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THE VERTEBRATE FAUNA OF THE LOWER PLIOCENE CONTINENTAL DEPOSITS IN THE EBRO DELTA (BAIX EBRE BASIN, NE SPAIN)

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Abstract. The Pliocene faunas of the northeastern Iberian Peninsula are poorly known due to the scarcity of deposits from this interval. In this context, the site of Sant Nofre-Campredó (Baix Ebre, Catalonia, Spain), comprising two contemporaneous outcrops belonging to geologically correlated sections (Sant Nofre and Campredó-Via Fèrria), makes a significant contribution to the study of Pliocene faunas in this region. The first vertebrate remains were recovered in the late 1970s in clay deposits close to the Sant Nofre Hill. Later, intensive sampling in the 1980s at the Campredó-Via Fèrria outcrop led to the recovery of more than a hundred fossil specimens, including small vertebrates and large mammals. Here, we revise these collections to expand and update the vertebrate list, better constrain the age of the continental deposits, and characterize the environment and climate around the mouth of the Ebro River during the formation of the site. Up to 24 vertebrate species have been identified at Sant Nofre-Campredó, including amphibians, reptiles, and mammals. The presence of the rodents *Paraethomys baeticus* Piñero & Verzi, 2020*,* *Apocricetus barrierei* (Mein & Michaux, 1970), and *Occitanomys brailloni* Michaux, 1969 implies an early Ruscinian age (MN14 unit) for the two outcrops. Biostratigraphic correlations with other well-dated sites in the Iberian Peninsula refine the estimated age of Sant Nofre-Campredó to approximately 4.6 Ma. The ecological affinities of the identified fauna reveal a landscape dominated by woodland habitats in the surroundings of the site during the Early Pliocene, with presence of open humid meadows and water bodies under warm and moist climatic conditions.

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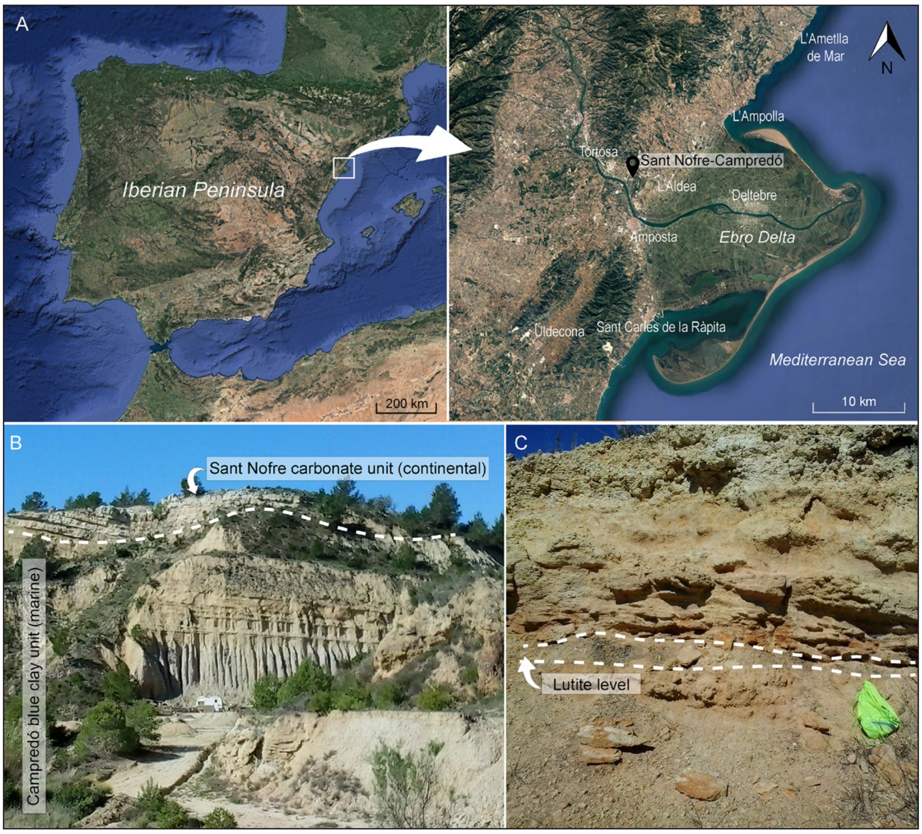

Fig. 1 - Geographic and stratigraphic context. A) Location of the Sant Nofre-Campredó site (source: Google Earth Pro). B) General view of the Sant Nofre outcrop. The vertebrate remains come from the mudstone and lutite interbedded in the carbonate unit. C) Detail of a dark lutite level in the lacustrine Sant Nofre carbonate unit.

INTRODUCTION

The Pliocene (5.33 to 2.58 Ma) marked the last significant warm period in Earth's climate history preceding the onset of Pleistocene glacial-interglacial dynamics. That is why this epoch can help us understand climate change patterns and climate sensitivity (Pagani et al. 2010). The warm phase peaked with the mid-Pliocene warm period (3.29 to 2.97 Ma), an interesting analogue to present climate change (Haywood et al. 2011). The Early Pliocene coincided with an important sea-level rise of about 25 m (Miller et al. 2020), in addition to the refilling of the Mediterranean basin (Zanclean flood), so that coastal basins along the Mediterranean, including the Baix Ebre Basin (NE Spain), were covered by shallow seas. Warm temperatures allowed for the presence of subtropical to tropical molluscs (Martinell 1988), but not of well-developed reef systems or mangroves as in previous warm periods, such as the Miocene Climatic Optimum (see Bessedick & Cabrera 1985; Rull et al. 2024).

The Pliocene marine record is well known from several sections and cores, but continental sections are limited in the western Mediterranean. In contrast to the central and southern Iberian Peninsula (Teruel, Guadix-Baza, Granada, Fortuna, and Alcoy basins), the Lower Pliocene faunas of the northeast are poorly understood due to the scarcity of deposits from this sub-epoch. Besides the material from the Baix Ebre Basin described here, in the Catalan record, the sites of Vilafant (Gibert et al. 1980), Far d'Empordà (Llenas et al. 2002), and Cornellà de Terri (Sanz et al. 1987) are known from the Empordà Basin. The former two have solely yielded small vertebrates, whereas the latter has provided remains of both small and large mammals. Only one additional site is recognized in the northeastern Iberian Peninsula, the impressive lagerstätte of Camp dels Ninots in the La Selva Basin (Gómez de Soler et al. 2012). In this regard, the Pliocene sediments of Sant Nofre-Campredó provide a key contribution to the study of Pliocene faunas in this region.

The site of Sant Nofre-Campredó—also known in the literature as Sant Onofre and Via Fèrria (Agustí et al. 1983; Agustí & Gibert 1985) or simply Tortosa (Aldana Carrasco 1992)—is situated within the Baix Ebre region, near the delta of the Ebro River, close to Tortosa (SW of Tarragona province, NE Spain; Fig. 1). This locality comprises two outcrops, one at the Sant Nofre Hill (Sant Nofre), near the Venta del Ranchero and a second one (Campredó-Via Fèrria) close to the railway between Tarragona and Tortosa, close to the town of Campredó. They represent two contemporaneous sections comprising marine and continental units that are correlated to both the marine and the terrestrial realm, the latter containing vertebrate remains (Magné 1978; Agustí et al. 1983). The Pliocene deposits in the Baix Ebre region have been recognized since the early 20th century, as documented by Font y Sagué (1905) and Gignoux & Fallot (1922). Subsequent studies dealt with various aspects of the palaeontology and geology of the area. Bataller & López (1929) and Solé et al. (1965) published lists of macrofossils (fauna and flora). Maldonado (1972) described the stratigraphic succession of Pliocene and Quaternary sediments in the area, being the first work citing vertebrate fossils in this area. Magné (1978) presented the sections of Sant Nofre and Campredó-Via Fèrria along with extensive lists of foraminifera, confirming the Pliocene age attributed since the beginning of the 20th century. Agustí et al. (1983) and Agustí & Gibert (1985) focused on micromammal palaeontology. Martinell & Domènech (1984) studied marine molluscs. Solé de Porta & Valle (1986) and Bessais & Cravatte (1988) provided a detailed palaeoenvironmental reconstruction based on palynological data. Stratigraphy and sedimentology were explored by Martinell (1988), Arasa (1990), and Arasa-Tuliesa & Cabrera (2018). Ichnology was addressed in works by Martinell & Domènech (1995), de Gibert & Martinell (1996, 1998), and de Gibert et al. (1998). Additionally, Aguirre et al. (2014) examined vermetid-coralline algal bioconstruction in the area.

The first small vertebrate remains were recovered in the late 1970s in clay levels close to the Sant Nofre Hill. Later, intensive sampling in the 1980s at the Campredó-Via Fèrria (Campredó-VF) outcrop led to the recovery of more than a hundred vertebrate remains, including herpetofauna, small mammals, and large mammals. Previous works presented a preliminary faunal list, suggesting a Ruscinian (Early Pliocene) age for the site (Agustí et al. 1983; Agustí & Gibert 1985). Here, we revise these collections to expand and update the vertebrate list, providing detailed descriptions for all taxa (amphibians, reptiles, and mammals). This is a good basis to better constrain the age of the site and infer the prevailing palaeoenvironmental conditions during its formation.

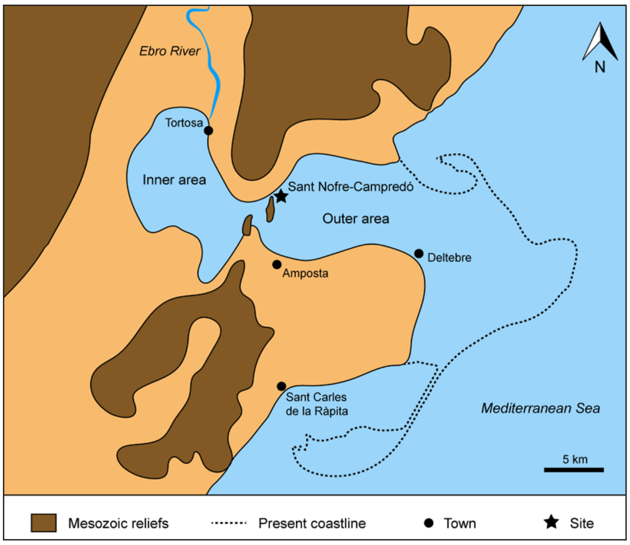

Fig. 2 - Palaeogeography of the Baix Ebre Basin at the time of the carbonate unit deposition during the Early Pliocene (modified from Fleta et al. 1991).

Geological setting

The Baix Ebre Basin is the result of the overprinting of Neogene extensional faulting over the tectonic unit known as the Linking Zone, which connects the Catalan Coastal Ranges (northernly) and the Iberian Range (westerly) (Guimerà & Álvaro 1990). Fleta et al. (1991), who reconstructed the palaeogeography of the Baix Ebre Basin during the Pliocene, characterized the basin as a bay featuring two closely connected sectors (Fig. 2). The inner area was confined and notably exhibited brackish conditions, while the outer segment was more open to marine influences. The Sant Nofre-Campredó outcrop is situated in the transitional area between these two zones, where freshwater influences were significant (Martinell & Domènech 1984).

The Lower Pliocene of Baix Ebre in the Sant Nofre area has been divided into three informal lithostratigraphic units (Arasa 1990; Fleta et al. 1991; de Gibert & Martinell 1996; Arasa-Tuliesa & Cabrera 2018). From base to top, these units are:

1) The basal detritic marine unit formed by calcareous and siliceous gravel and massive sandstone. The lithofacies and fossil evidence are indicative of littoral environmental conditions (Arasa 1990; Martinell & Domènech 1995; Arasa-Tuliesa & Cabrera 2018).

2) The Campredó blue clay unit (Fig. 1B) consisting of a 65 m thick sequence of mudstone

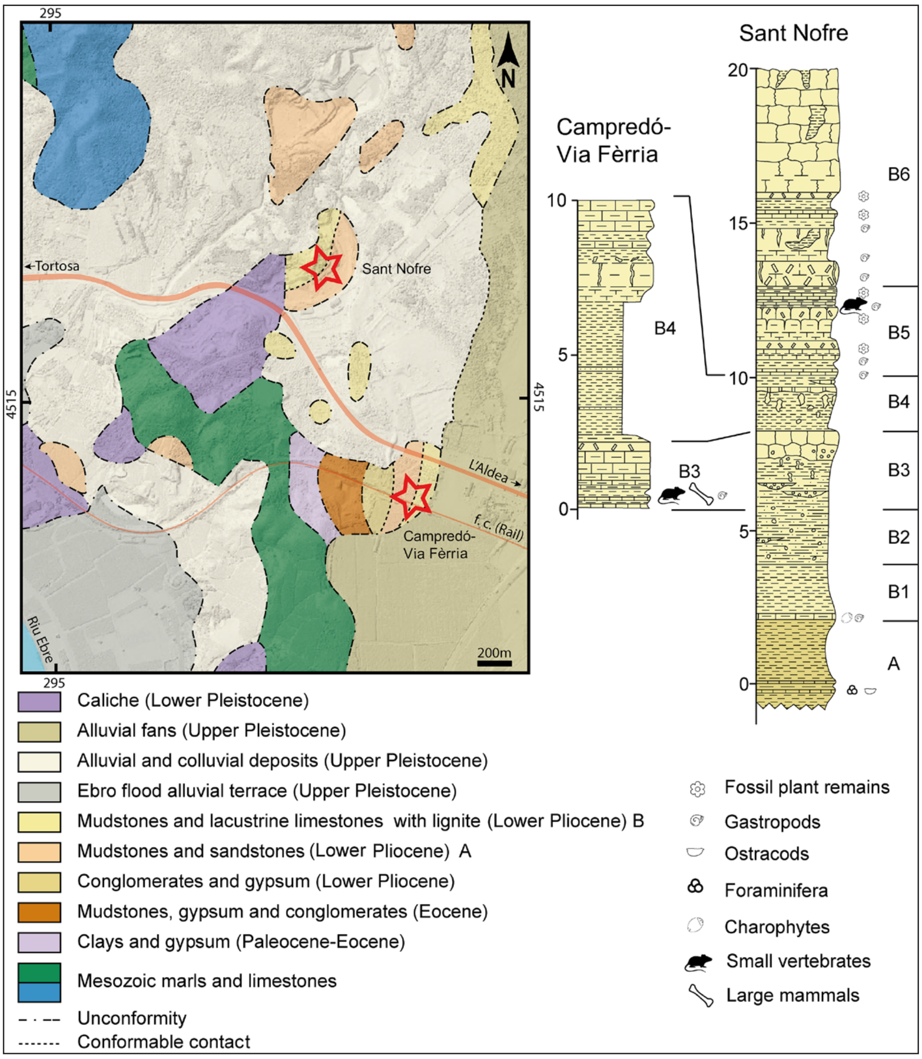

Fig. 3 - Geological map of the studied area and stratigraphic logs of the continental Lower Pliocene succession at Sant Nofre and Campredó-Via Fèrria (modified from Agustí et al. 1983) and Mapa Geològic Comarcal de Catalunya 1:50,000).

and sandstone that records sedimentation in a shallow marginal bay (Martinell & Domènech 1984; de Gibert & Martinell 1996). It is subdivided into three subunits: the lower sandy clay subunit, the intermediate blue clay subunit, and the upper sandy clay subunit.

3) The Sant Nofre carbonate unit (Fig. 1B) composed of lacustrine mudstone and carbonate with interbedded lutite (Fig. 1C) bearing vertebrate remains. This unit constitutes the top of the Lower Pliocene succession in this area (Agustí et al. 1983).

Agustí et al. (1983) designated the marine deposits as Unit A, while the overlying lacustrine sediments containing continental vertebrates were referred to as Unit B. These authors subdivided the Sant Nofre carbonate unit into six subunits (B1 to B6) (Fig. 3). B1 is 1.7 m thick and consists of grey-greenish calcareous mudstone. B2 is 2 m thick and is composed of red mudstone with siliceous pebbles. B3 is 2.4 m thick and is formed by greyish-whitish mudstone with ochre stains and carbonate nodules. B4 is 1.9 m thick and is composed of gray and brown mudstone with calcareous intercalations and white chalky nodules. B5 is 2.9 m thick and consists of an alternation of dark greyish-black mudstone levels with abundant freshwater gastropods and sporadic microvertebrate remains, and limestone levels with occasional accumulations of algal remains. Dark lutite layers are interbedded (see Fig. 1C). The microvertebrates studied here come from a level at the top of this subunit. B6 is 7 m thick and consists of limestone with vertical burrowing and molds of gastropods, with interbedded levels of mudstone containing gastropod remains (Fig. 3).

In the Campredó-VF outcrop, the Lower Pliocene succession is less developed as compared to the Sant Nofre section (Maldonado 1972; Canerot et al. 1975; Magné & Viallard 1977; Magné 1978). The series exhibits numerous visible faults and is also likely affected by additional faults not observable due to the poor quality of the outcrop and the presence of recent Quaternary materials, which, in part, cover the Pliocene deposits (Agustí et al. 1983). B1 is represented by a 12.5 m-thick mudstone interval with bioturbated limestone intercalations. Overlying this deposit is a sandy limestone bed (B2) with irregular stratification. Subunit B3 consists of a 0.3 m-thick level of travertine, with an intercalation of carbonaceous black mudstone. It is covered by 0.3 m of black clay containing abundant plant remains and freshwater gastropods. This level has yielded the remains of small vertebrates and large mammals studied in this work (Agustí et al. 1983). Above it lies 1.5 m of clayey limestone. Subunit B4 is composed of 4.5 m of mudstone with sandy intercalations at the base, followed by 3.5 m of clayey limestone. Subunits B3 and B4 are depicted in Fig. 3.

Material and Methods

The fossil material referred to here consists of disarticulated elements collected by wet screen-washing the sediments obtained in sampling campaigns a few decades ago. The collection from Sant Nofre includes 17 identified small mammal teeth, representing eight different taxa, and 20 disarticulated cranial and postcranial bones of amphibians and squamate reptiles representing five taxa. The material from Campredó-VF comprises 98 teeth of at least 13 small mammal species, 20 disarticulated cranial and postcranial bones ascribed to seven herpetofaunal taxa, seven dentognathic remains of one castorid species, and 17 dental and postcranial remains of artiodactyls representing two taxa (see Tab. 1). These fossils are housed in the collections of the Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA; Sabadell, Barcelona, Spain).

All the measurements are expressed in millimeters. For the small mammal remains, they were taken in the occlusal plane of the teeth with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. For the castorid remains, measurements were taken with Mitutoyo digital calipers. The measurements of micromammal taxa with a high number of specimens are presented in the manuscript as summary tables. The measurements of each of these specimens are available in the Supplementary material. The upper teeth are denoted by capital letters and the lower teeth by lowercase letters. Small mammal 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), except for the lagomorphs, which have been drawn. The large mammals, amphibians, and reptiles are illustrated by means of digital photographs. For the latter two, a Digital Microscope AM7915MZTL Dino-Lite Edge was employed, alongside the DinoCapture 2.0 software for photo-stacking.

