pliocene boundary.

Therefore, according to this correlation, Puerto de la Cadena is closely coeval of the Tomea Eksi 3 level, at the other edge of the Mediterranean Basin, in the Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece; Hordijk and de Bruijn, 2009), also placed within chron C3n.3r. However, when we compare the two small mammal assemblages, striking differences are evident. The rodent fauna from Tomea Eksi 3 is composed of a diversified fauna of murids related to *Apodemus* (*Micromys bendai*, *Rhagapodemus primaevus*, *Apodemus atavus*, *Apodemus dominans*?) together with an archaic arvicolid (*Mimomys* aff. *davakosi*). This association suggests a forested environment, with predominant humid conditions, which is confirmed by the other rodent associations present in closer levels of the basin, including, among others, flying squirrels of the species *Pliopetaurista dehneli* (Vorio 3/3a; Hordijk and de Bruijn, 2009).

In contrast, Puerto de la Cadena has a very different small mammal association, with most of the rodent species indicating open-dry conditions. This is the case of the hamsters *Apocricetus* cf. *barrierei* and *Ruscinomys lasallei* (a selenodont/hypsodont cricetid), the gerbil *Debruijnimys* sp. and the stephanodont murid *Stephanomys* cf. *dubari*. These evidences point to the existence of very different environmental conditions at the two extremes of the Mediterranean. In the Western Mediterranean there is the persistence of an open landscape, with prevalent dry conditions, which most possibly are reminiscent of the Messinian Salinity Crisis (as indicated by the persistence of gerbils of African origin). In contrast, the conditions in South Eastern Europe suggest a forested environment in a humid context. This difference can be explained by the influence of the neighboring Black Sea, which possibly increased precipitation due to lake effect.

7. Conclusions

The Puerto de la Cadena site, in the upper part of the Cigarrón Unit, at the northern flank of the Carrascoy range mountain (Murcia, Spain), has yielded diverse vertebrate continental fauna, and up to 26 different species were recorded. The recovered assemblage can be correlated to the base of MN14 (earliest Ruscinian of the early Pliocene). The small mammal association consists of *Stephanomys* cf. *dubari*, *Paraethomys* cf. *meini*, *Debruijnimys* sp., *Apocricetus* cf. *barrierei*, *Ruscinomys lasallei*, *Trischizolagus maritsae,* and *Prolagus* cf. *michauxi*. The large mammal record comprises *Macaca* sp., *Eucyon monticinensis*, *Anancus arvernensis*,

Hipparion aff. *fissurae*, *Dihoplus schleiermacheri* vel *Dihoplus megarhinus*, Cervidae indet., *Sivatherium* cf. *hendeyi*, *Gazella* aff. *baturra*, *Gazella* aff. *lydekkeri*, *Parabos* sp., and three additional indeterminate bovids. Among the reptiles, Puerto de la Cadena records Crocodylia indet., *Malpolon* gr. *monspessulanus-mlynarski*, *Vipera* sp., Trionychidae indet., *Titanochelon* sp., and one indeterminate testudinid. This fauna includes a number of elements of African origin, such as *Debruijnimys* sp., *Macaca* sp., and *Sivatherium* cf. *hendeyi*, which most likely settled on the Iberian Peninsula during the Messinian Salinity Crisis (as has been reported in previous studies).

Puerto de la Cadena is one of the youngest localities of the MN14 (early Pliocene), with the joint presence of typical elements of this unit, like *Apocricetus* cf. *barrierei Sivatherium*, *Gazella* aff. *baturra*, and *Hipparion fissurae*. According to the magnetostratigraphic correlation proposed in this work, the faunal association from Puerto de la Cadena is dated to the early Pliocene. Our results allow us to establish the boundary between MN13 and MN14 within the reversed polarity interval C3n.3r (4.997–4.896 Ma). In addition, this study confirms the persistence of crocodiles in the early Pliocene of Europe.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2017.04.020.

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SUPPLEMENTARY INFORMATION

1. The vertebrate paleontological record

A preliminary faunal list of the vertebrate remains yielded by the Puerto de la Cadena site was published by Mancheño et al. (2013). However, in the present work we provide the results of a more thorough study of the faunal remains, including some measurements and photographs that led to minor amendments and additions to the previously reported faunal list (Table 1).

1.1. Mammals

1.1.1. Small mammals

Among the small mammals, rodents are represented by the families Muridae and Cricetidae, while lagomorphs include representatives of the families Prolagidae and Leporidae. The murid association comprises the species *Stephanomys* cf. *dubari*, *Paraethomys* cf. *meini*, and *Debruijnimys* sp., represented by four, three and two teeth, respectively.

The two M^1 of *Stephanomys* cf. *dubari* (2.58 x — mm; — x 1.73 mm) display the t1 displaced backwards, the labial crest is well developed, and the lingual crest is low in one specimen and high in the other one. They have both t1bis and t2bis (Fig. 5A). The two M_1 (2.25 x 1.47 mm; 2.05 x — mm) have a well-developed longitudinal crest connecting the hypoconid-entoconid to the protoconid-metaconid. The labial cingulum is moderate, with a low oval c1 attached to the hypoconid, and accessory cusps are absent. The tma is very weak and low, and the posterior heel is oval and of medium size (Fig. 5B). These teeth show the typical features of *Stephanomys*, such as a high crown, longitudinal crest in the lower teeth, and posterior crests and spurs on t1 and t3 in the

upper teeth. The studied material shows morphological and biometrical differences with respect to the older representatives of the genus, *Stephanomys stadii* and *Stephanomys ramblensis*. The late Pliocene species of *Stephanomys* have a higher crown, larger size, and greater development of the stephanodonty than the studied molars (Minwer-Barakat et al., 2011). In contrast, the described specimens are similar to those of *Stephanomys dubari* and *Stephanomys cordii*. The moderate size and rather poorly developed longitudinal connections agree better with *S. dubari* than with *S. cordii*, although given the restricted sample we prefer to be cautious and use open nomenclature. *Stephanomys dubari* is present in late Miocene to Early Pliocene assemblages of the Iberian Peninsula (García-Alix et al., 2008a; Mansino et al., 2015a).