The systematic nomenclature generally follows Speybroeck et al. (2020) for extant herpetofaunal taxa. Osteological nomenclature mainly follows Estes (1981) for urodeles; Roček (1994), Sanchiz (1998), and Blain et al. (2016) for anurans; Hervet (2000) and Bailon (2010) for chelonians; Hoffstetter (1962), Augé (2005), and Barahona & Barbadillo (1997) for lizards; and Szyndlar (1984) for snakes. In describing and measuring the sciurid tooth, we have followed the nomenclature and methods proposed by Sinitsa & Pogodina (2019) and Casanovas-Vilar et al. (2015), respectively. Freudenthal (2004) was followed in the description and measurements of the glirid teeth. The nomenclature and measurement methods of castorid remains follow Stirton (1935) and Casanovas-Vilar et al. (2008), respectively, whereas the terminology for masticatory muscles follows Cox & Baverstoc (2016). For the nomenclature and measurements of cricetids, we have followed Mein & Freudenthal (1971). The terminology and measuring methods employed in the descriptions of the murid teeth are those of Van de Weerd (1976) and Martín-Suárez & Freudenthal (1993), respectively. The terminology and measurements used to describe lagomorphs remains follow Angelone & Sesé (2009). We used the terminology and methods of Furió et al. (2015) for the Erinaceidae, and of Reumer (1984) for the Soricidae.

Systematic Palaeontology

The vertebrate association from Sant Nofre-Campredó is highly diversified, comprising urodeles, anurans, lizards, snakes, turtles, insectivores, rodents, lagomorphs, and artiodactyls (see Tab. 1).

Class **AMPHIBIA** Linnaeus, 1758
Order **Urodela** Duméril, 1805
Family Salamandridae Goldfuss, 1820
Subfamily Pleurodelinae Tschudi, 1838
Pleurodelinae indet.

Fig. 4A

Material: *Campredó-VF*. One incomplete left posterior thoracic rib (IPS128916).

Description. *Rib*. A subcomplete rib is present in Campredó-VF, including approximately the proximal half of the total length of the shaft (Fig. 4A). It is a quite large rib, with a preserved length of 5.0 mm, indicating its total length may have reached 10 mm. In dorsoposterior view, the head of the rib is unicapitate with a large and shallow fossa. The crest of the head of the rib possesses a straight proximal margin. In proximal view, the articular facets of the head of the rib are different in shape and size. The capitulum (articulating with the parapophysis) is larger and circular, while the tuberculum (articulating with the diapophysis) is smaller and slightly laterally flattened. The crest of the head between both articular facets is narrow, long and slightly curved. The length of this crest suggests a posterior thoracic position for this rib, whereas this crest is usually shorter in anterior thoracic ribs (Scholtes et al. 2022). The shallow fossa between the two heads, together with the orientation of the facets, indicate that IPS128916 corresponds to a left rib.

Order	Family	Species
Urodela	Salamandridae	Pleurodelinae indet.* †
Anura	Alytidae	*Latonia* sp.* †
	Pelobatidae	*Pelobates* sp.†
Chelonii	Geoemydidae/Emydidae	Geoemydidae vel Emydidae indet.*
Squamata	Lacertidae/Scincidae	Lacertidae vel Scincidae indet.* †
	Anguidae	cf. *Ophisaurus* sp.* †
	Natricidae	cf. *Natrix* sp.*
	Colubridae/Psammophiidae	Colubridae vel Psammophiidae indet.*
Eulipotyphla	Soricidae	Soricinae indet.*
		*Plioblarinella dubia**
	Erinaceidae	*Parasorex* sp.*
Rodentia	Sciuridae	Xerinae indet.*
	Gliridae	*Muscardinus* cf. *meridionalis** †
	Castoridae	*Castor fiber**
	Cricetidae	*Apocricetus* cf. *barrierei** †
	Muridae	*Stephanomys* sp.* †
		*Apodemus gorafensis** †
		*Apodemus atavus** †
		*Paraethomys baeticus** †
		*Occitanomys alcalai**
		*Occitanomys brailloni** †
Lagomorpha	Prolagidae	*Prolagus* sp.* †
Artiodactyla	Suidae	*Propotamochoerus provincialis**
	Bovidae	cf. Caprini indet.*

Tab. 1 - Vertebrate faunal list of the site of Sant Nofre-Campredó. The taxa marked with an asterisk are present at Campredó-Via Fèrria, while taxa marked with a dagger are found in Sant Nofre.

Remarks. Because of the size of IPS128916, small newts (such as genera *Chioglossa*, *Mertensiella*, *Ichtyosauria*, *Lissotriton*, *Ommatotriton*) can reasonably be disregarded. Based on biogeographic arguments, the Asian genera *Cynops*, *Hypselotriton*, *Paramesotriton*, *Pachytriton*, and *Laotriton* can also be disregarded. When compared with the extant "large" Iberian genera *Salamandra*, *Triturus*, and *Pleurodeles* (Fig. 4B–F), IPS128916 differs from *Salamandra* and *Triturus* by the absence of a deep notch on the crest of the head of the rib. Moreover, the articular facets of *Triturus*, especially the capitulum, are usually antero-posteriorly flattened and not circular like in IPS128916. The specimen shares greatest similarities with extant *Pleurodeles waltl* Michaehelles, 1830, such as a unicapitate head, a shallow fossa in posterodorsal view, and a crest of the head of the rib with a straight proximal margin, but the articular facets have a different outline, again slightly antero-posteriorly flattened. Urodele ribs are apparently not very common in the fossil record, unless in sites where articulated specimens are available, such as in the fossil localities of Enspel and Rott (Rhineland-Palatinate, southwestern Germany; Estes 1981; Hellmund & Böhme 1987; Roček & Wuttke 2010; Schoch et al. 2015) or in the Pliocene site of Camp dels Ninots (Girona, northeastern Spain; Gómez de Soler et al. 2012; Blain et al. 2022). In the case of Enspel, the comparison between IPS128916 and *Chelotriton paradoxus* Pomel, 1853 shows some similarities in terms of the dimensions of the proximal part. However, morphologically, only the very last caudal ribs show the same morphology as that observed in IPS128916. The lack of preservation of the distal part in IPS128916 hampers any further comparisons. The same is true for the disarticulated ribs of *Chelotriton* sp. from Mokrá-Western Quarry (Czech Republic; Ivanov 2008) or in the extant consulted specimens of *Tylototriton*: *Tylototriton shanjing* Nussbaum, Brodie & Yang, 1995 (without number) from the osteological collections of Tübingen (Germany) and *Tylototriton verrucosus* Anderson, 1871 (MDHC-251) from the osteological collections of Torino (Italy). When compared with the posterior thoracic ribs of the Pliocene unnamed Pleurodelinae from Camp dels Ninots (Fig. 4G), IPS128916 differs slightly in having a slightly to well-developed notch on the proximal margin of the crest of the head, and by a more flattened tuberculum. Based on the large size of IPS128916, we can also discount the small unnamed species of *Pleurodeles* from Valalto-1A (Middle Miocene, Teruel Basin, Spain), even if only represented by vertebrae (Blain, personal observations). We also stress that the presence or absence of a notch is highly variable among elements of a single individual (e.g., in *T. shanjing)*, and the notch seems to be more developed on the anterior ribs than on the posterior ones. Consequently,

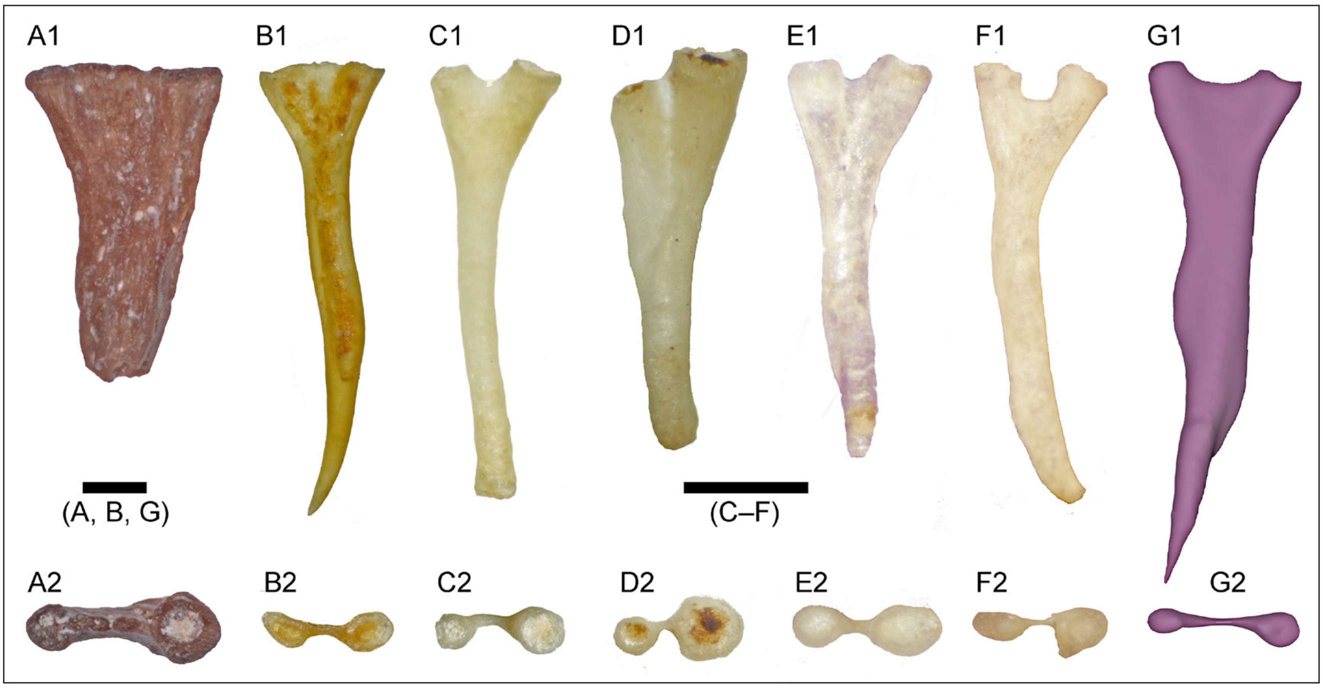

Fig. 4 - Newt rib from the Lower Pliocene of Sant Nofre-Campredó and comparison with extant and fossil large Iberian urodeles. Pleurodelinae indet. from Campredó-VF: A - left rib (IPS128916), in posterodorsal (A1) and proximal (A2) views. B - *Pleurodeles waltl* (BHC-PlWa1): left rib in posterodorsal (B1) and proximal (B2) views. C - *Salamandra salamandra bejarae* (BHC-SaSa3): left rib in posterodorsal (C1) and proximal (C2) views. D - *Salamandra salamandra salamandra* (BHC-SaSa7): left rib in posterodorsal (D1) and proximal (D2) views. E - *Triturus pygmaeus* (MNCN-13092): left rib in posterodorsal (E1) and proximal (E2) views. F - *Triturus marmoratus* (MNCN-16067): left rib in posterodorsal (F1) and proximal (F2) views. G - Pleurodelinae indet. from the Pliocene of Camp dels Ninots: left rib in posterodorsal (G1) and proximal (G2) views. Scale bars equal 1 mm.

all our comparisons with extant and fossil taxa must be taken cautiously. Nevertheless, IPS128916 clearly corresponds to an indeterminate Pleurodelinae, most probably to a representative of the unnamed clade containing the extant genera *Pleurodeles*, *Echinotriton*, and *Tylototriton* and the extinct genus *Chelotriton*.

Order **Anura** Duméril, 1805
Family Alytidae Fitzinger, 1843
Genus *Latonia* von Meyer, 1843

Latonia sp.

Fig. 5A–K

Material: *Campredó-VF*. Five maxillae (IPS128914, IPS128915, IPS128919, IPS128920, IPS128921), two vertebrae (IPS128912, IPS128928), two fragments of a radioulna (IPS128909 and IPS128911), one tibiofibula (IPS128910), and one phalanx (IPS128922). *Sant Nofre*. Seven vertebrae (IPS128931, IPS128935, IPS128936, IPS128938, IPS128941, IPS128942, IPS128943), one urostyle (IPS128949), one coracoid (IPS128946), one right humerus (IPS128930), four ilia (IPS128933, IPS 128936, IPS128937, IPS128944), and two distal phalanges (IPS128948, IPS128940).

Description. *Maxillae*. These are mainly represented by small-sized toothed fragments impossible to localize precisely within the element, except for IPS128921 (Fig. 5A). Most of the fragments document the insertions of numerous pedicellate teeth, the horizontal lamina is always relatively thick, and their lateral surface is smooth. IPS128921 corresponds to the posterior end of the crista dentalis at the level of the processus pterygoideus. Even if rather incomplete, a posterior depression seems to be present posterodorsal to the processus pterygoideus. Such a posterior depression is suggested by the dorsal part of the insertion of the processus pterygoideus, which becomes gradually vertical.

Vertebrae. All the fossil vertebrae are small (centrum length = 0.90 – 3.00 mm, average 1.50 mm, n = 7), and only the centrum and the base of the transverse processes are preserved (Fig. 5B). The vertebrae are opisthocoelous with an anterior condyle and a posterior cotyle that are rounded or slightly dorsoventrally flattened. In ventral view, the lateral edges of the centrum are generally parallel. On all the fossil vertebrae, the insertion of the transverse processes is wide. Only one vertebra preserves a longer part of the transverse processes, which appear relatively thin in anterior view.

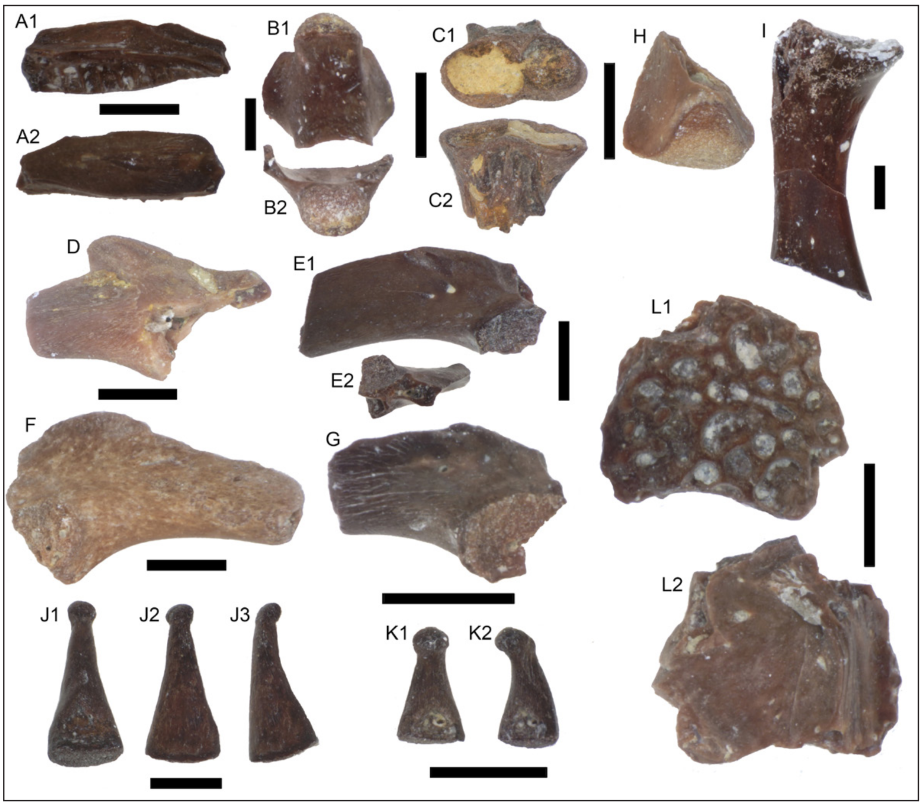

Fig. 5 - Anurans from the Lower Pliocene of Sant Nofre-Campredó. A–K - *Latonia* sp.: (A) right maxilla (IPS128921), in medial (A1) and lateral (A2) views; (B) vertebra (IPS128912), in ventral (B1) and anterior (B2) views; (C) urostyle (IPS128949), in anterior (C1) and dorsal (C2) views; (D) left ilium (IPS128933), in lateral view; (E) left ilium (IPS128944), in lateral (E1) and posterior (E2) views; (F) right ilium (IPS128936), in lateral view; (G) left ilium (IPS128938), in lateral views; (H) right humerus (IPS128930), in ventral view; (I) radioulna (IPS128909 and IPS128911), in medial view; (J) distal phalanx (IPS128948), in ventral (J1), dorsal (J2), and lateral (J3) views; (K) distal phalanx (IPS128940), in ventral (K1) and lateral (K2) views. L - *Pelobates* sp.: left squamosal (IPS128939), in lateral (L1) and medial (L2) views. Scale bars equal 1 mm.

Urostyle. Only the anterior part of this element is preserved, lacking the dorsal crest (Fig. 5C). Two cotylar cavities, corresponding to the articulation with the sacrum, are located anteriorly and are well separated by a vertical septum. This septum appears incomplete in the described fossil, likely due to the worn pattern of this element. These cavities are strongly dissymmetric, with the left cotyle being circular, while the right one is slightly dorsoventrally flattened. Although broken, there is evidence of the insertion of a small and cylindrical transverse process on the right side of the element.

Ilia. The four small fossil ilia (three left and one right) correspond to the posterior part of this bone, and they mainly document the acetabular cavity, the tuber superior, and the posterior part of the dorsal crest (Fig. 5D–G). These ilia bear a dorsally swollen tuber superior, followed by a low dorsal crest on its anterior branch. The supraacetabular fossa is relatively well developed. The pars ascendens is always incomplete but seems to have been rather elongate and with a relatively wide base. The pars descendens seems to be very narrow and is intercepted by the ventral margin of the acetabulum in one of the ilia. In posterior view, the junction surface with the ischium and pubis is thin and shows a rather wide and deep interiliac groove. The interiliac tubercle seems to have been well developed.

Other bones. A coracoid, humerus, radioulna, tibiofibula, and three phalanges that are highly fragmented or of a lesser diagnostic value are tentatively assigned to the family Alytidae. The only coracoid is highly incomplete and documents a well-developed subcircular intumescentia glenoidalis. The medial part of the element is thin, but the morphology and length of the distal end are unknown. The humerus (Fig. 5H) is highly incomplete and only documents the distalmost part of the element. The condyle is subcircular and seems to have been slightly displaced laterally in relation to the axis of the diaphysis. The cubital fossa is small and deep. The ulnar epicondyle is well developed and does not reach the distal margin of the humeral condyle. The radial epicondyle is more reduced. The ulnar epicondyle is topped by a crest, while it is unclear for the radial one. The maximal width (MW) of the whole condyle and epicondyles is 1.52 mm. The radioulna is reconstructed from two fragments (Fig. 5I). It is rather large (maximum preserved length is around 7.1 mm). However, it seems to have been relatively gracile, with a well-constricted collum antibrachii. A fragment of a tibiofibula only documents the medial part of this element. It is very small and narrow in its whole preserved length. In addition, three phalanges are represented in the fossil assemblage, one in Campredó-VF and two distal phalanges in Sant Nofre. The distal phalanges (Fig. 5J, K) are slightly curved and characterized by a shallow ventral concavity, followed distally by a well-developed bulge.

Remarks. There are some differences in size among the fossil remains, but morphologically they are very homogeneous, suggesting that they all pertain to a single species. This species is mainly represented by juvenile specimens, with very few sub-adults or adults. Besides the small size of all the available material, the presence of a posterior depression on the medial side of the maxilla is clearly a characteristic of the genera *Latonia* and *Latoglossus* (Roček 1994; Hossini 2000). In contrast, such a depression is absent or appears very rarely in *Discoglossus* (e.g., Roček 1994; Bailon 1999; Blain et al. 2013). The Moroccan Miocene genus *Latoglossus* can reasonably be excluded for biogeographical reasons. *Latonia* has been described from several Iberian Miocene localities, with two different species: *Latonia* cf. *ragei* from the Ramblian of Navarrete del Río (Teruel Basin, Aragon, east-central Spain), and *Latonia gigantea* (Lartet, 1851) in the upper Aragonian and lower Vallesian sites of the Vallès-Penedès Basin (Catalonia, Spain; Villa et al. 2019; Böhme & Ilg 2003). Among species of the genus *Latonia*, a smooth lateral surface of the maxilla is typical of the species *Latonia ragei* Hossini, 1993, *Latonia nigriventer* Mendelssohn & Steinitz, 1943 and *Latonia vertaizoni* (Friant, 1944). In contrast, *L. gigantea* shows an ornamentation consisting of tubercles that form parallel ridges posteriorly (Roček 1994, 2013; Biton et al. 2016; Villa et al. 2019). Because the studied fossils may mainly represent juveniles and the portion of preserved lateral surfaces on the maxillae is relatively small, however, no definitive conclusion can be reached beyond a cautious attribution at the genus rank. If confirmed, Campredó-VF would represent the first Pliocene (and youngest) record of the genus *Latonia* in the Iberian Peninsula.