With regard to the teeth from Puerto de la Cadena assigned to *Paraethomys* cf. *meini* (Fig. 5C, 5D), there is an M_1 (2.24 x 1.50 mm) with a slightly asymmetrical anteroconid and no tma. It displays a poorly developed longitudinal spur. The labial cingulum is moderate, and the c1 is large and round. There is a small elongated posterior heel. The two M_2 (1.53 x 1.48 mm; 1.65 x 1.5 mm) have a weak labial cingulum. The c1 is small, low and separated from the hypoconid. The anterolabial cusp is poorly preserved. The posterior heel is weak and laminar. The teeth of *Paraethomys* from Puerto de la Cadena are clearly smaller than those of *Paraethomys jaegeri*, and also slightly smaller than those of *Paraethomys abaigari* (see Adrover et al., 1988) and *Paraethomys belmezensis* (Castillo Ruiz, 1992), more closely resembling the maximum values reported for *Paraethomys meini* from Sète (type locality; Adrover, 1986). The morphology of the described specimens also agrees with that of *Paraethomys meini*, given the presence of a weak labial cingulum and the lack of tma. However, we use open nomenclature due to the scarcity of remains. According to Agustí et al. (2006), the first occurrence of *Paraethomys* in the Iberian Peninsula is recorded in the neighboring Fortuna Basin

(Southern Spain; few kilometers north of our site) prior to the MSC (ca. 6.2 Ma), although this taxon further persisted during the Ruscinian (Mein et al., 1990; Adrover et al., 1993; García-Alix et al., 2008a; Minwer-Barakat et al., 2012; Mansino et al., 2015a; Piñero et al., in press.). Agustí et al. (2006) associated the *Paraethomys* dispersal with the entry of camels of the genus *Paracamelus* into southern Spain, being likely part of the same dispersal event from northern Africa. Similarly, Gibert et al. (2013) indicated the first entry of *Paraethomys* and *Paracamelus* in the Iberian Peninsula in Venta del Moro (Spain) at 6.23 Ma.

Gerbils are represented by *Debruijnimys* sp. (Fig. 5E). The sample consists of two M^1, one of them fragmentary (2.88 x 2.07 mm; 2.76 x — mm). The anterocone is composed of two lobes, which are widely confluent. There is a spur on the posterior side of the anterocone, which does not reach the paracone. Protocone and paracone are connected by a transverse ridge, the paracone being larger than the protocone. The posterior wall of the paracone is projected towards the metacone without reaching this cusp. The hypocone and the metacone are connected. The metacone is much smaller than the hypocone and it is connected to the anterolabial wall of this cusp. *Debruijnimys* sp. from Puerto de la Cadena agrees in size and occlusal morphology with the molars ascribed to *Debruijnimys* sp. from the early Pliocene localities of Sifón 413 (Agustí et al., 2006), Alcoy 4B (Agustí, 1991), Botardo C (Martín Suárez, 1988), Gorafe 1 and Caravaca (Bruijn, 1974), and La Gloria 4 (Adrover et al., 1993). According to Agustí and Casanovas-Vilar (2003), the genus *Debruijnimys* settled on the Iberian Peninsula at least two times during the Miocene-Pliocene transition, migrating in two different waves from North Africa. The first one corresponds to *Debruijnimys almenarensis*, recorded in some late Miocene localities, like Almenara-Casablanca M (Agustí, 1990; Agustí et al., 2011), Negratín-1 (Minwer-Barakat et al., 2009a), Salobreña (Aguilar et

al., 1984), Zorreras-3A (Martín-Suárez et al., 2000), and Gafares 2B (García-Alix et al., 2016), while the second one comprises *Debruijnimys* sp. from the previously mentioned early Pliocene localities (Castillo and Agustí, 1996; Agustí and Casanovas-Vilar, 2003), which might be the ancestors of *Debruijnimys julii* (see Agustí and Casanovas-Vilar, 2003).

Cricetids are represented at Puerto de la Cadena by *Apocricetus* cf. *barrierei* and *Ruscinomys lasallei*. The remains of *Apocricetus* cf. *barrierei* consist of a single mandible with the M_1 (2.53 x 1.40 mm), M_2 (2.12 x 1.54 mm) and M_3 (2.10 x 1.59 mm; Fig. 5F, 5G, 5H), all these teeth being very worn. In the M_1, the anteroconid is crest-like and simple, with a double anterolophulid and very short prelophid. The protolophid and metalophid are anterior and there is no evidence of mesolophid. The M_2 and M_3 display the same occlusal pattern as the M_1, with a well-developed labial cingulum, no lingual cingulum, anterior protolophid and metalophid, and no mesolophid. The crest-like anteroconid and the presence of a short prelophid are common traits in both *A. barrierei* and *A. alberti* (see Ruiz Sánchez et al., 2014; Mansino et al., 2014). In addition, the size fit well with this species, enabling to distinguish the described specimen from *Apocricetus plinii*, *Apocricetus alberti* and *Apocricetus angustidens*. We tentatively attribute the studied teeth to *Apocricetus* cf. *barrierei*. The presence of a single mandible leads us to use open nomenclature. *Apocricetus barrierei* was originally identified in the early Pliocene of Southern France (Hautimagne, Chabrier, Celleneuve, Vendargues; Mein and Michaux, 1970), but later recognized in many sites from Spain (Freudenthal et al., 1988). This species is considered a key element of MN14 by several authors (Mein et al., 1990; Freudenthal et al., 1998; Kälin, 1999; García-Alix et al., 2008a).