Family Pelobatidae Bonaparte, 1850
Genus *Pelobates* Wagler, 1830

Pelobates **sp.**

Fig. 5L

Material: *Sant Nofre*. One fragment of squamosal (IPS128939).

Description. *Squamosal*. Only the central part of the lamella alaris of a left squamosal has been found in Sant Nofre (Fig. 5L). None of the processes is preserved, nor the ramus paroticus. The outer surface of the lamella alaris shows a dense sculpture composed of a few isolated tubercles that mainly coalesce into anastomosing, bony ridges (i.e., pits and grooves). The inner surface of the squamosal is smooth and shows the fused part of the processus posterolateralis.

Remarks. Among the possible attributions, *Chelotriton* and *Latonia* also bear dermal sculpture on their cranial elements (and on the osteoderms in the case of *Chelotriton*). In *Chelotriton*, the dermal sculpture is described as consisting of tall, densely set tubercles (Schoch et al. 2015), while according to Roček & Wuttke (2010), the sculpture is said to be of a pit-and-ridge type rather than pustular. In *Latonia*, a dense and well-developed dermal ornamentation is also present, consisting mainly of small tubercles (pustular) that can more rarely fuse with one another forming ridges (e.g., Roček 1994; Villa et al. 2019). If the ornamentation pattern is inconclusive, the morphology of the medial surface, with what we interpret as a fused processus posterolateralis, is characteristic of the squamosal of a pelobatid. Although the specimen is largely incomplete, the development of the lamella alaris and the dense dermal ornamentation on the squamosal match *Pelobates cultripes* Cuvier, 1829 (Iberian Peninsula and southwestern France), *Pelobates syriacus* Boettger, 1889 (southeastern Balkan Peninsula, Caucasus, and the Middle East), and *Pelobates varaldii* Pasteur & Bons, 1959 (northwestern Morocco). By contrast, in *Pelobates fuscus* (Laurenti, 1768) (eastern France to eastern Asia; northern Italy to the Baltic countries), the dermal sculpture is much sparser (e.g., Bailon 1999; Blain et al. 2016). In addition, three fossil species have been described from Europe (Sanchiz 1998; Roček 2013): *Pelobates decheni* Troschel, 1861 (Late Oligocene of Germany: Böhme et al. 1982; Roček & Wuttke 2010); *Pelobates fahlbuschi* Böhme, 2010 (Early Miocene of Germany: Böhme 2010) and *Pelobates sanchizi* Venczel, 2004 (Middle Miocene of Hungary: Venczel 2004; Venczel & Hír 2013). All present a dense dermal sculpture, at least on the maxilla and frontoparietal. The dermal sculpture on the squamosal in *Pelobates sanchizi* is similarly dense as on IPS128939, but does not present any isolated tubercles (Ivanov 2008). In conclusion, only attribution to *Pelobates fuscus* can be ruled out, but a more precise attribution at the species rank within the genus *Pelobates* cannot be securely determined. Therefore, IPS128939 is indeterminate at the species rank.

Class **REPTILIA** Laurenti, 1768
Order **Chelonii** Brongniart, 1800
Geoemydidae vel Emydidae indet.

Fig. 6A, B

Material: *Campredó-VF*. One indeterminate shell plate (IPS128917), and one indeterminate plate of the plastron (IPS128918).

Description. *Shell bones*. Two small fragments of indeterminate shell bones have been recovered from Campredó-VF. Both remains are relatively thin and no growth lines are present in dorsal view. IPS128917 shows several sulci that cannot be determined given the highly fragmentary nature of the specimen (Fig. 6A1). Based on its slight curvature in anterior and posterior view (Fig. 6A2), IPS128917 probably belongs to a costal plate. IPS128918 is ornamented on its external face with small, shallow, elongated holes (Fig. 6B). IPS128917 also shows them but in a lesser density (Fig. 6A1). IPS128918 is flat and probably represents a fragment of plastron.

Remarks. The poor preservational state of the studied specimens complicates their identification, resulting in the use of open nomenclature. Nevertheless, some remarks can be made. The relative thickness of the plates and the absence of any growth line in the dorsal surface discount attribution to Testudinidae (e.g., Bailon 2010). Thus, both elements may be related to freshwater turtle taxa. Around the Miocene-Pliocene boundary, the diversity of these chelonians included up to three different families: Trionychidae, Geomydidae, and Emydidae (Pérez-García 2017). Among them, Trionychidae is easily distinguishable from the rest based on its characteristic sculptured ornamentation pattern consisting of ridges, pits, and knobs (Scheyer et al. 2007), which is absent in the studied remains. Due to the fragmentary nature of the studied specimens, no more precise attribution can be proposed.

Order **Squamata** Oppel, 1811
Lacertidae vel Scincidae indet.

Fig. 6C, D

Material: *Campredó-VF*. One left hemipelvis (IPS128913). *Sant Nofre*. One right dentary (IPS128945).

Description. *Dentary*. The fragment from Sant Nofre documents the central part of a right dentary (Fig. 6C). The maximum preserved length is about 3.9 mm. No teeth are preserved, but they were probably cylindrical and their insertion on the bone was pleurodont. On the lateral side, two large lateral foramina are visible. In medial view, the Meckelian groove seems to have been opened along its entire length.

Hemipelvis. A small left hemipelvis is represented in Campredó-VF. Its maximum preserved length is 2.1 mm. It is composed of three fused bones: ilium, pubis, and ischium (Fig. 6D). Only their proximal portion around the acetabulum is preserved. All three bones participate in the formation of a rounded and quite large acetabulum. The pubis and ischium are joined immediately ventral to the acetabulum along a weakly visible, more or less vertically oriented suture. The pubis and ischium are separated by a large thyroid fenestra. The preacetabular process is short and robust, but well distinct from the ilium main shaft. A large obturator foramen is located on the pubis.

Remarks. The dentary clearly pertains to a pleurodont lizard. Blanids and anguids can be disregarded because the teeth do not seem to have been cone-shaped, knife-like or laterally compressed. Geckonids can also be ruled out because the teeth do not appear to have been densely packed and thin, and above all, due to the open Meckelian groove. The specimen can therefore be attributed to a scincid or a lacertid. However, in the absence of any teeth and the coronoid process, no more precise attribution can be made.

Concerning the hemipelvis, its composition of fused ilium, pubis, and ischium is characteristic of limbed lizards and sphenodontids. Attribution to anguines and limbless skinks can be disregarded, as in most species the pubis and ischium are indistinguishably fused together (e.g., Čerňanský & Klembara 2017; Miralles et al. 2015; Camaiti et al. 2019). IPS128913 matches the morphology of a lacertid; nevertheless, because a small preacetabular process can also be present in some species of limbed scincids (see, for example, Čerňanský & Klembara 2017), a cautious attribution to Lacertidae vel Scincidae indet. is preferred.

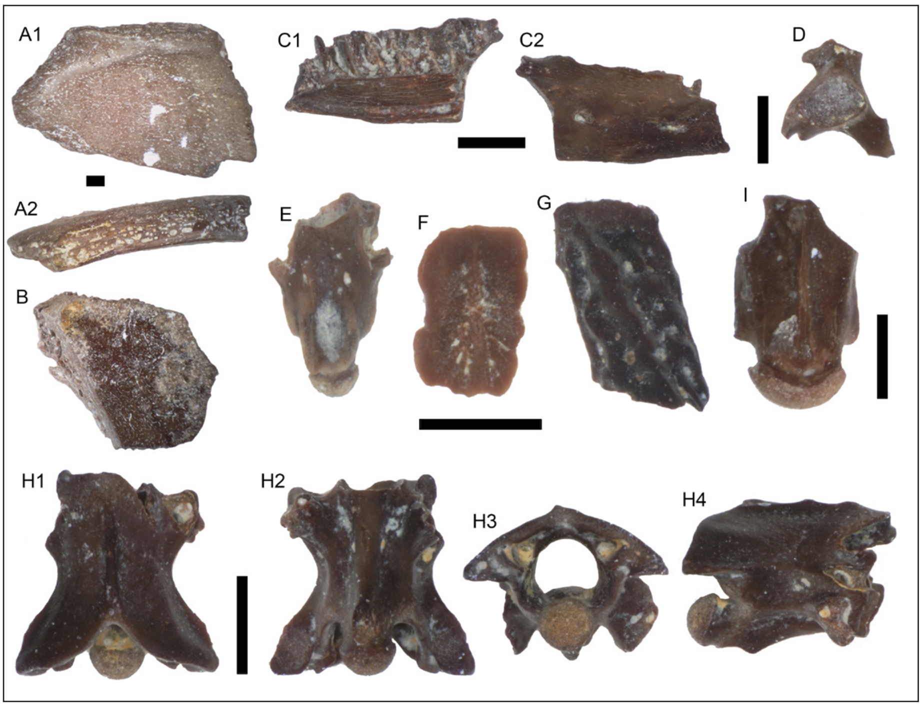

Fig. 6 - Chelonians and squamate reptiles from the Lower Pliocene of Sant Nofre-Campredó. A, B - Chelonii indet. (Geoemydidae or Emydidae): (A) indeterminate plate (IPS128917), in dorsal (A1) and anterior/posterior (A2) views; (B) indeterminate plate (IPS128918), in dorsal view. C, D - Lizard indet. (Lacertidae or Scincidae): (C) right dentary (IPS128945), in medial (C1) and lateral (C2) views; (D) left hemipelvis (IPS128913), in lateral view. E–G - cf. *Ophisaurus* sp.: (E) caudal vertebra (IPS128947), in ventral view; (F) mediodorsal osteoderm (IPS128929), in dorsal view; (G) laterodorsal osteoderm (IPS128932), in laterodorsal view. H - cf. *Natrix* sp.: trunk vertebra (IPS128923), in dorsal (H1), ventral (H2), posterior (H3), and right lateral (H4) views. I - Colubridae vel Psammophiidae indet.: trunk vertebra (IPS128924), in ventral view. Scale bars equal 1 mm.

Family Anguidae Gray, 1825
Genus *Ophisaurus* Daudin, 1803

cf. ***Ophisaurus*** sp.
Fig. 6E–G

Material: *Campredó-VF*. One mediodorsal osteoderm (IPS128929). *Sant Nofre*. One caudal vertebra (IPS128947), and one laterodorsal osteoderm (IPS128932).

Description. *Caudal vertebra*. The caudal vertebra is only represented by the centrum (Fig. 6E). It is small (centrum length = 1.4 mm) and relatively elongated and narrow, suggesting a posterior position for this vertebra. The condyle and cotyle are dorsoventrally flattened. The condyle is separated from the centrum of the vertebra by a sharp incision. The ventral face of the centrum is flat. It bears the insertion of two haemapophyses fused to its posterior half. Two large subcentral foramina are present, even if filled with sediment. On the anterior region of the centrum, the insertion of the transverse processes appears to be narrow, possibly indicating the presence of an autotomy line, although this is difficult to discern.

Osteoderm. The osteoderm from Campredó-VF (IPS128929) is small (length = 1.4 mm), relatively thin, and rectangular in shape (Fig. 6F). It exhibits a relatively narrow, smooth overlap surface on the anterior and both lateral sides, with a greater development on the left side compared to the right. Even if rather worn, its outer surface displays an ornate, vermicular surface. The ornamentation appears to have been densely spaced, albeit fine rather than strong. The presence of a well-marked medial ridge suggests a mediodorsal position for this osteoderm. The osteoderm from Sant Nofre (IPS128932) is small (length = 1.8 mm), elongated, and appears to have been rhomboid (or parallelogram) in shape (Fig. 6G). A narrow, smooth overlap surface is present on the anterior margin, and possibly also, but much narrower, on its left lateral side. The ornate vermicular surface appears rougher than on IPS128929, and a relatively wide medial ridge is present, located transversally to the longitudinal axis of the bone. All these characteristics suggest a laterodorsal position for this osteoderm.

Remarks. None of the recovered elements is diagnostic at genus rank by itself. Nevertheless, the association of a caudal vertebra with a possible autotomy line and osteoderms bearing a medial ridge suggests the occurrence of the genus *Ophisaurus*, at least in Sant Nofre.

The autotomic split in caudal vertebrae is absent in the genus *Pseudopus*, where only autotomic foramina are developed. However, in the genera *Anguis* and *Ophisaurus*, an autotomic split is present and generally well visible (Hoffstetter & Gasc 1969; Čerňanský et al. 2019). Subrectangular and parallelogram trunk osteoderms, with external surficial sculpting, are commonly associated with modern anguid genera. Subtle differences in the external surface sculpting of osteoderms are commonly used for taxonomic distinction in fossil and modern anguid lizards. Among European anguids, only the genera *Ophisaurus* and *Pseudopus* present a medial ridge on their mediodorsal osteoderms, whereas the osteoderms in *Anguis* have an oval or irregular shape and lack a bony ridge on their sculptured surface (Hoffstetter 1962; Augé 2005). Moreover, the osteoderm IPS128929 may differ from those of the genus *Pseudopus* by its smoother sculpture and both IPS128929 and IPS128932 from glyptosaurines, which bear granular ornamentation (Augé 2003; de Buffrénil et al. 2011). In the genus *Pseudopus*, the osteoderms are usually more thickened in the middle, that is not the case of our fossil osteoderms. The transversally located medial ridge visible on IPS128932 is due to its position on the body (laterodorsal), as stressed by Hoffstetter (1962), and not a characteristic exclusive to diploglossine and cordylid lizards.

Family Natricidae Bonaparte, 1840
Genus *Natrix* Laurenti, 1768

cf. ***Natrix*** sp.

Fig. 6H

Material: *Campredó-VF*. One trunk vertebra (IPS128923).

Description. *Vertebra*. The vertebra is small (centrum length = 1.9 mm) and, even if highly incomplete, possesses a somewhat robust hypapophysis (Fig. 6H). The neural arch is vaulted posteriorly. The condyle and cotyle are small and circular. None of the parapophyseal process is preserved, but the parapophyses are well defined. In ventral view, the centrum is flat, and its lateral margins are well marked.

Remarks. All these characteristics seem to be consistent with an attribution to the extant genus *Natrix*. When compared with extant species, IPS128923 presents a mosaic of features between *Natrix maura* (Linnaeus, 1758) (well-defined parapophyses) and *Natrix* gr. *N. natrix* (Linnaeus, 1758) (the flat centrum). IPS128923 also differs from the extinct taxa *Natrix longivertebrata* Szyndlar, 1984, *Natrix sansaniensis* Lartet, 1851 and *Natrix merkurensis* Ivanov, 2002, which have much more elongated trunk vertebrae (Szyndlar 1984; Ivanov 2002). Moreover, *N. sansaniensis* and *N. merkurensis* have very distinctive epizygapophyseal spines (Ivanov 2002). However, such developed epizygapophyseal spines are also present on the anterior trunk vertebra of *N. longivertebrata*, but seem to be less developed on the mid-trunk vertebrae (Szyndlar 1984). *Natrix merkurensis*, *N. sansaniensis*, and to a lesser extent *Natrix mlynarskii* Rage, 1988 have a high neural spine, whereas on IPS128923 it is broken but does not appear to have been very high. In ventral view, IPS128923 does not show the triangular, protruding area below the cotyle formed by the base of the hypapophysis observed in *N. mlynarskii* (see Rage 1988). Judging by its size, IPS128923 is a juvenile, and therefore attribution to the genus *Natrix* is tentative. The oldest occurrence of the genus in the Iberian Peninsula is recorded in the Late Pliocene (MN16) of Las Higueruelas (Castile La Mancha, central Spain) and Camp dels Ninots (Blain et al. 2024). Thus, if the presence of the genus *Natrix* is demonstrated in the Early Pliocene of Campredó-VF, it may constitute the earliest mention of the genus in the Iberian Peninsula, while already present in western and central Europe since the Oligocene (Rage 1988).

Colubridae vel Psammophiidae indet.

Fig. 6I

Material: *Campredó-VF*. One centrum of a trunk vertebra (IPS128924).

Description. *Vertebra*. Only the centrum of the trunk vertebra is preserved (Fig. 6I). It is relatively small (preserved centrum length = 2.6 mm) and appears to be rather elongated. The haemal keel is narrow and well developed along its whole length, ending as a slightly spatulate point. A precondylar constriction is well marked. The condyle is subcircular in posterior view.

Remarks. IPS128924 does not bear any hypapophyses, as seen in Colubridae and Psammophiidae, unlike the trunk vertebrae of the families Natricidae, Elapidae, and Viperidae. Due to its incompleteness, no further comparison is feasible.

To conclude with herpetofauna, there are three centra (IPS128925, IPS128926, IPS128927) from Campredó-VF with a maximum length of 2 mm.

Due to the fragmentation of these small vertebral fragments, a more precise attribution than Serpentes indet. is not feasible. IPS128925 is a fragment of centrum bearing a broken hypapophysis. IPS128926 corresponds to the posterior half of a centrum with the insertion of what can be either a large haemal keel or a robust hypapophysis. IPS128927 is a very small condyle, with a diameter of around 1 mm.

Class **MAMMALIA** Linnaeus, 1758
Order **Eulipotyphla** Waddell, 1999
Family Erinaceidae Fischer, 1814
Subfamily Galericinae Pomel, 1848
Genus *Parasorex* Von Meyer, 1865

Parasorex **sp.**
Fig. 7A

Material and measurements: *Campredó-VF*. One partial left m2 (IPS126953) (measurements of the trigonid: L = 1.41 mm; W = 2.24 mm).

Description. *m2*. The specimen is broken. Only the trigonid is preserved. The talonid is completely missing. The protoconid is the highest cusp of the trigonid. The metaconid is only a bit lower than the protoconid. The paraconid is lower than the other two cuspids, and is not clearly isolated as an elevation, but is only visible as the mesial end of the paralophid. The base of the anterior margin of the tooth is curved and there is a small cingulid covering part of it. The trigonid basin opens to the anterolingual edge of the tooth.

Remarks. The only fragment recovered does not allow the identification of the species, as additional elements would be needed. However, the generic attribution is beyond any doubt, as the genus *Parasorex* is almost invariably present in Upper Miocene and Lower Pliocene localities from Spain (Furió & Agustí 2017). Indeed, this is the only galericine genus documented in this interval in southwestern Europe (Furió et al. 2018). The wide geographic and biostratigraphic range of *Parasorex* species indicate that they were more generalist than their extant Asian relatives (Van den Hoek Ostende 2001; Furió et al. 2011). Therefore, the occurrence of this genus in Campredó-VF does not provide much to inform about the age and palaeoenvironmental conditions of this site.

Family Soricidae Fischer, 1814
Subfamily Soricinae Fischer, 1814
Tribe Blarinellini Reumer, 1998
Genus *Plioblarinella* von Koenigswald & Reumer, 2020

Plioblarinella dubia (Bachmayer & Wilson, 1970)
Fig. 7B

Material and measurements: *Campredó-VF*. One right M1 (IPS126951) (AW = 1.46 mm; PW = 1.55 mm; BL = 1.45 mm; LL = 1.42 mm; PE = 1.35 mm).