Ruscinomys lasallei is represented by one M_1 (3.08 x 2.01 mm), two M_2 (3.03 x 2.15 mm; 2.91 x 1.90 mm), one M_3 (2.92 x 1.96 mm), and two M^1 (one fragmentary; 4.28 x 2.61 mm; — x 2.28 mm). In the M^1, an anterior groove separates the two lobes of the anterocone (Fig. 5I). There are well-developed ectolophs, and the anterior one reaches the anterior wall of the paracone, being placed in a lower position with respect to this cusp. The posterior ectoloph is connected to the anterior wall of the metacone, and it is placed at the same level than this cusp. The M_1 has a very simple dental pattern, with a small and rounded anteroconid, and lacking the anterolophid (Fig. 5L). There is a short mesolophid that does not reach the posterior wall of the metaconid. The posterolophid does not close the posterosenid. The M_2 follows the same pattern as the M_1, with no anterolophid and a short mesolophid (Fig. 5J, 5K). In one specimen, this mesolophid does not reach the posterior wall of the metaconid, while it does in the other one, closing the mesosinusid. In the M_3, the anterolophid is also absent, and there is a short mesolophid that reaches the posterior wall of the metaconid, closing the mesosinusid (Fig. 5M). An alternate assignment to *Ruscinomys schaubi*, *Ruscinomys gilvosi*, or *Ruscinomys bravoi* is ruled out because of their smaller size, whereas an attribution to *Ruscinomys europaeus* is discounted by the larger dimensions of the latter. The great crown height of the studied molars, their large size, and some morphological traits (such as the lingual lobe of the M^1 anterocone directed forward with a sharp lingual angle, and the rounded M_1 anteroconid lacking the anterolophid) allows us to ascribe these teeth to *Ruscinomys lasallei* (see García-Alix et al., 2008b).

Two lagomorph species are represented at Puerto de la Cadena: the leporid *Trischizolagus maritsae* and the prolagid *Prolagus* cf. *michauxi*. The former is the most abundant small mammal species at the site. It is represented by nearly a hundred of upper and lower isolated teeth. Most of them are damaged, probably due to transport

prior to the deposition of the sandy sediments in which they are included, as it is shown by the frequent abraded or polished surfaces of these teeth. The sample includes several P_3 and P^2, which are the most diagnostic elements from a taxonomic perspective in lagomorphs. The P_3 display a typical archaeolagine structure, with five reentrant folds, although the development of the mesoflexid is variable (Fig. 6A). None of the specimens exhibit crenulations on the enamel of the posterior wall of the hypoflexid. The P^2 show a simple structure (Fig. 6C). The paraflexus is the deepest reentrant fold, followed by the mesoflexus, whereas the hypoflexus appears in all the specimens as a very shallow enamel invagination. No specimen exhibits crenulations on the enamel of the lingual wall of the paraflexus. All of the upper molariform teeth (Fig. 6D) display crenulations on the enamel of the anterior wall of the hypoflexus. In some of them, crenulations are also visible on the enamel of the posterior wall, although they are usually smoother than those of the anterior wall. All these features agree with the morphology of *T. martisae* from Maritsa (Greece), the type locality of the species (Bruijn et al., 1970). The size of the teeth from Puerto de la Cadena (length of P_3 ranges from 2.25 to 2.99 mm) is slightly larger than in those from Maritsa. This slight difference might be due to the fact that most specimens from Maritsa correspond to juvenile teeth, whereas within the Puerto de la Cadena sample there are both juvenile and adult specimens.

In the nearby La Alberca site, *Hispanolagus crusafonti* was originally described by Janvier and Montenat (1971), being later transferred to *Trischizolagus* by López Martínez (1989). The material from Puerto de la Cadena differs from *T. crusafonti* in the presence of a mesoflexid and the lack of crenulations on the enamel of the posterior wall of the hypoflexid of the P_3, as well as in having a simple paraflexus (instead of double as in *T. crusafonti*, at least judging from the illustrations) without crenulations

on the enamel of its lingual wall. La Alberca is currently considered to be slightly older (latest Miocene; Mein et al., 1973; Bruijn et al., 1975) than Puerto de la Cadena (earliest Pliocene). Therefore, the record of two different species of the genus *Trischizolagus* in two sites so geographically close might be due to the slight differences in age. However, their close chronological proximity suggests that this fact might also stem from a misinterpretation of the material from La Alberca, as it was yet suggested by López Martínez (1989).

In Puerto de la Cadena, the prolagid *Prolagus* cf. *michauxi* is much less abundant than *T. maritsae*, and only a few teeth can be ascribed to the former species. For the same reasons as in the case of *T. maritsae* (see above), in general these teeth are poorly preserved. The only available P_3 (Fig. 6E) displays a large and rounded anteroconid, similar in size to the metaconid, protoconid and hypoconid. The metaconid is connected to the entoconid by a narrow metaisthmus. The protoconid shows an elongated protonoculid projected forward. The protoconid is connected to the entoconid-hpoconid complex by a narrow protoisthmus. The crochet is absent. These characteristics agree with those of *Prolagus michauxi*. However, taking into account the scarcity of the sample and the lack of more diagnostic material, we provide a species identification with open nomenclature. *Prolagus michauxi* was also identified in the nearby La Alberca site (López Martínez, 1989). According to Sesé (2006), in Spain *T. maritsae* and *P. michauxi* occur around the Mio-Pliocene boundary, from MN13 to MN15.

1.1.2. Large mammals

The large mammal assemblage from Puerto de la Cadena comprises primates (family Cercopithecidae), carnivorans (Canidae), proboscideans (Gomphotheriidae),

perissodactyls (Equidae and Rhinocerotidae), and artiodactyls (Cervidae, Giraffidae, and Bovidae).

The primate remains from Puerto de la Cadena consist of two isolated cercopithecid teeth (a damaged and partial male upper canine, and a well preserved and only slightly worn upper molar crown) attributable to genus *Macaca*. They come from distinct outcrops and therefore belong to different individuals. The canine is dagger-like and labiolingually compressed, and displays a conspicuous mesiolingual sulcus extending from the crown onto the root. The upper molar is an M^3, as indicated by its distally-tapering contour, the lack of distal contact facet, and the presence of a distal accessory cuspule. It displays a bilophodont and generalized papionin occlusal pattern, which is characteristic of the dentally-conservative cercopithecid genus *Macaca* (Delson, 1973, 1975). The moderate occlusal relief and shallow median notches rule out an alternate attribution to the papionin *Theropithecus* and the colobine *Mesopithecus*. An assignment to the latter is further discounted by the restricted mesial fovea and the moderately developed median lingual cleft, among other features. In turn, a referral to the larger papionin *Paradolichopithecus* is discounted by the dimensions of the M^3, which only minimally exceed those of living Barbary macaques from North Africa (*Macaca sylvanus sylvanus*), and fit well with those of the early Pliocene *Macaca sylvanus prisca* and the younger *Macaca sylvanus florentina* (see Alba et al., 2011). Although cercopithecid canines are less informative from a taxonomic viewpoint (Delson, 1973), the specimen from Puerto de la Cadena similarly resembles in size and shape those of living and fossil *Macaca sylvanus* subspp. (Alba et al., 2011). Given current uncertainties about the distinctiveness of European macaque subspecies and the taxonomic identity of latest Miocene macaques from Europe, as well as the scarcity of the sample, pending more detailed comparisons we attribute the material from Puerto de

la Cadena to *Macaca* sp. Macaques have also been recorded from the late Miocene of North Africa (Delson, 1973, 1975, 1980; Szalay and Delson, 1979) and the latest Miocene of Spain (Almenara-Casablanca M; Köhler et al., 2000) and Italy (Moncucco Torinese; Alba et al., 2014), undoubtedly representing an immigrant element of African origin.

The canid *Eucyon monticinensis* (Fig. 7J) is represented by three mandibular fragments (with P_4-M_1, M_2, and the talonid of the M_1 and M_2, respectively), as well as by two isolated M^1, one of them with the lingual wall broken. The morphology and size are identical to those of *Eucyon monticinensis* from Brisighella, Italy (Rook, 1992), which mainly differs from *Eucyon debonisi* of Venta del Moro, Spain, in the larger size of its dentition (Montoya et al., 2009).

Proboscidean remains include a D^2 (Fig. 7L) and a molariform tooth (Fig. 7C) with at least four lobes. The latter has crenulated enamel, it is worn flat, and there is no lophodonty, unlike in *Mammuthus* or *Zygolophodon* and the lobes are not anteroposteriorly compressed as the plates of the Elephantidae. An assingment to *Gomphotherium* or *Tetralophodon* can be discounted because these tend to have molariform teeth with three and four lobes, respectively and relatively large D^2. It seems more likely the material belongs to *Anancus*. The only European species of this genus is *A. arvernensis*. The size of the molariform tooth suggests a D^3 or D^4, and considering the small size of the D^2 compared to this tooth it might be a D^4. In the Iberian Peninsula, *Anancus* appeared not later than MN12 and lasted at least until the beginning of the Pleistocene (Mazo and Van der Made, 2012). In central Europe it is recorded since MN11 (Göhlich, 1999).

The large mammal assemblage of Puerto de la Cadena includes two perissodactyls:

the equid *Hipparion* aff. *fissurae*, and the rhinocerotid *Dihoplus schleiermacheri* vel *Dihoplus megarhinus*. *Hipparion* aff. *fissurae* is represented by a fragment of right $D^{3/4}$, three right P^2, two right and one left $M^{1/2}$ (Fig. 7O), two right M^3, one left D_2, one right P_2, two right and one left $P_{3/4}$, one right (Fig. 7B) and a fragment of a left $M_{1/2}$, two left M_3, a partial humerus, a tuber calcis fragment of calcaneum, two left astragali, a right third metacarpal and a diaphyseal fragment of a third metacarpal, a fragment of a third metatarsal, and a proximal central phalanx. The dentition is of intermediate size and fairly hypsodont. The occlusal pattern is moderately complex, the caballine fold is of type 1, the protocone varies between square-oval and elongate-oval, and the fossettes do not have many folds. The lower teeth have a simple morphology, with the double knot (metaconid and metastylid) displaying an elongate oval shape, a wide linguaflexid, and a deep ectoflexid with a fold in the premolars. The ectoflexid may reach the lingualflexid. The protostylid is usually present and isolated on the occlusal surface, depending on the degree of wear. The postcranial skeleton is gracile. The third metacarpal is very similar to those from Layna (the type locality of *H. fissurae*), but a little shorter, and therefore closer in morphology, like the proximal phalanx, to the remains from Orrios 1, assigned by Alberdi and Alcalá (1999) to *Hipparion* aff. *fissurae*.