Description. *M1*. In overall shape the tooth is rather square, but its posterior margin is somewhat wider than the anterior. The ectoloph is asymmetrical, with a longer posterior arm of the metacone than the anterior arm of the paracone. The parastyle is slightly curved in a distal direction. The mesostyle is not divided. The metastyle is labiodistally elongated. The posterior emargination is not much pronounced, being only faintly visible. The protocone is the highest point of a rather discontinuous endoloph, which is divided into two segments. The first segment connects the base of the paracone with the posterior arm of the protocone. The other segment covers the lingual base of the hypoconal flange. The hypocone is a tiny elevation at the anteriormost point of this second segment. The posterior arm of the protocone is not connected to the base of the metacone. There is a small protruding cingulid at the lingual base of the protocone.

Remarks. The rather square shape of the occlusal outline, the size, and the discontinuous endoloph are the key points for generic and specific identification. Compared with other samples of the same species found in Spain (Furió & Agustí 2017), the only element found is somewhat larger than the same elements from Can Vilella (MN13, Cerdanya Basin, Catalan Pyrenees), but similar in size to the largest specimens from Romanyà d'Empordà (MN13; Empordà Basin, Catalonia). The size of this M1 from Campredó-VF is larger than its equivalents found in the assemblage of Osztramos 9 (MN15; Hungary), according to the data provided by Reumer (1984).

The classification and status of the genera nowadays included in the Blarinellini has been challenged several times in the last decades (see Bachmayer & Wilson 1970; Reumer 1984, 1998; Storch

1995; Furió et al. 2011; Furió & Agustí 2017; von Koenigswald & Reumer 2020) and, indeed, there are some controversies regarding the generic ascription of this European species. In the absence of a synthetic work on the tribe providing a complete landscape about the taxonomy of this group of shrews, we follow the proposal of von Koenigswald & Reumer (2020) to include this species in *Plioblarinella*, a genus established 'ad hoc' to allocate it. The occurrence of Blarinellini shrews in Spanish localities is somehow linked to environments with abundant moisture (Furió et al. 2018).

Soricinae indet.

Fig. 7C

Material and measurements: *Campredó-VF*. One right m1 (IPS126952) (L = 1.43 mm; TRW = 0.85 mm; TAW = 0.89 mm).

Description. *m1*. The trigonid and the talonid are quite similar in length and width. The metaconid is the highest cuspid of the tooth, but there is not much difference from the protoconid. In occlusal view the metaconid occupies a slightly more posterior position than the protoconid. The paraconid is projected anteriorly. The paralophid is rather straight and its base is covered by a marked cingulid, whose anterior half strongly protrudes from the occlusal outline. The talonid basin is closed on its lingual side by a strong entoconid cristid, and it is only open to the posterolingual corner of the tooth by means of a marked notch separating the entoconid and the entostylid. The oblique cristid ends anteriorly at the central part of the protolophid. The reentrant valley is quite pronounced. The base of the distal margin is covered by a thin but well-delimited cingulid.

Remarks. Unfortunately, the only element recovered attributable to this taxon does not display clearly derived characters to specify its taxonomic attribution below subfamily. The talonid is similar in length to the trigonid, so ascription to the subfamilies Crocidurinae or Crocidosoricinae is discounted. The moderate opening of the trigonid and the presence of an entoconid cristid do not support ascription to the subfamilies Allosoricinae and Paenelimnoecinae. Thus, this tooth can only be confidently attributed to a member of the subfamily Soricinae. The medium size of the tooth makes its ascription to the tribes Anousorsoricini, Beremendiini or Blarinini extremely unlikely. Similarly, the pronounced reentrant valley and the non-rectangular outline in occlusal view indicate that it does not belong to a Blarinellini species. As it is, this tooth most likely belongs to a Soricini or to a Soriculini species. Nothing else can be added to refine the identification from either the biostratigraphy or the palaeoenvironment of the site, as the species of these two tribes cover a wide range of chronologies and ecological preferences. Interestingly, two similar elements were recovered from the Upper Miocene (MN13) site of Bàscara Superior (Empordà Basin, Catalonia, Spain; Furió & Agustí 2017).

Order **Rodentia** Bowdich, 1821
Family Sciuridae Fischer, 1817
Subfamily Xerinae Osborn, 1910
Xerinae indet.

Fig. 7D

Material and measurements: *Campredó-VF*. One right dp4 (IPS126946) (L = 1.25 mm; W1 = 0.89 mm; W2 = 1.02 mm).

Description. *dp4*. The only available specimen is considerably worn. This milk molar is rectangular, its anterior margin being only slightly narrower than the posterior one. The crown is relatively high for a sciurid dp4. It presents four clearly delimited cuspids: protoconid, metaconid, hypoconid and entoconid. The protoconid and metaconid are very large, opposite, and close together but not connected by means of any ridge. The protoconid is conspicuously larger than the metaconid. The trigonid basin is just a tiny slit-like valley between these cuspids. There is no anteroconulid or any trace of the anterior cingulid, so that the anterosinusid is also absent. The hypoconid is crescent-shaped and connected to the protoconid by means of a thick ectolophid. The sinusid is absent. There is no mesoconid. The posterior margin of the tooth is straight and defined by the thick posterolophid, which connects with a large and prominent entoconid. The posterolophid shows a slight constriction as it approaches the posterolingual corner of the tooth. This may indicate the presence of a greatly reduced hypoconulid. There is no mesostylid but the talonid basin is closed by a thin cingulid that merges the entoconid with the metaconid. The talonid basin is shallow and faint. There is some very minor enamel wrinkling near the main ridges, but this could be related to dental wear.

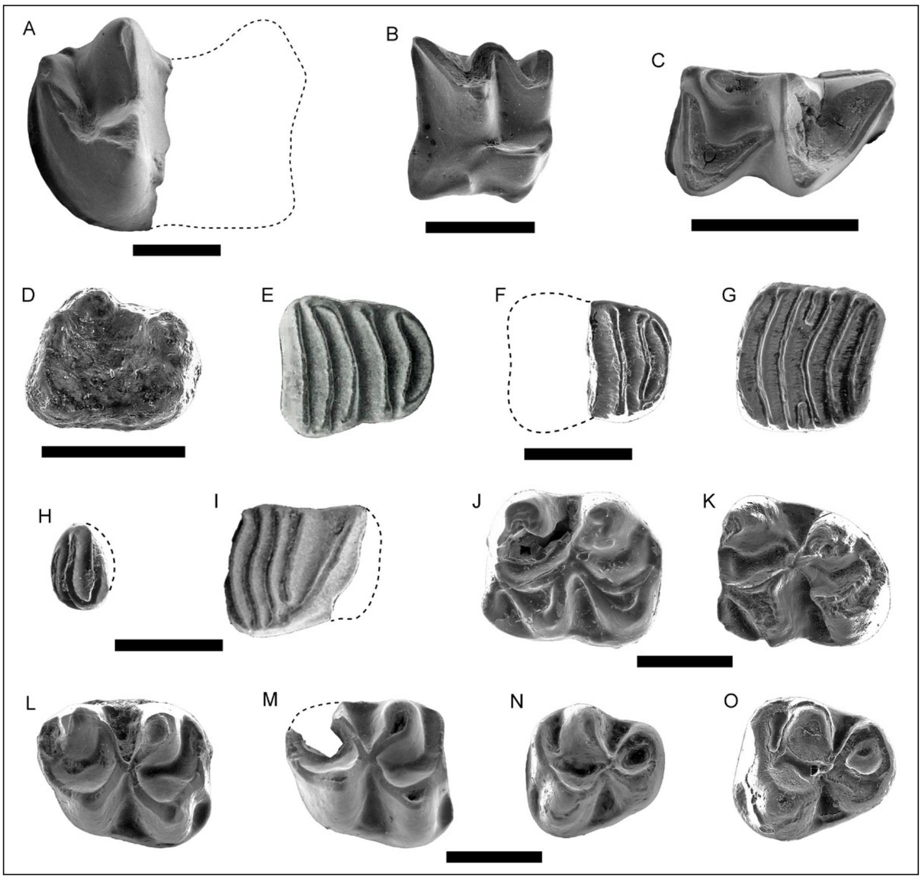

Fig. 7 - Insectivores and rodents from the Lower Pliocene of Sant Nofre-Campredó. A - *Parasorex* sp.: broken left m2 (IPS126953). B - *Plioblarinella dubia*: right M1 (IPS126951). C - Soricinae indet.: right m1 (IPS126952). D - Xerinae indet.: right dp4 (IPS126946). E–I - *Muscardinus* cf. *meridionalis*: (E) right m1 (IPS127159); (F) anterior fragment of right m1 (IPS127172); (G) left m2 (IPS127158); (H) right P4 (IPS126948); (I) right M1 (IPS126945). J–O - *Apocricetus* cf. *barrierei*: (J) left m2 (IPS126943); (K) left m3 (IPS126947); (L) right M2 (IPS20637); (M) right M2 (IPS126940); (N) left M3 (IPS126941); (O) left M3 (IPS126942). The dashed lines represent an approximation of the original (expected) shape of the broken teeth. Scale bars equal 1 mm.

Remarks. The dp4 from Campredó-VF stands out because of its small size, much smaller than common representatives of the Sciuridae in Late Miocene and Pliocene Iberian faunas, such as *Sciurus*, *Pliopetaurista*, *Spermophilinus* or *Atlantoxerus*. It is only comparable in size to small-sized flying squirrels such as *Pliopetes* and *Blackia* on the one hand, and to small-sized ground squirrels such as *Tamias*, *Sinotamias,* and some species of *Heteroxerus* on the other. The presence of a well-developed entoconid may suggest affinities with flying squirrels, but the absence of enamel crenulations and overall different morphology rules out this option. In both *Blackia* and *Pliopetes*, the protoconid and metaconid are smaller than in the studied specimen and the protoconid is always posterior to the metaconid rather than opposite. Furthermore, both flying squirrel genera show an anteroconulid and/or anterior cingulid. The relatively high crown, large and appressed protoconid and metaconid, together with the absence of anteroconulid and/or anterior cingulid fits better with ground squirrels. The Marmotini *Tamias* and *Sinotamias* show a similar morphology (see Sinitsa 2018) but these genera, as well as most marmotins, do not present a well-defined entoconid and the occlusal contour is not rectangular, the posterior margin being wider and curved. On the other hand, the long-ranging (Late Oligocene to Late Miocene; see Cuenca-Bescós 1988) Xerini ground squirrel *Heteroxerus* includes some small-sized species, such as *Heteroxerus rubricati* Crusafont, Villalta & Truyols, 1955, close in size to the Campredó-VF specimen. These would similarly present a reduced or absent anteroconulid and/or anterior cingulid, as well as large and appressed protoconid and metaconid. But, most importantly, *Heteroxerus* and other xerins are characterized by the presence of an entoconid, which results in square premolars. *Heteroxerus rubricati* is known from the Ramblian (MN3) to the upper Vallesian (MN10), and other small-sized species, such as *Heteroxerus paulhiacensis* Black, 1965 are even older (see García-Alix et al. 2007). *Heteroxerus mariatheresae* Adrover, Mein & Moissenet, 1993 is the youngest species of the genus, being known from a few middle to upper Turolian (MN12–MN13, Late Miocene) sites from Spain: La Gloria-5 (Teruel Basin; Adrover et al. 1993a), Venta del Moro (Cabriel Basin; Mansino et al. 2018), and Jun-2B (Granada Basin; García-Alix et al. 2007). All these collections include very few specimens (less than 10) and no dp4s, thus precluding comparisons with the Campredó-VF material. Nevertheless, *H. mariatheresae* is a relatively large-sized species of the genus (Adrover et al. 1993a), so one may expect the dp4 to be larger than the studied specimen. The small size of the described specimens precludes an ascription to the genus *Atlantoxerus*, which is widespread in the Iberian Lower Pliocene (see Adrover et al. 1993a; García-Alix et al. 2007). Considering that only a single specimen has been recovered, we prefer to assign the Campredó-VF material to Xerinae indet. However, we note that it shows many affinities with *Heteroxerus*. The recovery of further material may confirm the presence of this genus at Campredó-VF, which would then become its youngest record.

Family Gliridae Muirhead, 1819
Subfamily Dryomyinae De Bruijn, 1967
Genus *Muscardinus* Kaup, 1829

Muscardinus cf. ***meridionalis*** García-Alix, Minwer-Barakat & Martín-Suárez, 2008

Fig. 7E–I

Material and measurements: *Campredó-VF*. One right P4 (IPS126948) (L = 0.58 mm; W = 0.83 mm), and one right M1 (IPS126945) (W = ca. 1.26 mm). *Sant Nofre*. One right m1 (IPS127159) (L = 1.51 mm; W = 1.41 mm), anterior fragment of right m1 (IPS127172), and one left m2 (IPS127158) (L = 1.47 mm; W = 1.43 mm).

Description of the material from Campredó-VF. *P4*. The occlusal pattern is very simple. The anterior part is missing, so there is no evidence of the anteroloph. The protoloph and metaloph are fused lingually. An isolated posteroloph is present.

M1. The anterior part of the tooth is missing, so the anteroloph is lacking. The remaining ridges include the protoloph, precentroloph, postcentroloph, metaloph, and posteroloph. The posteroloph, metaloph, and postcentroloph are slightly curved backward. The postcentroloph is long, being lingually connected to the anteroloph. The precentroloph is isolated and does not reach the lingual side.

Description of the material from Sant Nofre. *m1*. The occlusal pattern of this tooth is composed of six ridges. All the ridges are somewhat curved forward. The anteriormost ridge (anterolophid) and the next one (anterotropid) are labially and lingually fused. All the remaining ridges are isolated.

m2. The occlusal pattern of this tooth comprises six main ridges. All are isolated and curve strongly forward. There are two small symmetric extra ridges between the third and the fourth ridges, one on the labial side and the other on the lingual side.

Remarks. The scarce material of *Muscardinus* from Sant Nofre and Campredó-VF was initially attributed to *Muscardinus* aff. *vireti* Hugueney & Mein, 1965 (see Agustí & Gibert 1985; Agustí et al. 1983), although it was acknowledged that its size was somewhat larger than the specimens from the type locality of Lissieu (MN13, Late Miocene, France; Hugueney & Mein 1965). These authors distinguished it from the early Late Miocene (Vallesian) species *Muscardinus hispanicus* De Bruijn, 1966 by its long postcentroloph and absence of anterotropid, as well as from the Late Pliocene *Muscardinus pliocaenicus* Kowalski, 1963 due to its smaller size, less elongated M1 and m1, and the persistence of extra ridges between the centrolophid and mesolophid. García-Alix et al. (2008a) later described the species *Muscardinus meridionalis* from the Early Pliocene (Ruscinian, MN14) of the Granada Basin (type locality Purcal-4), which is morphologically similar to *M. vireti* but larger. The material from Sant Nofre (m1, m2) presents dimensions that fit within the variability of *M. meridionalis*, while the P4 and the fragment of M1 from Campredó-VF are slightly smaller. Due to the limited material of *Muscardinus* recovered at Sant Nofre and Campredó-VF, we refer the specimens to *Muscardinus* cf. *meridionalis*.

Family Castoridae Hemprich, 1820
Subfamily Castorinae Hemprich, 1820
Genus *Castor* Linnaeus, 1758

Castor fiber Linnaeus, 1758

Fig. 8

Material and locality: *Campredó-VF*. Two partial mandibles with p4–m3 belonging to the same individual (IPS88860; labelled as TRM-1 and TRM-2 in Aldana Carrasco 1991, 1992), one left partial mandible with p4–m3 (IPS88861; TRM-3 in Aldana Carrasco 1991, 1992), one left p4–m3 series (IPS88862; TRM-4 in Aldana Carrasco 1991, 1992), one left P4 (IPS88863; TR-1 in Aldana Carrasco 1991, 1992), one right M3 (IPS88864; TR-2 in Aldana Carrasco 1991, 1992), and one damaged left lower incisor fragment (IPS88865).

Measurements: Measurements of the dental elements with the exception of incisors are shown in Tab. 2 and 3.

Fig. 8 - *Castor fiber* from the Lower Pliocene of Sant Nofre-Campredó. A - left partial mandible with p4–m3 (IPS88860a), in occlusal (A1), lateral (A2) and medial (A3) views. B - left partial mandible with p4–m3 (IPS88861), in occlusal (B1), lateral (B2) and medial (B3) views. C - left p4–m3 series (IPS88862), in occlusal (C1), lateral (C2) and medial (C3) views. D - left P4 (IPS88863). E - right M3 (IPS88864). Scale bar equals 1 cm in all pictures. Abbreviations: *aadm*, attachment area for the anterior deep masseter; *aat*, attachment area the anterior fibers of the temporalis; *aopf*, anterior opening of the paraflexid; *di*, diastema; *lmc*, lower masseteric crest (attachment area for the superficial masseter); *mef*, mental foramina; *mf*, masseteric fossa; *myld*, mylohyoid depression; *ppf*, proparaflexid.

Lower incisor IPS88660a: anterior width at the occlusal level, 7.0 mm; posterior width at the alveolar level, 3.6 mm; anteroposterior length of the wear facet, 9.5 mm. Lower incisor IPS88865: anterior width at the occlusal level, 8.4 mm; other measurements could not be taken reliably.

Description. This material was already described by Aldana Carrasco (1991, 1992), so here we only provide some remarks on a few morphological features that were not noted. The M3 (IPS88864) was not described by the latter author, who also made no comments or comparisons on mandible morphology. Hence, these are given here. Furthermore, this author only gave mean measurements. In Tab. 2 and 3 we provide detailed measurements for the whole collection, including the mandibles.

Age classes. All specimens except IPS88861 are only moderately worn, with no fossetes/ids defined. IPS88861 only has a single fossetid in each tooth, the metafossetid. Stefen (2009) defined five age classes based on tooth wear. IPS88861 would be older than her age class D, meaning that it is more than 80 months old. All other specimens are intermediate between age classes B and C, which would imply an age between 39 and 48 months old.

Mandible. The recovered mandibular fragments only preserve part of the corpus below the cheek tooth series. IPS88860a is the best-preserved specimen and also includes the anterior part of the mandible and the lower incisor. Overall, the mandible is robust and comparable in size to extant *Castor*.

The ventral part is broken in all specimens, so the characteristic digastric eminence of this genus is not preserved. The tip of the incisor is only slightly higher than the molar plane. The incisor is clearly proodont, its cutting edge being anterior to the vertical-incisive plane of the mandible. On the other hand, the wear surface of the cheek tooth series is markedly concave. The diastema is relatively shallow, flat, and asymmetric, with a deeper posterior margin. The mental foramen is placed anteriorly to the cheek teeth and located to the ventral side of the diastemal portion of the mandible, aligned with the anterior end of the masseteric fossa. Interestingly, the foramen is small and double, the lower aperture being slightly larger than the upper one. The mental foramen tends to be larger in older beavers (see Cuenca-Bescós et al. 2017), which would indicate that IPS88860 is a relatively young individual, in agreement with the age inferred from the cheek tooth wear stage. All *Castor* specimens we have examined have a single mental foramen, but double foramina have been reported for the Miocene genus *Steneofiber* (see Stefen 2005). The insertion area for the masseteric muscles is strongly built. There is a marked bulge on the lateral surface of the mandible below the p4 for the attachment of the anterior fibers of the anterior deep masseter. From this point, a faint ridge for the insertion of the superficial masseter extends postero-ventrally. The lateral surface of the mandible covered by the masseters does not define a fossa as in other rodents (masseteric fossa), being somewhat inflated and presenting a rugose surface defined by vascular impressions, which also occurs in extant *Castor*. The dorsal border of the 'masseteric fossa' is defined by an oblique ridge which uniquely in beavers serves for the attachment of the anterior fibers of the temporalis. All the recovered mandibles are badly broken on their medial side, allowing us to observe the lower incisor extending below the cheek teeth. On the medial side, there is a shallow depression as long as the cheek teeth row and placed just below it: the mylohyoid depression for the attachment of the muscle of the same name.