Rhinocerotidae are represented by a carpal bone, some fragments of deciduous teeth (Fig. 7E), and a mandibular symphysis (Fig. 7A), which has two rounded and not very large alveoli for the incisors. The latest Miocene and Pliocene rhinoceroses from Europe belong to *Stephanorhinus, Ceratotherium, Chilotherium*, as well as *Dihoplus scheleiermacheri* and *Dihoplus megarhinus* (Heissig, 1996, 1999). Although a discussion on the generic affinities of *Dihoplus megarhinus* is outside the scope of this paper, it should be noted that it has been classified in different genera (Guérin, 1980;

Fortelius et al., 1993; Heissig, 1999; Lacombat, 2007): *Dicerorhinus*, *Dihoplus*, *Stephanorhinus* and *Lartetotherium*. *Ceratotherium* and *Stephanorhinus* reduced the incisors (Heissig, 1999), whereas *Chilotherium* is characterized by large incisors. *Dihoplus schleiermacheri* and *Dihoplus megarhinus* might belong to a single lineage and have relatively small incisors (Heissig, 1999, p. 184, fig. 16.18). Most probably the material from Puerto de la Cadena belongs to this lineage, but it is not possible to conclusively discern, whether it belongs to *D. schleiermacheri* or to *D. megarhinus*. The former species ranged MN9–MN12/13 and the latter MN 14-15 (Heissig, 1996; Guérin, 1980), though recently material from MN 12 was been assigned to *D. megarhinus* (Pandolfi et al., 2015, 2016).

The artiodactyls of Puerto de la Cadena include a cervid (Cervidae indet.), a giraffid (*Sivatherium* cf. *hendeyi*), and six bovids (Bovidae indet. sp. 1, *Gazella* aff. *baturra*, *Gazella* aff. *lydekkeri*, Bovidae indet. sp. 2, Bovidae indet. sp. 3, and *Parabos* sp. The only indication of the presence of a deer in this locality is an antler fragment of an indeterminate cervid (Fig. 7G). The giraffids remains are assigned to *Sivatherium* cf. *hendeyi*. The taxonomically most significant specimens are a complete metacarpal III-IV and some isolated dental remains (Fig. 7I). The great degree of robustness of the metacarpal is remarkable, as well as the large size of the dentition, compared to the giraffids known from the late Miocene of the Iberian Peninsula, which include the genera *Decennatherium* and *Birgerbohlinia* (Crusafont, 1952; Morales and Soria, 1981; Montoya and Morales, 1991; Alcalá and Montoya, 1994; Montoya 1994; Ríos et al., 2016). Morphologically and morphometrically, the specimens from Puerto de la Cadena compares very well with *Sivatherium hendeyi* from the early Pliocene of Langebaanweg, South Africa (Harris, 1976). Other giraffid bones from this locality have a smaller size, either indicating the presence of a second taxon or the existence of

very wide range of intraspecific variation. It is possible that two astragali from other nearby localities might belong to *Sivatherium* cf. *hendeyi*: IPS34709 (housed at the Institut Català de Paleontologia Miquel Crusafont, in Sabadell) is from La Alberca and was previously identified by Montenat and Crusafont (1970) as belonging to a sivatheriine of large size. The other one is from the early Pliocene of La Gloria 4 (Teruel), and was reported as cf. *Birgerbohlinia* sp. by Alcalá and Montoya (1994).

The Puerto de La Cadena fauna has a great bovid diversity, with as much as six different species. Bovidae indet. sp. 1 is represented by a nearly complete metatarsal (Fig. 7H). This bone is robust for a gazelle, and more robust but smaller than another metatarsal, which we attribute to *Gazella* aff. *baturra*. The proximal articular surface is damaged, but it seems to have been relatively wider than in *Gazella*.

The small antelope *Gazella* aff. *baturra* is represented by numerous specimens, which include postcranial remains, dentition, a cranial fragment, and a horn core (Fig. 7M). All remains are of small size, clearly smaller than those attributed to *Gazella* aff. *lydekkeri*, and even smaller than *Gazella baturra* from the locality Gloria 4 (Alcalá and Morales, 2006).

A second *Gazella* species, *Gazella* aff. *lydekkeri,* is represented by three fragments of male horn core (two of which are of the same individual) and a fragment of frontal with a female horn core. Of the two fragments of horn core from the same male individual, one includes the upper part of the orbit and the lower part of the horn core, in which there is no sinus, but spongious bone. A little postcornual fossa is present. The frontal is thick. The basal section of the horn core is ca. 28 x 27 mm, nearly circular. The other fragment is the part of the horn core above the pedicle, but the two specimens do not fit together, because a small part is lacking. The surface is ornamented with wide and deep

vertical grooves. There is an anterior faint keel and a wide and deep posterior groove. There is a gentle "anti-clock screw torsion". The other male horn core has a similar morphology. The grooves are less marked and discontinuous on the anterior side and absent posteriorly. There is a slight indication of an anterior keel. The most common late Miocene gazelle is *Gazella deperdita*, but its horn cores are more flattened and the females do not have horn cores. The shape and morphology of the horn cores from Puerto de la Cadena are close to those of *Gazella lydekkeri* described by Pilgrim (1937) from the Dhok Pathan stage of the Middle Siwaliks. Another similar form is *Gazella* sp. from Maramena, Greece (Köhler et al., 1995). The frontal with horn core, attributed to a female, is short and has a circular section, and resembles the females of *Gazella borbonica* (see Heintz, 1975), and the specimen from the Baynunah Formation (Abu Dhabi), attributed by Gentry (1999) to *Gazella* aff. *lydekkeri*. It is difficult to relate these specimens to teeth or postcranial remains, though possibly a nearly complete but crushed metacarpal (Fig. 7K) and an intermediate phalanx may belong to this species. The shape of the articular surfaces of the second phalanx resembles those of *Gazella*. The metapodial is large and relatively short (robust) for a gazelle. In recent species, the metapodials tend to be much more elongated.