Lower incisor. Aldana Carrasco (1991) provided a very sketchy description of this element. The incisors are stout and show a triangular section with a flattened anterior surface. The wear facet is also triangular and not much elongated. The enamel is restricted to the ventral side only extending minimally in lateral and medial view of the incisor. The characteristic orange pigmentation of beaver incisors is not preserved, the recovered specimens being colored black or brown.

Collection number	Element	Length	Width	Height
IPS88860a	p4	8.8	7.0	–
IPS88860a	m1	7.3	7.2	–
IPS88860a	m2	7.1	7.3	–
IPS88860a	m3	7.6	6.5	15.7
IPS88860b	p4	8.8	7.3	–
IPS88860b	m1	7.2	(6.7)	–
IPS88860b	m2	7.0	(7.1)	–
IPS88860b	m3	7.1	6.2	–
IPS88861	p4	12.8	7.6	–
IPS88861	m1	9.0	8.1	–
IPS88861	m2	8.9	7.7	–
IPS88861	m3	8.9	6.6	9.0
IPS88862	p4	10.6	7.1	23.8
IPS88862	m1	8.0	7.9	23.9
IPS88862	m2	8.1	7.4	21.9
IPS88862	m3	6.9	6.5	15.6
IPS88863	P4	9.5	8.3	22.5
IPS88864	M3	6.1	5.6	20.3

Tab. 2 - Dental measurements (in mm) of *Castor fiber* from Campredó-VF, Early Pliocene, northeastern Spain. Estimated measurements due to minor breakage of the specimens are given within brackets.

Lower cheek teeth. For a detailed description of these elements the reader is referred to Aldana Carrasco (1991, 1992). Here, we only add some comments on morphological features not noted by that author. All the striids extend to the base of the crown in the teeth in which this character can be assessed. The striids are infilled with cement, which is thicker near the base of the crown. Regarding the p4, the roots can be observed in IPS88861, whereas they are not formed in all other specimens. There is an anterior flattened root as well as a posterior one. It is worth noting that in IPS88862, which shows very slight wear, the paraflexid opens at the anterior border of the p4 marking a very short striid there. Apparently, this soon becomes closed so that the paraflexid is only open lingually in all the other specimens. The mesoflexid in the p4 is variable. In IPS88861 and IPS88862 it curves anteriorly, whereas it is straighter in IPS88860a and IPS88860b, with its labial end being further posteriorly directed to face the hypoflexid. In IPS88860b, the m3 presents an additional reduced flexid on the lingual side anterior to the paraflexid, the so-called proparaflexid. This element forms a very short striid on the lingual side, which quickly disappears with wear. The

Collection number	Length of p4–m3		Height by breath of the mandibular body at the lingual side							
	occlusal level	alveolar level	p4		m1		m2		m3	
			L	W	L	W	L	W	L	W
IPS88860a	30.1	(32.5)	(22.2)	(10.0)	(22.1)	(12.3)	(22.06)	(15.3)	–	–
IPS88860b	29.9	(31.9)	(23.0)	(11.4)	(19.9)	(13.3)	(19.56)	(15.5)	(20.3)	(14.9)
IPS88861	35.0	36.8	–	–	–	–	–	(18.9)	–	–
IPS88862	32.3	–	–	–	–	–	–	–	–	–

Tab. 3 - Mandible measurements (in mm) of *Castor fiber* from Campredó-VF, Early Pliocene, northeastern Spain. Abbreviations: L, length; W, width. Estimated measurements due to breakage of the specimens are given within brackets.

proparaflexid also wears down quickly, to the point that it is already absent in the right hemimandible of the same individual (IPS88860b).

Upper cheek teeth. These include a P4 and a M3. The M3 was reported by Aldana Carrasco (1991, 1992) but was not described, so we describe it here. The occlusal contour is quadrangular, with a straight posterior border. In side view, the molar curves posteriorly. It presents two flattened roots separated by the parastria and hypostria. The anterolabial corner is broken. The paraflexus merges with the hypoflexus, so that the first loph is isolated. The protocone is marked by a small constriction on the posterior wall of the first loph. The mesoflexus curves posteriorly, almost reaching the posterior wall of the molar. The metaflexus is straight, its lingual end facing the posterior end of the mesoflexus. The hypostria reaches the crown basis. The para-, meso- and metastria are equally long and extend to the crown basis. All the striae are infilled with cement, which is thicker near the crown base.

Remarks. The described material can be unambiguously assigned to the genus *Castor* because of its hypsodont cheek teeth with tetralophodont occlusal pattern and abundant cement infilling all striae/iids. It fits the size range of the extant genus *Castor* (see for example Stefen 2009), albeit most of the recovered specimens are relatively small. Mandible morphology of European fossil beavers is rarely described in detail. Here, we show that the mandible of the Campredó-VF specimens is very similar to that of extant *Castor*, except for its somewhat smaller size and the presence of a double mental foramen in one specimen (IPS88860a). Insertion areas for the masticatory muscles are analogous to those of the extant species. Three *Castor* species have been reported from the Pliocene and Pleistocene of Europe: *Castor praefiber* Depéret, 1897, *Castor plicidens* Forsyth Major, 1875, and *Castor fiber*. *Castor plicidens* is known from Early Pleistocene sites of Italy, Germany, and France (Barisone et al. 2006). It is distinguished from *C. fiber* by the frequent occurrence of pronounced secondary enamel folds (plicatures) on the occlusal surface. The taxonomic value of these plicatures is debated because they are known to occur in old *C. fiber* specimens, so various authors consider *C. plicidens* either a junior subjective synonym of *C. fiber* (see Hugueney 2004) or just a subspecies (Barisone et al. 2006), whereas others consider it a distinct species (Cuenca-Bescós et al. 2017). In any case, the studied material does not present enamel plicatures, so affinities with *C. plicidens* can be ruled out. *Castor praefiber* is a debated species too. It generally occurs in older sites than *C. fiber*, dating back to the Pliocene. It is distinguished from *C. fiber* by its smaller size, pronounced roots and striae/striids not reaching the crown base (see Barisone et al. 2006). However, Wessels et al. (2011) argued that *C. praefiber* specimens fit the variation in size and morphology of extant *C. fiber* (see Stefen 2009). We concur with this observation and consider *C. praefiber* a junior subjective synonym of *C. fiber*. Therefore, the oldest records of *C. fiber* in Europe would date back to the Early Pliocene (MN14) of France (Barisone 2004). To date, the oldest occurrence of the genus *Castor* in the Iberian Peninsula is in the Villanyan (MN16) sites of Huélago (Sesé 1989) and Villarroya (Friant 1964). In turn, Cuenca-Bescós et al. (2017) reported the presumed oldest occurrence of the species *Castor fiber* in the Iberian Peninsula from various Lower Pleistocene localities at the Sierra de Atapuerca. In their review of the Iberian record of the genus *Castor*, Cuenca-Bescós et al. (2017) did not mention the record from Campredó-VF, even though Aldana Carrasco (1991, 1992) had already noted that this was the oldest occurrence of *Castor fiber* in the Iberian Peninsula. Indeed, Campredó-VF dates back to

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
m2	Campredó-VF	2	1.98	2.02	2.06	1	–	1.66	–
m3	Campredó-VF	1	–	(1.93)	–	1	–	1.60	–
M2	Campredó-VF	2	1.95	2.00	2.05	2	1.65	1.69	1.72
M3	Campredó-VF	2	1.68	1.75	1.81	2	1.56	1.57	1.58

Tab. 4 - Dental measurements (in mm) of *Apocricetus* cf. *barrierei* from Sant Nofre-Campredó, Early Pliocene, northeastern Spain. Abbreviations: VF, Via Fèrria; N, number of specimens. Estimated measurements due to breakage of the specimens are given within brackets.

the early Ruscinian (MN14, see below) and would not only be the oldest Iberian record of *Castor fiber*, but also of the genus *Castor*. Older citations, such as that of *Castor vidali* Crusafont Pairó, De Villalta & Bataller, 1948 from the lower Vallesian (MN9, Upper Miocene) of Teuleria del Firal (Crusafont et al. 1948), are misidentifications of *Chalicomys jaegeri* Kaup, 1832 (see Casanovas-Vilar & Alba 2011), a common, large-sized beaver species of the European Late Miocene.

Family Cricetidae Fischer, 1817
Subfamily Cricetinae Fischer, 1817
Genus *Apocricetus* Freudenthal, Mein & Martín-Suárez, 1998

Apocricetus* cf. *barrierei (Mein & Michaux, 1970)

Fig. 7J–O

Material: *Campredó-VF*. Two left m2 (IPS126943; labial fragment, IPS126944), one left m3 (IPS126947), two right M2 (IPS20637, IPS126940), and two left M3 (IPS126941, IPS126942). *Sant Nofre*: Two left M3 (lingual fragment, IPS127165; posterior fragment, IPS127171).

Measurements: Tab. 4.

Description of the material from Campredó-VF. *m2*. The anterosinusid is absent. The well-developed labial cingulid reaches the base of the protoconid. There is an anterior metalophulid and an anterior hypolophulid. The mesolophid is absent. The sinusid and mesosinusid are closed by low cingulids. The posterolophid reaches the posterior wall of the entoconid, closing the posterosinusid.

m3. The anterosinusid is absent. The labial cingulid is well developed, reaching the base of the protoconid. There is an anterior metalophulid and an anterior hypolophulid. The small mesolophid reaches the posterior wall of the metaconid. The posterolophid reaches the posterior wall of the entoconid, closing the posterosinusid.

M2. A small lingual anteroloph is present at the base of the crown. There is a well-developed labial anteroloph. This ridge reaches the anterior wall of the paracone in one specimen, thus closing the anterosinus. There is a short posterior protolophule. A very small entoloph is present. The metalophule is anterior and connects to the anterior wall of the metacone. The posteroloph directly merges with the posterior wall of the metacone. The sinus and mesosinus are closed by cingula at the base of the crown.

M3. The labial anteroloph closes the anterosinus. A very small lingual anteroloph is present at the base of the crown. A very small anterior protolophule can be distinguished at the base of the anterosinus. A posterior protolophule is also present in one specimen (IPS126941; Fig. 7N). The metalophule is anterior and connects to the anterior wall of the metacone. The posteroloph is fused to the metacone, therefore closing a small posterosinus. The sinus and mesosinus are closed by cingula at the base of the crown.

Remarks. *Apocricetus* cf. *barrierei* from Campredó-VF is represented only by m2, m3, M2, and M3, lacking m1 and M1. In size, these molars fall within the range of variation of *Apocricetus barrierei* from the site of Baza-1 in the Guadix-Baza Basin (MN14, Andalucia, southern Spain; Piñero et al. 2017a), as well as those of the type locality of Chabrier (MN14, southern France; Mein & Michaux 1970), being smaller than *Apocricetus angustidens* (Depéret, 1890) from Serrat d'en Vaquer and Mont-Helène (MN15, southern France; Freudenthal et al. 1998). They are larger, however, than *Apocricetus alberti* Freudenthal, Mein & Martín Suárez, 1991 from Sifón-61 (MN13, Fortuna Basin, Murcia, east-southern Spain; Piñero & Agustí 2019). They also present a more simplified occlusal pattern than the latter species, with M2 and M3 lacking the anterior protolophule. The morphology of the lower molars (m2 and m3) also falls within the variability observed in the abundant sample from Baza-1, with a small mesolophid being present only in the m3. The two fragments of M3 from Sant Nofre also fit the size of *A. barrierei.*

Apocricetus barrierei is thought to have evolved from the smaller *A. alberti* near the Miocene-Pliocene boundary (Freudenthal et al. 1998). The earliest as-

Tab. 5 - Dental measurements (in mm) of *Occitanomys alcalai* from Sant Nofre-Campredó, Early Pliocene, northeastern Spain. Abbreviations: VF, Via Fèrria; N, number of specimens.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
m1	Campredó-VF	1	–	1.82	–	1	–	1.25	–
m2	Campredó-VF	2	1.31	1.35	1.38	2	1.27	1.29	1.30
m3	Campredó-VF	1	–	1.09	–	1	–	1.04	–
M1	Campredó-VF	–	–	–	–	1	–	1.32	–
M2	Campredó-VF	3	1.28	1.36	1.40	3	1.34	1.37	1.39

semblage clearly attributed to *A. barrierei* comes from Purcal-4, located in the Granada Basin (Andalucia, southern Spain; between 5.3 and 5.2 Ma; Martín-Suárez et al. 1998; García-Alix et al. 2008b). The species of *Apocricetus* are considered to constitute an anagenetic lineage including *A.* aff. *plinii* (Freudenthal, Lacomba & Martín Suárez, 1991)–*A. plinii*–*A. alberti*–*A. barrierei*–*A. angustidens*. This lineage shows an overall trend to size increase coupled with various morphological changes throughout the Late Miocene and Pliocene (MN11–MN16) (Freudental et al. 1998; Mansino et al. 2014).

Family Muridae Illiger, 1811
Subfamily Murinae Illiger, 1811
Genus *Occitanomys* Michaux, 1969

Occitanomys alcalai Adrover, Mein & Moissenet, 1988

Fig. 9A–H

Material: *Campredó-VF*. One left m1 (IPS126932), one right m2 (IPS126907), one left m2 (IPS126901), one right m3 (IPS126914), one left M1 (posterior fragment, IPS126920), two left M2 (IPS126917, IPS126918), and one right M2 (IPS126919).

Measurements: Tab. 5.

Description. *m1*. There is no tma. The nearly symmetrical anteroconid is connected to the metaconid-protoconid pair. A hint of a longitudinal spur is discernible. The labial cingulum is wide, distinctly separated from the protoconid by a valley, and extends to the labial face of the hypoconid. The posterior accessory cuspid (c1) is connected to the hypoconid by a spur. No other accessory cuspids are observed. The reduced posterior heel is very low.

m2. The anterolabial cuspid is large. The longitudinal crest is absent. The oval posterior heel is small and low. The labial cingulum is weak and does not present either c1 or any other accessory labial cuspids.

m3. The protoconid and metaconid are symmetrical. There is no longitudinal crest. The small anterolabial cuspid is low.

M1. Only a posterior portion is preserved. The connection between t6 and t9 is low. The reduced t12 is also low. Both the t4 and t9 are connected to the t8. The t7 is absent.

M2. The t1 is in contact with the anterolingual face of the t5 by a low spur. It is also basally connected to the t4–t5 intersection. The t1bis is present as a double t1 in one molar with minimal wear (IPS126918). In the two remaining specimens, which exhibit more wear, the t1 and t1bis wear to a comma shape. The small t3 may be connected basally to the anteriolabial side of the t5. The t9 is well developed. The t6–t9 connection is low but present. The t12 is absent.

Remarks. The *Occitanomys* sample from Sant Nofre-Campredó includes two species clearly distinguished by size. The small-sized species is more common, being represented by the eight specimens just described. These display distinctive features compared to *Occitanomys hispanicus* (Michaux, 1971), particularly evident in the better development of the t6–t9 connection. Although close in size to *Occitanomys sondaari* Van de Weerd, 1976, the teeth exhibit notable differences, including the presence of t1bis and t6–t9 connections in the upper molars without any isolated t4 or t9, and a well-developed labial cingulum in the m1 (Van de Weerd 1976). *Occitanomys brailloni* Michaux, 1969 can be distinguished from the Campredó-VF specimens by its larger size and better development of longitudinal connections in the lower teeth (Michaux 1969). *Occitanomys adroveri* (Thaler, 1966) is slightly larger and exhibits a higher frequency and better development of longitudinal connections in the lower molars (Van de Weerd 1976). The sample from Campredó-VF shows several diagnostic features consistent with *Occitanomys alcalai*, such as relatively elevated crown height, presence of t1bis, absence of isolated tubercles, well-developed spurs in the upper molars, and symmetrical anteroconid (Adrover et al. 1988). Furthermore, the size falls within the variability range of *O. alcalai* from its type locality, Peralejos-E (MN14, Teruel Basin; Adrover et al.

1988), as well as other localities such as Negratín-1 (MN13, Guadix-Baza Basin; Minwer-Barakat et al. 2009a), Romerales-2C (MN13, Fortuna Basin; Piñero et al. 2018a), Valdecebro-3 (MN13, Teruel Basin; Adrover et al. 1988), La Gloria-4, Celadas-9 (MN14, Teruel Basin; Adrover et al. 1993b), and Purcal-4 (MN14, Granada Basin; García-Alix et al. 2008c). Based on both morphological and biometrical criteria, the specimens from Campredó-VF are attributed to *Occitanomys alcalai*.

Occitanomys alcalai is very common in the Upper Miocene and Lower Pliocene record of the Iberian Peninsula (Van de Weerd 1976; Adrover et al. 1988, 1993b; García-Alix et al. 2008c; Minwer-Barakat et al. 2009a; Mansino et al. 2016, 2017; Piñero & Agustí 2019; Piñero et al. 2023a; among others). The earliest population of this species has been reported in Sifón-1, at about 6.9–6.7 Ma (Fortuna Basin; Piñero & Agustí 2019), whereas its last occurrence is recorded at Gorafe-4, between 4.30 and 4.19 Ma (Guadix-Baza Basin; Martín-Suárez 1988; Piñero et al. 2018b).

Occitanomys brailloni Michaux, 1969

Fig. 9I, J

Material and measurements: *Campredó-VF*. One left M2 (IPS126916) (L = 1.53 mm; W = 1.43 mm). *Sant Nofre*. One right M1 (IPS127167) (L = 2.34 mm; W = 1.59 mm).

Description. *M1*. The t1 is placed posteriorly, and is larger than the t3. The connection between the t1 and t2 is lower than that between the t2 and t3. The t1bis and t2bis are absent. The union between the t5 and t6 is somewhat lower than the union between the t4 and t5. There is no t7. The t6 and t9 are connected, the former being closer to the t9 than to the t3. The t4–t8 connection is basal. There is a small t12.

M2. The oval t1 is larger than the round t3. The former is basally connected to the t5. The t1bis is present as a duplicated t1. The t6–t9 connection is low. The t4 is larger than the t9. The t4 is connected to the t5 but separated from the t8. There is no t12.

Remarks. The stephanodonty observed in these two specimens from Sant Nofre-Campredó is more advanced than in *Apodemus* but less developed than in *Stephanomys* and *Castillomys*. Furthermore, they exhibit typical features of the genus *Occitanomys*: medium size, presence of a posteriorly positioned t1, and a notably inclined t6 that is much closer to the t9 than to the t3 (Michaux 1969; Martín-Suárez & Mein 1991). These specimens are clearly larger than *O. alcalai*, *O. hispanicus*, *O. sondaari*, *O. alcalai*, and *Occitanomys vandami* Suata-Alpaslan, 2009 (see Michaux 1971; Van de Weerd 1976; Adrover et al. 1988; de Giuli 1989; Suata-Alpaslan 2009). The two molars are, however, very close in size to *O. brailloni* from the type locality (MN15, Layna, Castile La Mancha, central Spain; Michaux 1969), Baza-1 (MN14, Guadix-Baza Basin; Piñero et al. 2017a), Sifón-Pista (MN14, Fortuna Basin; Piñero & Agustí 2019), Arquillo 3 (MN15, Teruel Basin; Adrover 1986), Nimes (France; Michaux 1969), and Kardia (MN14, Greece; Van de Weerd 1979). Additionally, they share similarities with the sample from the type locality, including the common presence of a reduced t12 in the M1, small t3 and large t1, and a connection between the t1 and t5 in the M2 (Michaux 1969). Consequently, we attribute these teeth to *Occitanomys brailloni*.

The oldest known record of *O. brailloni* is documented at Sifón-413 (5.3–5.2 Ma). This species has been recognized as a key element in distinguishing between the latest Miocene (MN13) and the earliest Pliocene (MN14) in the continental record of western Europe (Piñero & Agustí 2019). The stratigraphic range of this circum-Mediterranean species extends to the Upper Pliocene (Bachelet 1990; Castillo Ruiz 1990). Sant Nofre-Campredó and Sifón-413 are the only localities in which *O. brailloni* coexists with *O. alcalai* (see Piñero & Agustí 2019).

Genus *Stephanomys* Schaub, 1938

Stephanomys sp.

Fig. 9K, L

Material and measurements: *Campredó-VF*. One poorly preserved left M1 (IPS126924) (L = ca. 2.36 mm; W = 1.65 mm). *Sant Nofre*. One left M1 (posterior fragment, IPS127168) (W = ca. 1.76 mm).

Description. *M1*. The M1 from Campredó-VF is poorly preserved, but a complete stephanodonty can be observed. The posterior crests of t1 and t3 are well developed and connected to the t4–t5 and t5–t6 intersections, respectively. The t4, t5, t6, t9, and t8 are connected by a continuous crest. There is no t7. It is not possible to ascertain whether the t12 is present, as this portion is

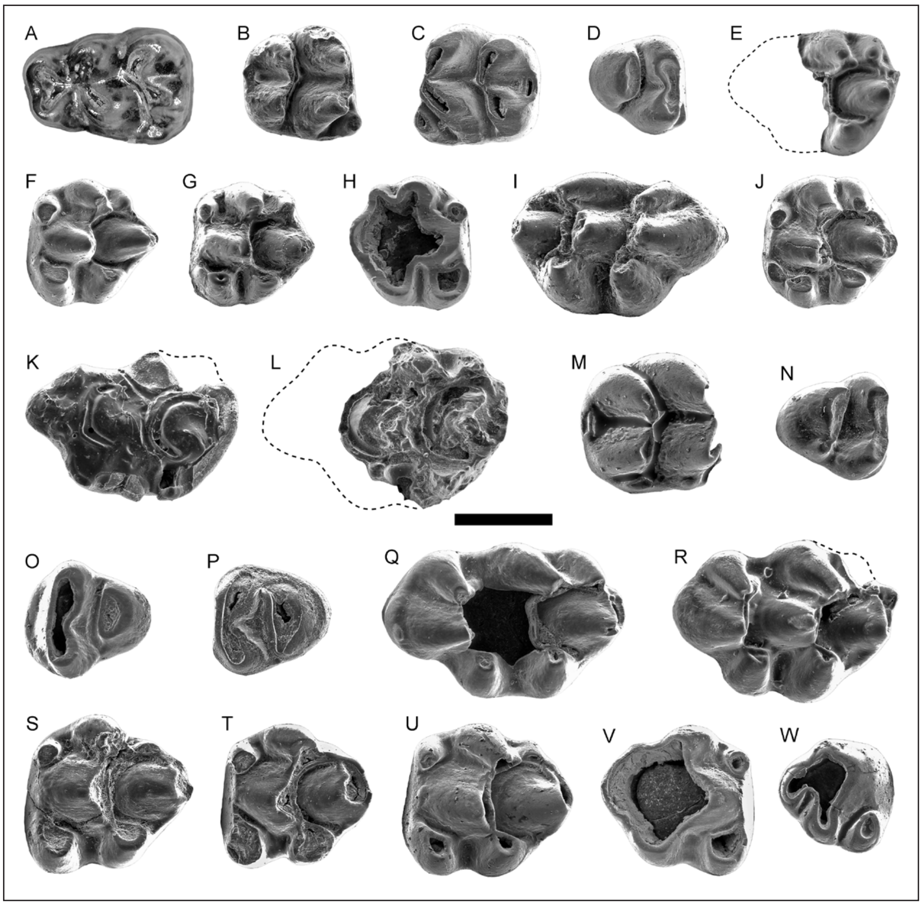

Fig. 9 - Murids from the Lower Pliocene of Sant Nofre-Campredó. A–H - *Occitanomys alcalai*: (A) left m1 (IPS126932); (B) right m2 (IPS126907); (C) left m2 (IPS126901); (D) right m3 (IPS126914); (E) posterior fragment of left M1 (IPS126920); (F) left M2 (IPS126917); (G) left M2 (IPS126918); (H) right M2 (IPS126919). I, J - *Occitanomys brailloni*: (I) right M1 (IPS127167); (J) left M2 (IPS126916). K, L - *Stephanomys* sp.: (K) left M1 (IPS126924); (L) posterior fragment of left M1 (IPS127168). M–W - *Paraethomys baeticus*: (M) anteriorly broken right m2 (IPS126930); (N) right m3 (IPS126936); (O) left m3 (IPS126934); (P) left m3 (IPS126935); (Q) left M1 (IPS20635); (R) left M1 (IPS126926); (S) left M2 (IPS126927); (T) left M2 (IPS126928); (U) left M2 (IPS127157); (V) right M2 (IPS126929); (W) right M3 (IPS20634). The dashed lines represent an approximation of the original (expected) shape of the broken teeth. Scale bar equals 1 mm.

not preserved. However, the posterior fragment of M1 from Sant Nofre preserves a small t12. A high ridge joining the t4, t5, t6, t9, and t8 is also visible. The t4 and t8 are likewise connected by a high crest. The t1, t2, and t3 are missing, but as in the Campredó-VF specimen, a posterior crest connected to the t4–t5 intersection, and another connected to the t5–t6 intersection can be discerned.

Remarks. The studied molars have typical characteristics of the genus *Stephanomys*, including a high crown, and well-developed posterior crests of t1 and t3 in the upper molars. Based on the approximate dimensions of the M1, we can assume that the material from Sant Nofre-Campredó is smaller than the Pliocene species *Stephanomys vandeweerdi* Adrover, 1986*, Stephanomys donnezani* (Depéret, 1890)*, Stephanomys thaleri* López-Martínez, Michaux & Hutterer, 1998, and *Stephanomys calveti* Bachelet & Castillo Ruiz, 1990 (see Gmelig Meyling & Michaux 1973; Cordy 1978; Adrover 1986). Similarly, the studied specimens show a markedly smaller size compared to the Pleistocene species *Stephanomys balcellsi* Gmelig Meyling & Michaux, 1973 and *Stephanomys progressus* Cordy, 1976 (e.g., Bachelet & Castillo Ruiz 1990; Minwer-Barakat et al. 2011; López-García et al. 2024). The dimensions of the studied molars are close to the maximum values of the Miocene species *Stephanomys ramblensis* Van de Weerd, 1976 from Valdecebro-3 (type locality, MN13, Teruel Basin, east-central Spain; Van de Weerd 1976) and *Stephanomys dubari* Aguilar, Michaux, Bachelet, Calvet & Faillat, 1991 from Castelnou 3, a karstic site mixing faunas from MN10 to MN14 (type locality, southern France; Aguilar et al. 1991), and to the minimum values of the Upper Pliocene species *Stephanomys minor* Gmelig Meyling & Michaux, 1973 from Moreda-1A and 1B (MN16, southern Spain; Castillo Ruiz 1990). The two molars also fall within the minimum size range of the Lower Pliocene species *Stephanomys cordii* Ruiz Bustos, 1986 from its type locality, Alcoy (MN14, Alcoi Basin, Valencia, eastern Spain; Cordy 1976). They are somewhat smaller than those of *Stephanomys margaritae* Adrover, 1986 from Aldehuela (type locality, MN15, Teruel Basin, east-central Spain; Adrover 1986). The dimensions of the two M1s therefore show similarities to *S. ramblensis*, *S. dubari*, *S. cordii*, and *S. minor*. A more extensive and well-preserved sample would

Tab. 6 - Dental measurements (in mm) of *Paraethomys baeticus* from Sant Nofre-Campredó, Early Pliocene, northeastern Spain. Abbreviations: VF, Via Fèrria; N, number of specimens. Estimated measurements due to breakage of the specimens are given within brackets.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
m1	Campredó-VF	–	–	–	–	1	–	1.49	–
m2	Campredó-VF	1	–	(1.57)	–	1	–	1.51	–
m3	Campredó-VF	3	1.34	1.35	1.35	3	1.18	1.20	1.21
M1	Campredó-VF	2	2.44	2.53	2.61	2	1.63	1.68	1.73
M2	Campredó-VF	3	1.73	1.79	1.91	3	1.56	1.61	1.67
	Sant Nofre	1	–	1.90	–	1	–	1.64	–
M3	Campredó-VF	1	–	1.31	–	1	–	1.16	–

be necessary for an attribution to species. The absence of additional diagnostic material leads us to leave the studied specimens unassiged to species as *Stephanomys* sp.

The genus *Stephanomys* is a common rodent in the Upper Miocene to Lower Pleistocene faunas of the Iberian Peninsula and France (Van de Weerd 1976; Adrover 1986; Aguilar et al. 1991; Minwer-Barakat et al. 2011; Piñero et al. 2024a; among many others). Minwer-Barakat (2005) proposed the anagenetic evolutionary lineage *S. ramblensis–S. dubari–S. cordii–S. margaritae–S. vandeweerdi–S. donnezani*. Throughout the Late Miocene and Pliocene, there was a continuous increase in size, stephanodonty, and crown height within this lineage.

Paraethomys baeticus Piñero & Verzi, 2020

Fig. 9M–W

Material: *Campredó-VF*. One left m1 (posterior fragment, IPS126931), one anteriorly broken right m2 (IPS126930), one right m3 (IPS126936), two left m3 (IPS126934, IPS126935), two left M1 (IPS20635, IPS126926), two left M2 (IPS126927, IPS126928), one right M2 (IPS126929), and one right M3 (IPS20634).

Sant Nofre. One left M2 (IPS127157).

Measurements: Tab. 6.

Description of the material from Campredó-VF. *m1*. The anterior portion is not preserved. The protoconid and hypoconid are somewhat more posteriorly located with respect to the metaconid and entoconid. The longitudinal spur is absent. The labial cingulum is mostly missing. The large, oval posterior accessory cuspid is connected to the labial face of the hypoconid by a low crest. There is another accessory labial cuspid attached to the protoconid. The medium-sized posterior heel is elongated and displaced lingually.

m2. The anterolabial cuspid is not preserved, but its posterior edge can be observed. The moderate labial cingulum has an elongated posterior accessory cuspid. Another small, round accessory labial cuspid is attached to the protoconid. There is no longitudinal spur. The posterior heel is elongated and displaced lingually.

m3. The anterolabial cuspid is absent. The hypoconid-entoconid pair (posterior complex) is separated from the protoconid-metaconid pair. The labial cingulum is weak or absent. A reduced, round posterior accessory cuspid attached to the labial side of the posterior complex is present in one out of three specimens (IPS126936; Fig. 9N).

M1. The t1 is somewhat displaced backwards with respect to the t3. The union between the t1 and t2 is lower than the union between the t2 and t3. There is a very small distal spur on the t3 directed towards the t5–t6 intersection. The t4–t6, t9, and t8 are connected. The t4–t8 union is very low, while the t6–t9 connection is high. The t7 is absent. The t12 is present, being large in one specimen (IPS126926; Fig. 9R).

M2. The oval t1 is larger than the round t3. There is a small, low posterior spur on the t1 directed towards the t4–t5 intersection. The t3 is isolated. There is an inflated t9 in one specimen (IPS126927; Fig. 9S). In the other well-preserved molar (IPS126928; Fig. 9T), it is reduced to a crest connecting the t6 and t8. The t4 is connected basally to t8. The t12 is absent.

M3. The t1 is large and isolated. There is no t3. The t4–t6, t8 are connected.

Description of the material from Sant Nofre. *M2*. This tooth agrees with the morphology observed in Campredó-VF. The t9 is small but present. There is a low posterior spur on the t1 directed towards the t4–t5 intersection. The t1 is larger than the isolated t3. The union between the t4 and t8 is very low. There is no t12.

Remarks. The specimens found in Sant Nofre-Campredó have the diagnostic traits of the genus *Paraethomys*, including the presence of a t6–t9 connection, reduced or absent t9 in the M2, moderate

Tab. 7 - Dental measurements (in mm) of *Apodemus atavus* from Sant Nofre-Campredó, Early Pliocene, northeastern Spain. Abbreviations: VF, Via Fèrria; N, number of specimens.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
m1	Campredó-VF	3	1.60	1.67	1.71	4	0.94	0.99	1.02
m3	Campredó-VF	1	–	1.17	–	1	–	1.06	–
M1	Campredó-VF	5	1.77	2.00	2.15	5	1.12	1.29	1.43
M2	Campredó-VF	2	1.21	1.30	1.39	2	1.10	1.16	1.22
	Sant Nofre	–	–	–	–	1	–	1.26	–

labial cingulum in the lower molars, and reduced or absent anterolabial cuspids in the m3.

The studied material differs from *Paraethomys meini* (Michaux, 1969) in its larger size, while differing from *Paraethomys abaigari* Adrover, Mein & Moissenet, 1988 and *Paraethomys jaegeri* Montenat & De Bruijn, 1976 in its smaller size and less defined longitudinal spurs (Montenat & Bruijn 1976; Adrover et al. 1988). It is distinguishable from *Paraethomys belmezensis* Castillo Ruiz, 1992 by the presence of a connection between the t6 and t9 in the M1, and larger t3 on the M2 (Castillo Ruiz 1992). *Paraethomys balearicus* Torres-Roig, Piñero, Agustí, Bover & Alcover, 2019 has higher-crowned molars than the specimens from Sant Nofre-Campredó (Torres-Roig et al. 2019). The dimensions of the material from Sant Nofre-Campredó fit the size range of *Paraethomys baeticus* from the type locality, Baza-1 (MN14, Guadix-Baza Basin, Piñero et al. 2017a; Piñero & Verzi 2020). The size is also very close to that of *P. baeticus* from Sifón-Pista (MN14, Fortuna Basin; Piñero & Agustí 2019), Purcal-13 (MN14, Granada Basin, southern Spain; García-Alix et al. 2008c), Celadas-9, La Gloria-4 (MN14, Teruel Basin; Adrover et al. 1993b), Alcoi Barrranc Sud-2, 3 (MN14, Alcoi Basin; Mansino et al. 2015a), La Bullana-2B, 3 (MN14, Cabriel Basin; Mansino et al. 2015b), Gorafe-1, A, and 4 (MN14, Guadix-Baza Basin; De Bruijn 1974; Ruiz Bustos et al. 1984; Martín-Suárez 1988). In addition, the studied individuals show some diagnostic characteristics of this species, such as size intermediate between *Paraethomys meini* and *P. abaigari*, M1 with high t6–t9 and low t4–t8 connections, M2 with posterior spur on the t1 directed towards the t4–t5 intersection, and a moderate labial cingulum with a large posterior accessory cuspid (Piñero & Verzi 2020). All this evidence allows us to ascribe the studied *Paraethomys* specimens to *P. baeticus*. The specimen IPS127157 from Sant Nofre was initially attributed to *Occitanomys* sp. (Agustí et al. 1983; Fig. 9U), but it is reattributed here to *Paraethomys baeticus*.

Paraethomys baeticus from Sant Nofre-Campredó displays some primitive features when compared with other samples of the same species, such as the presence of a well-developed t12 in the M1, a small t9 in the M2, and weak longitudinal spurs in upper and lower molars. This places it among the earliest known populations of *P. baeticus*, along with that from Sifón-Pista (Piñero & Agustí 2019; Piñero & Verzi 2020). *Paraethomys baeticus* is considered to have diverged from the small-sized *P. meini* during the Early Pliocene. Piñero & Verzi (2020) proposed the anagenetic lineage *P. baeticus*–*P. abaigari*–*P. jaegeri*, which is marked by a gradual increase in size and stephanodonty. This lineage evolved in parallel with an essentially conservative *P. meini*. The coexistence of *P. meini* and its descendant lineage can be explained as the result of a cladogenetic speciation event via asymmetric speciation (Piñero & Verzi 2020). This cladogenetic event occurred at ca. 4.6 Ma. The trend towards increasing size underwent a strong acceleration in *P. abaigari* (between around 4.3 and 4.2 Ma), and *P. jaegeri* (between around 4.2 and 3.4 Ma), which may be an adaptive response to the climate cooling and aridity trend occurring in southern Spain after the Pliocene Climatic Optimum (4.35 Ma) and the glaciation at 4.1–4.0 Ma (Piñero et al. 2023b).

Genus *Apodemus* Kaup, 1826

Apodemus atavus Heller, 1936

Fig. 10A–J

Material: *Campredó-VF*. One right m1 (IPS126895), three left m1 (IPS126887; IPS126888; posterior fragment, IPS126889), one right m3 (IPS126915), four right M1 (IPS126870, IPS126871, IPS126872, IPS126938), two left M1 (IPS126865, IPS20638), one right M2 (IPS126884), and one left M2 (IPS20636).

Sant Nofre. One left m2 (IPS127163), and one broken right M2 (IPS127152).

Measurements: Tab. 7.

Description of the material from Campredó-VF. *m1*. There is a large anterocentral cuspid (tma). The protoconid-metaconid pair is connected to the lingual lobe of the anteroconid

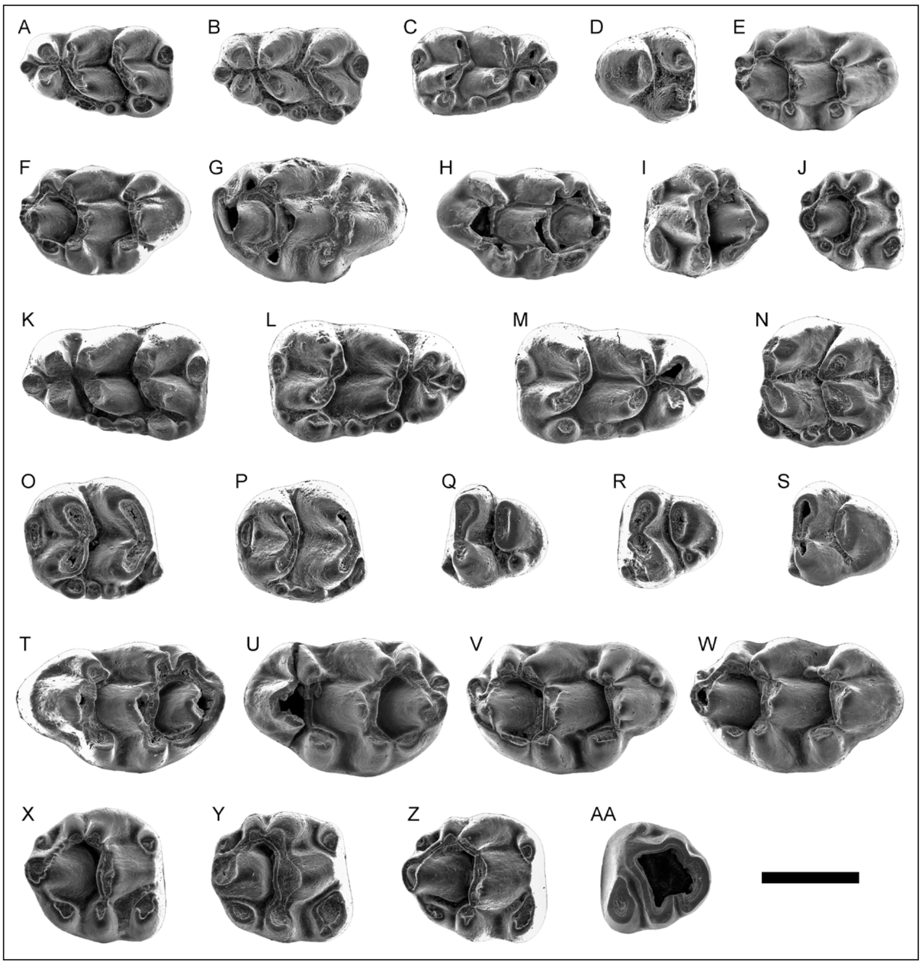

Fig. 10 - *Apodemus* from the Lower Pliocene of Sant Nofre-Campredó. A–J - *Apodemus atavus*: (A) left m1 (IPS126887); (B) left m1 (IPS126888); (C) right m1 (IPS126895); (D) right m3 (IPS126915); (E) right M1 (IPS126870); (F) right M1 (IPS126871); (G) right M1 (IPS126938); (H) left M1 (IPS20638); (I) left M2 (IPS20636); (J) right M2 (IPS126884). K–AA - *Apodemus gorafensis*: (K) left M1 (IPS20639); (L) right m1 (IPS126890); (M) right m1 (IPS126891); (N) left m2 (IPS20632); (O) right m2 (IPS126902); (P) right m2 (IPS126903); (Q) left m3 (IPS126909); (R) left m3 (IPS126910); (S) left m3 (IPS126912); (T) left M1 (IPS126866); (U) left M1 (IPS20633); (V) right M1 (IPS126875); (W) right M1 (IPS126876); (X) right M2 (IPS126880); (Y) right M2 (IPS126882); (Z) right M2 (IPS126883); (AA) left M3 (IPS126922). Scale bar equals 1 mm.

in two specimens (IPS126889, IPS126895), while they are separated in the other two cases. The labial cingulum is well developed. There is a large posterior accessory cuspid (c1), which is in contact with the hypoconid in three out of four specimens. Up to three additional accessory labial cuspids are present. The longitudinal crest is absent. The oval posterior heel is similar in size to the c1.

m3. The anterolabial cuspid is small and low. The hypoconid-entoconid pair is separated from the protoconid-metaconid pair. There is no labial cingulum. The posterior accessory cuspid is absent.