Bovidae indet. sp. 2 from Puerto de la Cadena is larger than *Gazella* aff. *lydekkeri*. It is represented by dental material (Fig. 7F) and postcranial bones. The teeth are moderately high crowned and the third molars are large and the premolars are reduced in size. These teeth are morphologically similar to those from the locality of La Gloria 4 (Teruel, Spain), described as *Tragoreas oryxoides* by Alcalá (1994), although the former are a little larger. The latter species is again similar to *Norbertia hellenica* described on the basis of material from Maramena (Köhler et al., 1995). However, both species appear to have P_4 with a more derived morphology than in Puerto de La Cadena.

Postcranial remains larger than those assigned to *Gazella* aff. *lydekkeri* include metapodial fragments and a second phalanx. This phalanx is morphologically clearly different from the specimen assigned to the large gazelle. Its morphology lacks derived features seen in *Gazella* and Caprinae. Notably, it differs from the phalanx of *Norbertia*, which is clearly caprine (Köhler et al., 1995, Pl.6, fig. 2). Either the teeth and bones belong to a single species, which is not *Norbertia*, or the teeth represent that genus and the bones still another taxon.

A maxilla with three deciduous teeth and the first molars (Fig. 7D) as well as a P^2 represent a still larger species identified as Bovidae indet. sp. 3. It is a little smaller than *Parabos*, which is represented by the same deciduous teeth. The anterior parts of the D^2 and P^2 are very reduced.

The remains of *Parabos* sp. consist of deciduous and adult dentition: a maxilla with D^2-M^1 and a mandible with D_2-M_1, M^2 (Fig. 7N), P^3 and postcranial bones. They can be attributed to a primitive Bovini, close to *Parabos soriae* from Venta del Moro (Morales, 1984), or to *Parabos cordieri* from Montpellier (Gromolard and Guérin, 1980). The absence of a horn core impedes a precise attribution.

1.2. Reptiles

The reptile record of Puerto de la Cadena includes representatives of Crocodylia, Testudines, and Ophidia. The crocodilians represented at Puerto de la Cadena are indeterminate (Crocodylia indet.). The sample consists of two well-preserved teeth (Fig. 8) and a few fragments of osteoderms (not available for study). One tooth is somewhat robust and pointed, with a rather short crown (8.1 mm tall and 7.6 mm wide at the base; these proportiosn are indicative of a posterior tooth) that displays an average crocodylian morphology: classic conical shape with a mesiodistal, non-serrated carina

separating the slightly swollen labial surface from the smaller lingual surface. Both surfaces are rather smooth, devoid of evident wrinkles, and the boundary between the crown and the root is marked by a small constriction. In contrast to the former tooth, which suggests that the crocodile died, the other corresponds to a shed tooth, so that only the tooth crown is preserved. The crown was at least 13 mm tall (it is slightly worn apically) and 8.3 mm wide at the base (mesiodistal diameter). It seems to be more elongated and curved, and rather slender, than the other tooth (indicative of an anterior maxillary tooth). The preserved morphology does not enable the precise taxonomic allocation of these specimens even to family rank, although it must be noted that they fit the typical tooth shape displayed by crocodyloids, only represented at that time in Europe by genus *Crocodylus* (Delfino and Rossi, 2013; Georgalis et al., 2016). Given that Puerto de la Cadena is here considered to be early Pliocene in age, the crocodilian bones described here (and attributed Crocodylia indet.) would represent, together with the fossils from Gargano (latest Messinian or early Zanclean; Apulia, Italy) attributed to *Crocodylus* sp. (Delfino et al., 2007), the youngest report of crocodilians in Europe. The oldest possible evidence of the presence of *Crocodylus* in Europe is from the early Tortonian Scrontone site (Abruzzo, Southern Italy; Delfino and Rossi, 2013), thus indicating that this taxon might have already reached Europe during the Tortonian, well before the MSC, which has been traditionally considered as the event that caused several trans-Mediterranean dispersals during the latest Miocene.

All the turtle remains identified in Puerto de la Cadena belong to the Cryptodira. The most abundant lineage is the family Testudinidae (i.e., tortoises or terrestrial turtles). It is relatively diverse, with three different forms being identified. In addition, a trionychid (softshell turtle) is also recognized.

One of the testudinids recognized in the area of study is *Titanochelon* sp. (Fig. 9A).

The presence of a large testudinid was already recognized by Montenat (1973) in La Alberca, based on fragmentary material. He interpreted that this taxon had a similar size to '*Testudo*' *perpiniana*, a French species recently reassigned to the genus *Titanochelon* (Pérez-García and Vlachos, 2014). New remains from La Alberca, corresponding to fragments of plates and to a phalanx, were also identified as assignable to a large testudinid, having been attributed to '*Cheirogaster*' cf. *bolivari* (Pérez-García et al., 2011). In turn, a carapace found in another locality westward from Puerto de la Cadena, Barranco del Cigarrón, was preliminarily attributed to '*Cheirogaster*' *bolivari* (Mancheño et al., 2001). All the large species of Testudinidae (i.e., whose shell length is greater than 1 m) recorded in the European Neogene record, including the Iberian species '*Cheirogaster*' *bolivari*, have recently been reassigned to *Titanochelon* by Pérez-García and Vlachos (2014). The currently confirmed stratigraphic distribution of the species *Titanochelon bolivari* is from the Aragonian to the lower Vallesian (Langhian to early Tortonian, MN5 to MN10), of both Spain and Portugal (Pérez-García and Vlachos, 2014; Pérez-García et al., 2016). The preparation and study of the specimen preliminarily presented by Mancheño et al. (2001), and the preliminary analysis of other specimens found both in that locality and in other outcrops of Puerto de la Cadena (including well-preserved and relatively complete shells, partial shells, isolated plates, vertebrae and appendicular elements), do not allow us to support this specific attribution. Therefore, this taxon is here recognized as *Titanochelon* sp. The detailed study of these specimens, currently in progress, will allow a specific determination. This genus is known from the early Miocene to the Pleistocene (Pérez-García and Vlachos, 2014; Pérez-García et al., 2017). This is the most abundant turtle so far found in Puerto de la Cadena.