M1. The t1 is in anterior position. It is larger than the t3. There is a weak t1bis in one specimen (IPS126871). A round and low extra cusp between the t2 and t3 is present in one specimen (IPS126870). The t7 is connected basally to the t8. The separation between the t4 and t7 may be deep. The t6 and t9 are connected. There is a well-developed t12, being fairly large in three cases (IPS126865, IPS126870, IPS126938).

M2. The oval t1 is larger than the round t3. Both cusps are isolated. The t7 is connected to the t8. The t4 and t7 are separated. This separation is deep and wide in one out of two specimens (IPS20636). A large t12 is present in one individual (IPS126884). There is a t6–t9 connection.

Description of the material from Sant Nofre. *M2*. The sole M2 of *Apodemus atavus* from Sant Nofre does not preserve its posterolabial portion. The tooth has a deep and wide separation between the t4 and t7. The oval t1 is larger than the round t3, both cusps being isolated. The t7 and t8 are joined.

Remarks. Sant Nofre-Campredó has yielded 70 molars exhibiting the common features of the genus *Apodemus*, including the presence of t7 and the t6–t9 connection in the M1 and M2, a large tma in the m1, and a well-developed labial cingulum and the absence of a longitudinal crest in the m1 and m2. This sample presents two distinguishable groups based on size, with 15 of the specimens being notably smaller when compared to the remaining teeth. These specimens are somewhat smaller than *Apodemus gudrunae* Van de Weerd, 1976, and significantly smaller than *Apodemus jeanteti* Michaux, 1967 and *Apodemus gorafensis* Ruiz Bustos, Sesé, Dabrio, Peña & Padial, 1984 (see Michaux 1967; Pasquier 1974; Ruiz Bustos et al. 1984). Therefore, attribution to these species can be ruled out. Instead, the size of the studied material closely matches that of the samples of *Apodemus atavus* from Csarnóta (type locality; MN15, Hungary; see Van de Weerd 1976), Pedrera del Corral d'en Bruach (Catalonia; López-García et al. 2024), Celadas-9, La Gloria-4, Orrios-3, Arquillo-3, Villalba Alta (MN14–MN15, Teruel Basin; Adrover 1986; Adrover et al. 1993b), Tollo de Chiclana-1B (MN15, Guadix-Baza Basin; Minwer-Barakat et al. 2005), Moreda-1B (MN16; Castillo Ruiz 1990), Dehesa-1 (Granada Basin; García-Alix et al. 2008c), Lo Fournas-13, Balaruc-2, Plà de la Ville, Seynes, Lo Fournas-4, Mas Rambault-2 (southern France; Bachelet 1990), Wèze, Schernfeld (MN15, Poland; Pasquier 1974), Rebielice-Królewskie (MN16, Poland; Pasquier 1974), Tomea Eksi-3, and Komanos-1 (MN15, Ptolemais lignite mines, Greece; Hordijk & De Bruijn 2009), among other sites. In addition, the studied specimens display some typical traits of *A. atavus* as defined by Heller (1936): small size, the protoconid-metaconid pair connected to the lingual lobe of the anteroconid, presence of accessory labial cuspids, a well-developed tma in the m1, and a frequent deep separation between the t4 and the t7 in the M1 and M2. Thus, considering both morphological and biometric criteria, the studied specimens are attributed to *Apodemus atavus*.

Apodemus atavus and *Apodemus dominans* Kretzoi, 1959 are considered to be extreme morphotypes of a single species by some authors, *A. dominans* being a subjective junior synonym of *A. atavus* (Fejfar & Storch 1990; Martín-Suárez & Mein 2004; Minwer-Barakat et al. 2005; García-Alix et al. 2008c; Colombero et al. 2014; López-García et al. 2024). We agree with these authors. The extensive geographic range of *A. atavus* encompasses a significant portion of the Palaearctic region, with documented occurrences ranging from western Europe across Georgia to China (Cai & Qiu 1993; Martín-Suárez & Mein 2004; Knitlová & Horáček 2017; Agustí et al. 2022). The temporal range of this species spans from the latest Miocene to the Early Pleistocene (Rietschel & Storch 1974; Fejfar & Storch 1990; Minwer-Barakat et al. 2005; Sala & Masini 2007; García-Alix et al. 2008c; Colombero et al. 2014). Some authors have considered *A. atavus* to be the direct ancestor of the extant *Apodemus sylvaticus* (Linnaeus, 1758) (see Rietschel & Storch 1974; Fejfar & Storch 1990; Martín-Suárez & Mein 1998; Piñero et al. 2022).

Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña & Padial, 1984

Fig. 10K–AA

Material: *Campredó-VF*. Seven right m1 (IPS126890; IPS126891; IPS126892; IPS126893; IPS126894; labial part broken, IPS126923; anterior and labial parts broken, IPS126925), three left m1 (IPS20639, IPS126885, IPS126886), five right m2 (IPS126902, IPS126903, IPS126904, IPS126905, IPS126906), seven left m2 (IPS20632; IPS126896; IPS126897; IPS126898; IPS126899; posterior part broken, IPS126900; IPS126939), two right m3 (IPS126913, IPS126937), six left m3 (IPS126908, IPS126909, IPS126910, IPS126911, IPS126912, IPS126933), four right M1 (IPS126873, IPS126874, IPS126875, IPS126876), six left M1 (IPS20633; broken, IPS126864; IPS126866; anterior part broken, IPS126867; IPS126868; central part broken, IPS126869), five right M2 (IPS126879, IPS1268780, IPS126881, IPS126882, IPS126883), three left M2 (IPS126877, IPS126878, IPS126921), and one left m3 (central part broken, IPS126922).

Sant Nofre. Two right m1 (IPS127153, IPS127154), three left m2 (anterior fragment, IPS127156; only preserved the external enamel, IPS127163; anterolingual part broken, IPS127170), and two right M1 (anterior part broken, IPS20609; lingual fragment, IPS127151).

Measurements: Tab. 8.

Description. *m1*. The well-developed tma is large and round. The anteroconid is rather symmetrical. The lingual lobe of the anteroconid is in contact with the metaconid, but the enamel is not fused. The protoconid and hypoconid are slightly displaced posteriorly in relation to the metaconid and entoconid, respectively. The well-developed labial cingulum has a large, oval posterior accessory cuspid (c1), which may be isolated or connected to the hypoconid. In addition to the c1, the labial cingulum possesses up to four accessory labial cuspids. The oval posterior heel is comparable in size to the c1. The longitudinal crest is absent.

m2. The large, oval anterolabial cuspid protudes beyond the outline of the tooth. It is basally connected to the anterior face of the protoconid. The labial cingulum is well developed. In addition to the small or medium-sized c1, there are up to three accessory labial cuspids. The large posterior heel is compressed to an oval shape. There is no longitudinal crest.

m3. A round c1 is present in four out of eight specimens. A low, reduced anterolabial cuspid is also present in six specimens. The protoconid and metaconid are either fused or in contact. They are

Tab. 8 - Dental measurements (in mm) of *Apodemus gorafensis* from Sant Nofre-Campredó, Early Pliocene, northeastern Spain. Abbreviations: VF, Via Fèrria; N, number of specimens.

Element	Locality	Length				Width			
		N	Min	Mean	Max.	N	Min.	Mean	Max.
m1	Campredó-VF	9	2.02	2.10	2.25	9	1.17	1.26	1.36
	Sant Nofre	2	2.03	2.12	2.20	2	1.32	1.33	1.33
m2	Campredó-VF	11	1.44	1.51	1.63	12	1.26	1.34	1.41
	Sant Nofre	1	–	1.45	–	3	1.27	1.30	1.33
m3	Campredó-VF	8	1.18	1.28	1.43	8	1.11	1.17	1.27
M1	Campredó-VF	9	2.24	2.34	2.57	10	1.43	1.48	1.57
	Sant Nofre		–	–	–	1	–	1.50	–
M2	Campredó-VF	8	1.48	1.59	1.64	8	1.38	1.43	1.52
M3	Campredó-VF	1	–	1.16	–	1	–	1.12	–

separated from the posterior complex. The longitudinal crest is absent.

M1. The t1 is slightly displaced backwards with respect to the t3. It is not in contact with the t5. The t2–t3 connection is higher than that of t1–t2. There is a small extra cusp between the t2 and t3 in one specimen (IPS126875; Fig. 10V). The t3 has a posterior spur directed towards the t5–t6 intersection. The t6 is the most inclined tubercle and is weakly connected to the t9. The elongated t7 may be in contact with the t4. It is connected to the t8. The t12 is well developed in all but one specimen (IPS126866), and is connected to the t8 but separated from the t9.

M2. The oval t1 is larger than the round, isolated t3. The former has an anterior spur directed towards the posterior side of the t2. The elongated t7 is connected to the t8 by a low crest and separated from the t4 by a medium-deep valley. The connection between the t6 and t9 is weak. There is a low t12 connected to the t8.

M3. The only M3 has a large t1 connected to the t5 by a low crest. The round t3 is very small. The t4, t5, t6, and t8 are connected.

The scarce material from Sant Nofre agrees with the morphology of the Campredó-VF specimens.

Remarks. The large *Apodemus* from Sant Nofre-Campredó is clearly larger than the Miocene species *Apodemus lugdunensis* (Schaub, 1938), *Apodemus barbarae* (Van de Weerd, 1976), and *Apodemus meini* Martín Suárez & Freudenthal, 1993 (Van de Weerd 1976; Martín-Suárez & Freudenthal 1993). Assignment to the Miocene-Pliocene *A. gudrunae* can be discounted because of the larger size of the specimens from Sant Nofre-Campredó (Van de Weerd 1976; Piñero & Agustí 2019). The studied molars are comparable in size to those of *A. jeanteti*, but they are distinguishable from the latter due to the presence of a well-developed tma, the development of a posterior spur in the t3 of the M1, the more posterior position of the t1 compared to the t3 in the M1, and the weaker connection between the t6 and t9 in the M1 and M2 (Michaux 1969; Adrover 1986; Castillo Ruiz 1990). The studied material is also close in size to *Apodemus agustii* Martín-Suárez, 1988. Nevertheless, it does not exhibit the typical characteristics of this species, such as the presence of a funnel in the m1 delimited by the anteroconid, protoconid, and metaconid (Martín-Suárez 1988). The measurenments of the material from Sant Nofre-Campredó are close to *Apodemus gorafensis* from the type locality, Gorafe-A (MN14, Guadix-Baza Basin; Ruiz-Bustos et al. 1984). The specimens are also close in size to *A. gorafensis* from Botardo-D (MN14, Piñero & Agustí 2020) in the Guadix-Baza Basin, La Bullana-2B, and Venta del Moro in the Cabriel Basin (MN13–MN14; Mansino et al. 2015b, 2017), Purcal-4, Purcal-24A, and Cacín-5 in the Granada Basin (MN13–MN14; García-Alix et al. 2008c), and Sifón-3, Sifón-52, and Sifón-61 in the Fortuna Basin (MN13; Piñero & Agustí 2019), among other localities. Additionally, the presence of an elongated t7, a greater inclination of t6 in relation to the other tubercles in the M1 and M2, a posterior spur in the t3 of the M1, a weak connection between the t6 and t9 in the M2, a large tma and posterior accessory cuspid (c1) in the m1, and a well-developed labial cingulum in the m1 and m2 are typical traits of this species. Thus, we attribute the large *Apodemus* specimens from Sant Nofre-Campredó to *Apodemus gorafensis*.

The highly worn specimen IPS126925 was initially identified as belonging to *Rhagapodemus* cf. *hautimagnensis* Mein & Michaux, 1970 by Agustí et al. (1983), whereas the remaining *Apodemus* material from Campredó-VF was attributed to *A.* aff. *jeanteti* in the same publication. Similarly, the specimens from Sant Nofre were originally assigned to *A. jeanteti* (Agustí & Gibert 1985). As stated above, we conclude that these specimens belong to *A. gorafensis*.

Apodemus gorafensis has been identified in many Upper Miocene and Pliocene localities from the Iberian Peninsula (Martín-Suárez 1988; García-Alix et al. 2008c; Mansino et al. 2013, 2015a, 2015b, 2017; Piñero & Agustí 2019, 2020; Piñero et al. 2017a, 2023a; Adrover et al. 1988, 1993b; Opdyke et al. 1997; among others). Piñero & Agustí (2019) reported the oldest occurrence of this murid at Sifón-3 (at about 6.7 Ma). It disappeared alongside other large-sized species, *A. jeanteti*, concurrently with the expansion of arvicolids (Martín-Suárez 1988). Subsequently, only medium- and small-sized *Apodemus* species persisted, a pattern that continues to the present day.

Order **Lagomorpha** Brandt, 1855
Family Prolagidae Gureev, 1962
Genus *Prolagus* Pomel, 1853

Prolagus sp.

Fig. 11

Material and measurements: *Campredó-VF*. One left M1 (IPS126949) (L = 1.24 mm; AA = - mm; PH = 1.88 mm; TH = 0.60 mm), and one left M2 (IPS126950) (L = 1.06 mm; AA = 1.96 mm; PH = 1.74 mm; TH = 0.42 mm). *Sant Nofre*. One left p3 (IPS127160) (L = 1.92 mm; W = 2.12 mm).

Description. *M1-2*. The M1 from Campredó-VF has no fossettes, whereas the M2 has a small, round fossette lying at the labial end of the hypoflexus. As for hypoflexa, in the M1 it is not possible to compare it to the tooth width; in the M2, the hypoflexus appears to have been quite long.

P3. The sole specimen from Sant Nofre is a large, bulky specimen, with quite thick enamel. The anteroconid has a roughly triangular shape and is displaced towards the lingual part of the tooth; it is apparently of the same size as the metaconid, though the fusion of metaconid and entoconid makes this comparison not obvious. The mesoflexid is thus lacking, and in the middle of the metaconid+entoconid area there is a fossette (mesofossette?). The enamel in correspondence to the entoconid is continuous. The centroflexid has a crenulated appearance on its lingual side (=the metaconid labial edge); the most distal of those crenulations should be the crochet, which appears medium-sized and located lingually. The protoconulid is very bulky and long, the protoconid is quite small and its distal end is forms a very thin protoisthmus, resulting in a bottlenecked appearance, whereas the metaisthmus is relatively wide.

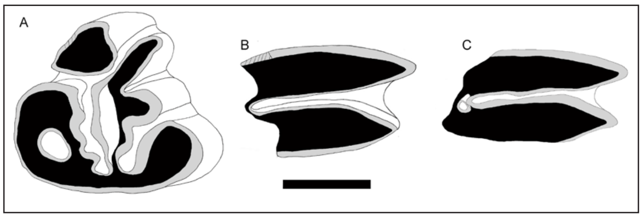

Fig. 11 - *Prolagus* sp. from the Lower Pliocene of Sant Nofre-Campredó. A) left p3 (IPS127160). B) left M1 (IPS126949). C) left M2 (IPS126950). Scale bar equals 1 mm.

Remarks. A specific taxonomic attribution for the fossil remains of Campredó-VF cannot be made with confidence, as the two available specimens are not diagnostic at the species level. It can be stated, however, that they pertain to a relatively derived species of the genus *Prolagus*, due to the fact that fossettes are lacking or very small. A trend noticed in the genus *Prolagus* during the entire Miocene and Pliocene is that fossetes reduce their size and become rarer in younger assemblages. The small size of the sample prevents statistics aimed to estimate the incidence of this trait for taxonomic purposes in the sample. Thus, at present we refrain from a specific determination of the prolagid materials from Campredó-VF, provisionally leaving them in open nomenclature, i.e., as *Prolagus* sp.

The measurenments of the p3 of Sant Nofre fall into the size range of latest Miocene-Pliocene species of westernmost Europe *Prolagus michauxi* López Martínez, 1975 and *Prolagus depereti* López Martínez, 1975. Its size appears greater than in *Prolagus calpensis* Major, 1905, a younger western European species. The morphological study of the p3 from Sant Nofre presents some difficulties due to some unusual features of the specimens, which prevent an accurate specific determination. To such difficulties should be added the taxonomic mayhem of Pliocene *Prolagus* of western Europe (see Angelone & Rook 2012). Nevertheless, some characteristics of the tooth occlusal surface fall in the range of Iberian Miocene-Pliocene samples of *P. michauxi*, such as the shape and size of the anteroconid and its size compared to the metaconid, the bulky protoconulid, the presence of the crochet. For such reasons, a taxonomic attribution of the specimen from Sant Nofre to *Prolagus* cf. *michauxi* may be a

Collection number	Tooth locus	MD	BL(m/d)
IPS100657	R i1	7.8	11.1
IPS100661a	R i2 germ	>7.7	>6.2
IPS100661a	L i2 germ	>7.9	>8.1
IPS100663	R p2? partial germ	>14.8	(9.3)
IPS100656	R m1 germ	20.3	13.1/13.9
IPS100662	R di3? crown	>8.0	5.5
IPS100658	R? dc1	8.0	6.0
IPS100659	R dp2 crown	10.0	4.3
IPS100660	L dp2	10.0	4.4

Tab. 9 - Measurements (in mm) of the suid teeth from Campredó-VF. Those preceded by the 'greater than' symbol denote incomplete preservation, while those within parentheses are estimates. Abbreviations: MD, mesiodistal length; BL, maximum labiolingual/buccolingual breadth; m, mesial lobe; d, distal lobe; R, right; L, left.

sensible choice, pending a revision of the species and hoping for the discovery of additional materials from the studied locality.