Apart from *Titanochelon* sp., Barranco del Cigarrón has yielded a partial shell that

probably corresponds to a new taxon of Testudinidae. This shell, attributable to an adult individual, has an estimated length of less than one meter. The general morphology of its carapace, as well as characters such as the morphology and proportions of the nuchal plate and the epiplastra, allow us to exclude its attribution to the genus *Titanochelon*. This putative new taxon is larger in size than the members of the lineage of *Chersine hermanni*, but smaller than the representatives of *Titanochelon*.

Several disjointed elements corresponding to carapace plates of a relatively small form of Testudinidae (i.e., whose shell is less than 30 cm in length) are recognized in Puerto de la Cadena. As in the other testudinids, these plates are relatively thick, and the pleuro-marginal sulci overlap or are very close to the costo-peripheral sutures. The degree of development of the ossification of these plates enables their attribution to adult specimens. This relatively small taxon probably corresponds to a member of the lineage of *Chersine hermanni*, a well-represented clade in the Iberian record, known from the early Miocene and being part of the current diversity (Llorente et al., 2002; Pérez-García, 2017). In this paper we leave these specimens unassigned to genus as Testudinidae indet.

The presence of Trionychidae indet. has been previously recognized both in La Alberca and in other outcrops of Puerto de la Cadena area (see Pérez-García et al., 2011). The plates of this taxon lack sulci due to the absence of scutes. The external surface of the plates attributed to this clade is decorated by circular to elongated depressions, with a maximum length between 2 and 4 mm, separated by narrower crests (Fig. 9B, 9C). The material published so far is very scarce, so a more precise determination cannot be proposed. The recent identification of Trionychinae in Puerto de la Cadena represents the youngest reference in Spain, where this clade was known the Eocene to the early Miocene (see Pérez-García et al., 2011 and references therein).

In addition, so far it corresponds to the only published reference to Trionychinae in the southern half of Spain.

Testudinids are terrestrial, whereas trionychids are aquatic turtles, with modifications in their appendicular skeleton which facilitated their dispersal both by continental freshwater environments and following the coasts (see Pérez-García et al., in press and references therein). The depositional environmental conditions interpreted for the top of Cigarrón Unit (where Puerto de la Cadena is placed), which is considered a continental setting related to fluvial systems near to the coast, is consistent with the environmental requirements of the turtles identified here.

At Puerto de la Cadena, ophidians are represented by the colubrine *Malpolon* gr. *monspessulanus-mlynarski* and the viperid *Vipera* sp. The former is represented by three large-sized trunk vertebrae with a centrum length (CL) longer than 6 mm and up to 7.2 mm. The trunk fossil vertebrae possess an elongated morphology of the neural arch wings in dorsal view as well as of the centrum in ventral view (CL/NAW > 1.3), a usually thin and sharp haemal keel, and straight posterior margins of the neural arch, which are characteristic of the representatives of the genus *Malpolon* (Szyndlar, 1988; Blain, 2005, 2009; Blain et al., 2007). The distinction between the extant *M. monspessulanus* and the extinct *Malpolon mlynarski* from the Pliocene (MN15) of Layna (Soria, Spain) is based on cranial elements (Szyndlar, 1988), thus precluding a species attribution within genus *Malpolon* for the material from Puerto de la Cadena.

The viperid is recorded by three large vertebrae (CL comprised between 8 mm and 11.8 mm) attributed to *Vipera* sp. "Oriental viper complex" sensu Szyndlar (1991). These isolated vertebrae can be referred to the genus *Vipera* on the basis of several characters (Rage, 1984; Szyndlar, 1991; Szyndlar and Rage, 2002): presence of a

hypapophysis, depressed neural arch in posterior view, anteroventrally oriented parapophyseal processes, and slightly tilted prezygapophyseal facets. The large size of the vertebrae clearly suggest a referral to the representatives of the 'Oriental vipers' group, which hosts the largest representatives of the genus. Although reaching a similar size to the extinct *Daboia maxima* from the Pliocene (MN15) of Layna, the material from Puerto de la Cadena differs from the latter in lacking the depressed cotyle and condyle and the rectangular shape of the prezygapophyseal articular facets. 'Oriental vipers' have been identified in the Iberian fossil record in various Miocene localities of the Vallès-Penedès Basin (Delfino et al., 2015), in the early Pliocene of Caló d'en Rafelino (Manacor, Mallorca), in the Pliocene of Zújar (Bailon, 1991), and in the early Pleistocene of Medes Islands and Cova Bonica (Bailon, 1991; Blain, 2005, 2009; Bailon and Blain, 2007; Blain et al., 2016). Interestingly, the largest vertebra is very similar in size and shape to the trunk vertebra from Caló d'en Rafelino (CL = 12.7 mm – thus far the largest-sized European specimen of belonging to the "Oriental vipers complex"; Bailon et al., 2010) with a similar chronology ("very early Pliocene"). This fact suggests that they may belong to the same species, which would have dispersed across the Western Mediterranean Basin probably during the MSC.

2. Extended small mammal biostratigraphy

Zorreras 3A (Martín Suárez et al., 2000), in the Sorbas Basin, has in common with the Puerto de la Cadena the presence of *Paraethomys meini* and *Stephanomys dubari*. However, the former site records a different species of *Debruijnimys* (*D. almenarensis*). Similarly, the localities of Negratín 1 (Guadix Basin; Minwer-Barakat et al., 2009a) and Almenara-Casablanca M (Eastern Spain; Agustí, 1990; Agustí et al., 2011) share with

Puerto de la Cadena the presence of *Paraethomys meini* and *Stephanomys dubari*. Moreover, *Ruscinomys lasallei* has been recognized in Almenara-Casablanca M, and *Ruscinomys* sp. in Negratín 1. However, these localities also record *Debruijnimys almenarensis* and *Apocricetus alberti*. The same applies to Gafares 2B, in the Almería-Níjar Basin, which has yielded remains of *Stephanomys dubari*, *Paraethomys meini*, and *Debruijnimys almenarensis* (García-Alix et al., 2016).

The arrival of *Debruijnimys* sp. is related to a second immigration wave after to that of *Debruijnimys almenarensis* (see Agustí and Casanovas-Vilar, 2003). Whereas *Debruijnimys* sp. has been reported from early Pliocene localities, *Debruijnimys almenarensis* has been found in sites assigned to the late Miocene (Castillo and Agustí, 1996; Agustí and Casanovas-Vilar, 2003). This fact suggests an older age for Almenara-Casablanca M, Negratín 1, Gafares 2B, Salobreña, and Zorreras 3A.

The Puerto de la Cadena site can be compared with the *Apodemus gudrunae* zone of the Guadix Basin, in which the reference locality is Negratín 1 (Minwer-Barakat et al., 2012). Other localities assigned to this biozone are Rambla Chimeneas 3 (Minwer-Barakat et al., 2009b), which has in common the occurrence of *Stephanomys dubari* and *Paraethomys meini*, and Bacochas 1 (Sesé, 1989) in which *Paraethomys meini* and probably *Debruijnimys* (see Minwer-Barakat et al., 2009a) have been identified. However, the presence of *Apocricetus alberti* suggests a somewhat older age than Puerto de la Cadena.

The locality of Purcal 4, in the Granada Basin, resembles Puerto de la Cadena in recording *Paraethomys meini*, *Stephanomys dubari, Apocricetus barrierei* and *Ruscinomys lasallei* (García Alix et al., 2008c). This assemblage suggests a similar age to Puerto de la Cadena. In this way, the latter site may be correlated with the lower part

of the *Apocricetus barrierei* zone in the Granada Basin (García-Alix et al., 2008c). The cricetid *Ruscinomys* aff. *schaubi* has been found in la Dehesa 16, suggesting a slightly older age. On the contrary, the appearance of a large-sized *Paraethomys* (*P.* aff. *abaigari*) in Purcal 13 (García-Alix et al., 2008a) indicates a younger age than for Puerto de la Cadena. *Paraethomys* aff. *abaigari* and *Paraethomys abaigari* are common elements in numerous localities assigned to the early Ruscinian (MN14; e.g., Mein et al., 1990; Adrover et al., 1993; García-Alix et al., 2008a; Mansino et al., 2013, 2015a; Piñero et al., in press).

Puerto de la Cadena may be correlated with other sites from the Iberian Peninsula. The Cabriel Basin has yielded a number of late Miocene/early Pliocene localities such as Venta del Moro (Montoya et al., 2006; Mansino et al., 2014, 2016a, 2016b), Fuente del Viso (Opdyke et al., 1997), and La Bullana 2B (Mansino et al., 2015b). The Puerto de la Cadena site has in common with Venta del Moro some rodent species, such as *Stephanomys dubari*, and *Paraethomys meini* (Mansino et al., 2014, 2016a). However, the record of *Apocricetus alberti*, and the ancestor of *Ruscinomys lasallei* (*Ruscinomys schaubi*) in Venta del Moro indicates an older age. In addition, this site was deposited before the start of the "Gerbil Event" (Agustí et al., 2006), unlike Puerto de la Cadena.

The presence of *Paraethomys* aff. *abaigari*, and *Debruijnimys* cf. *julii* in La Bullana 2B (Mansino et al., 2015b) indicates a younger age than Puerto de la Cadena. In contrast, Fuente del Viso may have a similar age, given the record of *Prolagus michauxi*, *Ruscinomys lasallei*, *Stephanomys medius* (=*S. dubari, S. cordii*), *Paraethomys anomalus* (=*P. meini*) and *Cricetus barrierei* (=*Apocricetus barrierei*) (Opdyke et al., 1997; Freudenthal et al., 1998), thereby suggesting a very close age to Puerto de la Cadena.

The small mammal association from Puerto de la Cadena may also be correlated with the *Apocricetus barrierei* zone proposed by Mansino et al. (in press) for the Alcoy Basin. The level of Alcoi Forn 1'07 resemble to Puerto de la Cadena in the occurrence of *Paraethomys meini*, *Stephanomys dubari* and *Apocricetus barrierei* (Mansino et al., 2015c).

Regarding the Teruel Basin, Puerto de la Cadena can be partly correlated with the upper part of the *Stephanomys ramblensis* Zone (Mein et al., 1990), in which the Arquillo 4 locality (Adrover et al., 1993) shares with Puerto de la Cadena the presence of *Paraethomys anomalus* (=*P. meini*), *Ruscinomys* cf. *lasallei*, and *Prolagus michauxi*, although the identification of *Stephanomys ramblensis* in Arquillo 4 suggests an older age. Similarly, Celadas 2 (Adrover et al., 1993) shares with Puerto de la Cadena the presence of *Ruscinomys lasallei* and *Prolagus michauxi*, but the occurrence of *Stephanomys ramblensis* and *Apocricetus* cf. *alberti* indicates a somewhat older age for the former. On the contrary, the presence of *Apocricetus barrierei* in Peralejos E (Adrover et al., 1988) indicates a close age to Puerto de la Cadena.

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