Order **Artiodactyla** Owen, 1848
Family Suidae Gray, 1821
Genus *Propotamochoerus* Pilgrim, 1925

Propotamochoerus provincialis (Gervais, 1859)

Fig. 12A, B

Material: *Campredó-VF*. One right i1 (IPS100657), one right and one left i2 (IPS100661a), one right p2? (partial germ, IPS100663), one right m1 (germ, IPS100656), one right di3? crown (IPS100662), one right? dc1 (IPS100658), one right dp2 crown (IPS100659), one left dp2 (IPS100660), and one proximal fragment of lateral metacarpal (IPS100664).

Measurements: See Tab. 9.

Description and remarks. A suid species is represented by nine teeth, which display a typically suine morphology, as well as a proximal fragment of lateral metacarpal. The most informative specimens are the complete i1 (Fig. 12B) and m1 germ (Fig. 12A), which can be readily compared with published measurements. Both teeth are larger than those of *Sus arvernensis* (Croizet & Jobert, 1828) (see Montoya et al. 2006; Pickford 2013; Pickford & Obada 2016), a species that is alternatively included in *Dasychoerus* by some authors (Pickford 2013; Pickford & Obada 2016). Both specimens fit well in size with those of *Propotamochoerus provincialis* from Montpellier, Çobanpinar 1, and Venta del Moro (Morales 1984; Van der Made 2003; Pickford 2013), being thus attributed to the latter species. The m1 germ is slightly longer than those previously reported, probably owing in part to the lack of interproximal wear. An alternative identification of this molar as an m2 would support an alternative assignment to *S. arvernensis*. This anatomical identification would be nevertheless be inconsistent with the large size of the incisor and is at odds with the occlusal contour of the molar, which is narrower on the mesial than on the distal lobe (more typical of m1s than m2s, in which the mesial lobe tends to be as broad or broader than the distal). The distinction between *P. provincialis* and *S. arvernensis*, and by extension the potential overlap of their respective chronostratigraphic ranges, are still controversial. Pickford (2013) revised the suid sample from Montpellier (the type locality of *P. provincialis*, customarily correlated to MN14) and concluded that multiple species of different ages are represented (including not only the two aforementioned ones, but also the younger *Sus strozzi* Forsyth Major, 1881 (not recorded in Europe until about 2.5 Ma; Cherin et al. 2020). Pickford (2013) designated a lectotype of *P. provincialis* to clarify its distinction from *S. arvernensis* and *S. strozzi*, while Pickford & Obada (2016) further considered that *P. provincialis* would be recorded from the Late Miocene (MN11) to the Early Pliocene (MN15), overlapping during the Early Pliocene with *S. arvernensis*. In contrast, Iannucci et al. (2021) argued that there is no conclusive evidence for *P. provincialis* during the Pliocene. In our opinion, the two species must have overlapped at least during the earliest Pliocene, as indicated at least by the size of the specimens from the MN14 of Montpellier and Măluşteni (Pickford 2013; Pickford & Obada 2016; contra Iannucci et al. 2021), and in further agreement with the attribution of the Campredó-VF remains to *P. provincialis*.

Family Bovidae Gray, 1821
Tribe Caprini Gray, 1821
cf. Caprini indet.

Fig. 12C, D

Material and locality: *Campredó-VF*. One right upper molar crown (damaged, IPS88866), fragments of molar (IPS88867), one left talus (IPS100650), and one proximal fragment of metatarsal (IPS100655).

Description and remarks. Bovids are represented by a slightly damaged right upper molar crown (Fig. 12C), fragments of another molar, a left talus (Fig. 12D), and a less informative proximal fragment of metatarsal, which all may be at-

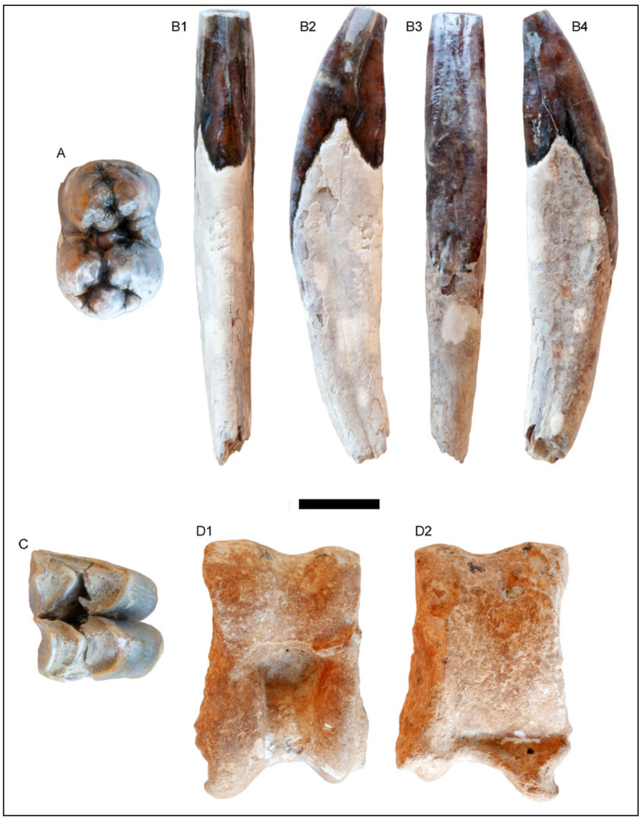

Fig. 12 - Most representative artiodactyl remains from the Lower Pliocene of Sant Nofre-Campredó. A, B - *Propotamochoerus provincialis*: (A) right m1 germ (IPS100656) in occlusal view; (B) right i1 (IPS100657), in lingual (B1), mesial (B2), labial (B3), and distal (B4) views. C, D - cf. Caprini indet.: (C) right M2 (IPS88866), in occlusal, lingual, and buccal views (from left to right); (D) left talus (IPS100650), in dorsal (D1) and plantar (D2) views. Scale bar equals 1 cm.

tributed to a single species. The comparatively long mesial lobe of the complete upper molar suggests that it corresponds to an M2 rather than an M1. In turn, tooth wear appears moderate (given that the anterior fossa is still open), indicating a moderate degree of hypsodonty. Based on overall shape, the specimen may be attributable to either the Antilopini or the Caprini, as both groups are present during the Late Miocene and Early Pliocene in the Iberian Peninsula (Alcalá 1994; Köhler et al. 1995; Alcalá & Morales 1997, 2006; Piñero et al. 2017b, 2023a). The large size of the M2 (L: 16.5 mm; W: 16.8 mm) discounts an attribution to Early Pliocene antilopins such as *Gazella* and *Hispanodorcas* (Alcalá 1994; Alcalá & Morales 2006) and is more similar to that of Late Miocene/Early Pliocene caprins from Europe (*Aragoral* and *Norbertia*; Alcalá 1994; Köhler et al. 1995; Alcalá & Morales 1997). The moderate crown height, the mesial lobe about as wide as the distal (instead of clearly narrower), and other occlusal details (rounded contour of the protocone, unrestricted fossae, and neocrista originating from the postprotocrista) further discount an attribution to the Antilopini. An alternative assignment to *Protoryx*, variously considered to be related to hippotragins and/or caprins (see discussion in Bibi & Güleç 2008), cannot be discounted based on dental size and proportions (see in particular *Protoryx* sp. 1 from the MN14 of La Gloria 4; Alcalá 1994). This is because damage on the buccal crown wall does not allow us to ascertain the development of the mesostyle (particularly well developed in *Protoryx*; Alcalá 1994) in the described specimen. Such an assignment is not supported based on the seemingly lesser hypsodonty of the Campredó-VF M2, which is more broadly consistent in morphology with the caprin *Norbertia*. The latter was originally described from Maramena (MN13–MN14) in Greece (Köhler et al. 1995), but might also be present at the MN14 site (5.0–4.9 Ma) of Puerto de la Cadena (Piñero et al. 2017b). However, more complete dental remains or horn cores would be required to provide an attribution to genus rank for the Campredó-VF material, which we therefore tentatively attribute to cf. Caprini indet.

AGE OF SANT NOFRE-CAMPREDÓ

The high evolutionary rates, rapid diversification, adequate fossil record, and cosmopolitanism of rodents make them an excellent tool for the dating of continental sediments (e.g., Maul et al. 1998; Piñero et al. 2018b). Hence, the chronology of Sant Nofre-Campredó can be estimated based on its rodent content, enabling us to correlate the site with other Iberian localities.

The highly similar faunal content of Sant Nofre and Campredó-VF (see Tab. 1), particularly the common presence of *Paraethomys baeticus*, suggests contemporaneous deposition of the two closely spaced deposits, as observed by Agustí et al. (1983) when correlating both sections. The two levels share most rodent taxa: *Paraethomys baeticus*, *Stephanomys* sp., *Apodemus gorafensis*, *Apodemus atavus*, *Apocricetus* cf. *barrierei*, *Occitanomys brailloni*, and *Muscardinus* cf. *meridionalis*. In addition, the rodent list of Campredó-VF includes *Occitanomys alcalai*, Xerinae indet., and *Castor fiber*.

Apodemus atavus, *Apodemus gorafensis*, and *Occitanomys alcalai* have a wide stratigraphic range, being documented in both Upper Miocene (late Turolian, MN13) and Lower Pliocene (early Ruscinian, MN14) localities (Martín-Suárez 1988; Adrover et al. 1988, 1993b; Mein et al. 1990; García-Alix et al. 2008c; Minwer-Barakat et al. 2009a, 2009b; Mansino et al. 2015a, 2015b, 2016, 2017; Piñero & Agustí 2019, 2020; Piñero et al. 2017a, 2018a, 2023a; among others). The temporal distribution of *Apodemus atavus* even extends up to the Early Pleistocene (e.g., Agustí et al. 2022; López-García et al. 2024). Considering biochronological criteria, however, the occurrence of *Occitanomys brailloni*, *Paraethomys baeticus,* and *Apocricetus barrierei* implies an Early Pliocene age for Sant Nofre-Campredó. *Occitanomys brailloni* has been used to characterize the beginning of the Early Pliocene in the continental record of western Europe (Piñero & Agustí 2019), its chronological range reaching the Late Pliocene (Michaux 1969). *Paraethomys baeticus* and *Apocricetus barrierei* are restricted to sites assigned to the early Ruscinian (MN14, García-Alix et al. 2008b; Piñero & Agustí 2019; Piñero & Verzi 2020; among others). Among them, *Paraethomys baeticus* is the most diagnostic biochronological element, being considered a marker of the later part of the MN14 unit (late early Ruscinian) in the Iberian Peninsula (Piñero & Verzi 2020).

The upper Turolian sites of Negratín-1 in the Guadix-Baza Basin and Purcal-3 in the Granada Basin (between 6.2 and 5.3 Ma; Martín-Suárez et al. 1998; Piñero et al. 2018b) are clearly older than Sant Nofre-Campredó due to the presence of *Apocricetus alberti*, considered the ancestor of *Apocricetus barrierei* (García-Alix et al. 2008d; Minwer-Barakat et al. 2009a).

In the Fortuna Basin, the lowermost Pliocene locality of Sifón-413, dated to 5.3–5.2 Ma (Garcés et al. 2001; Agustí et al. 2006; Piñero & Agustí 2019), shares with Sant Nofre-Campredó the presence of *Occitanomys alcalai*, *Occitanomys brailloni,* and *Apocricetus* cf. *barrierei*. The site of Puerto de la Cadena (Eastern Bethic Range, Murcia, southeastern Spain), dated to 5.0–4.9 Ma, shares with the studied locality the occurrence of *Apocricetus* cf. *barrieri* (Piñero et al. 2017b). The rodent assemblage from Botado-C and D (Guadix-Baza Basin; between 4.8 and 4.6 Ma), like Sant Nofre-Campredó, includes *Apodemus gorafensis* and *Occitanomys alcalai* (Martín-Suárez 1988; Maldonado-Garrido et al. 2017; Piñero & Agustí 2020). In the Granada Basin, Purcal-4 (dated to 5.2–5.3 Ma; Martín-Suárez et al. 1998) has some rodent taxa in common with Sant Nofre-Campredó, such as *Apodemus gorafensis*, *Apodemus* cf. *atavus*, *Occitanomys alcalai*, *Apocricetus barrierei,* and *Muscardinus meridionalis* (García-Alix et al. 2008d). Similarly, in the Teruel Basin, the locality of Perales-jos-E shares with the former site *Apocricetus barrierei*, *Apodemus gorafensis*, *Apodemus atavus,* and *Occitanomys alcalai* (Adrover et al. 1988; Mein et al. 1990). La Piquera, in the Duero Basin, also records *Apocricetus* cf. *barrierei*, *Apodemus gorafensis,* and *Occitanomys alcalai* (Piñero et al. 2023a). The absence of a large-sized *Paraethomys* species (i.e., *P. baeticus*, *P. abaigari*, *P. jaegeri*) in all these early Ruscinian (MN14) sites is a further argument to indicate an older age than the studied locality, however. They were deposited prior to the speciation event that gave rise to *P. baeticus* from *P. meini* (Piñero & Verzi 2020).

Sant Nofre-Campredó is close in age to the localities recording *Paraethomys baeticus*, such as Sifón-Pista in the Fortuna Basin (Piñero & Agustí 2019), La Bullana-2B and 3 in the Cabriel Basin (Mansino et al. 2015b), La Gloria-4 and Celadas-9 in the Teruel Basin (Adrover et al. 1993b), Gorafe-1, A, 4, and Baza-1 in the Guadix-Baza Basin (De Bruijn 1974; Ruiz Bustos et al. 1984; Martín-Suárez 1988; Piñero et al. 2017a), Calicasas-5A and Purcal-13 in the Granada Basin (García-Alix et al. 2008c), and Alcoi Barranc Sud-2, 3, 3A, Alcoi Cristian-0, 0B, and Alcoy-2C, 2D in the Alcoy Basin (Mansino et al. 2013, 2015a). All these sites are within the *Paraethomys baeticus* Zone of the Guadix-Baza Basin, with a chronological span ranging from ca. 4.6 to 4.3 Ma (Piñero et al. 2018b). It is noteworthy that *Paraethomys baeticus* from Sant Nofre-Campredó shows some plesiomorphic features, such as the presence of an inflated t9 in the M2. Taking these data into consideration, the site of Sant Nofre-Campredó would be biochronologically correlated to Sifón-Pista, the site recording the first occurrence of *Paraethomys baeticus* (Piñero & Verzi 2020).

In the Teruel Basin, the lower Ruscinian sites of Villalba Alta Río-1 (at about 4.3–4.2 Ma; Opdyke et al. 1997), La Judería, and Celadas-6 record *Paraethomys abaigari*, considered a descendant of *Paraethomys baeticus* (Adrover et al. 1988; Mein et al. 1990), indicating a somewhat younger age than Sant Nofre-Campredó. Similarly, Sant Nofre-Campredó

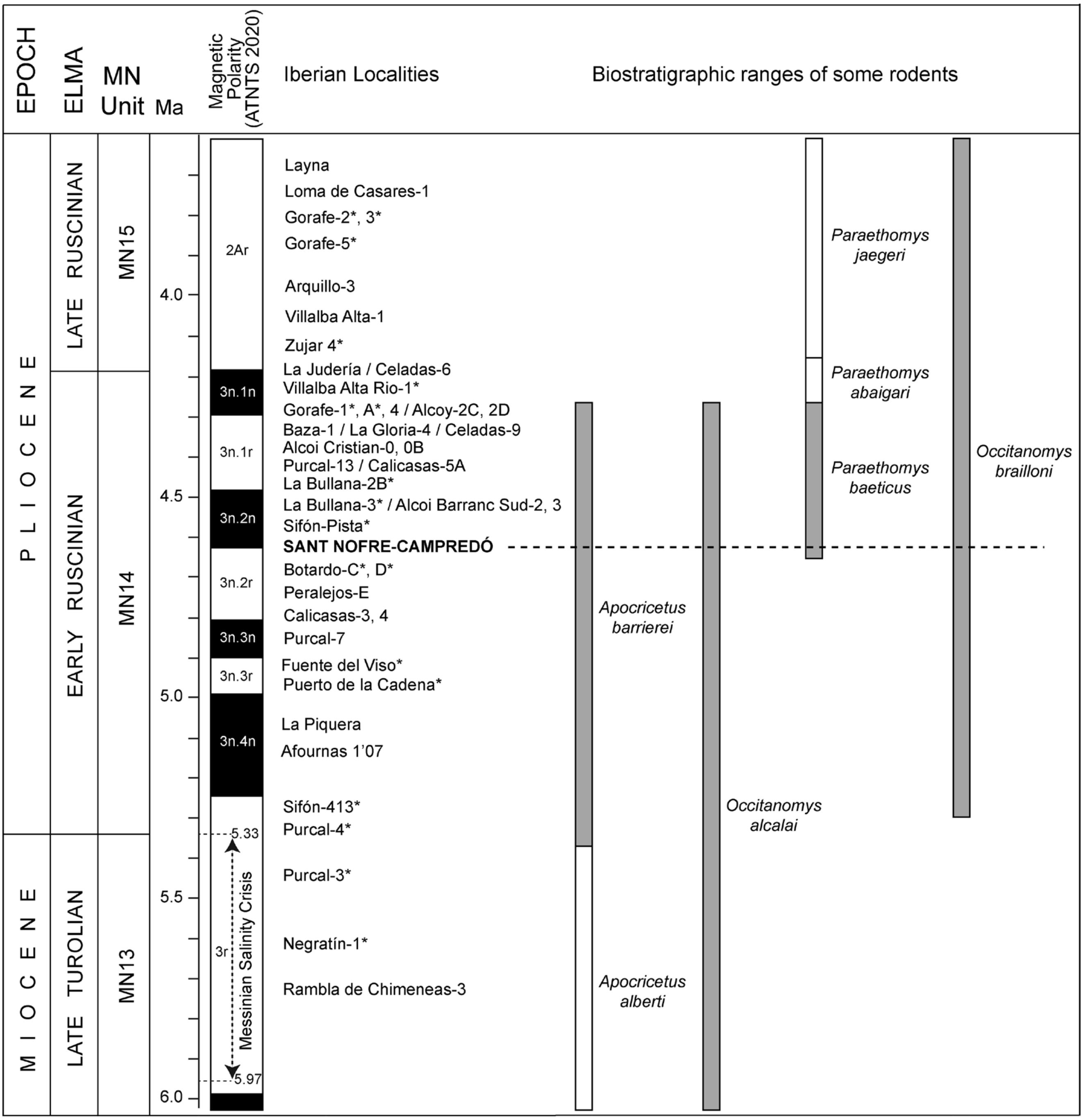

Fig. 13 - Biochronologic correlation of the Sant Nofre-Campredó site and comparison with other Iberian localities. The localities marked with an asterisk are calibrated with paleomagnetic data (Opdyke et al. 1997; Martín-Suárez et al. 1998; Oms et al. 1999; Garcés et al. 2001; Mansino et al. 2015b; Piñero et al. 2017b, 2018b). The position of La Bullana 2B and 3 is after Piñero & Verzi (2020). Abbreviations: ATNTS, Astronomically Tuned Neogene Time Scale (Ogg, 2020); ELMA, European Land Mammal Ages; MN, Mammal Neogene (Agustí et al. 2001; Piñero & Agustí 2019).

predates the late Ruscinian (MN15) sites of Gorafe 2, 3, and 5 from the Guadix-Baza Basin (between 3.9 and 3.3 Ma; Piñero et al. 2018b), which record *Paraethomys jaegeri* (descendant of *P. abaigari*).

The rodent association from Sant Nofre-Campredó thus indicates an early Ruscinian age (later part of the MN14 unit; *Paraethomys baeticus* Zone), and an intermediate age between the levels of Botardo D and Villalba Alta Río-1, being chronologically close to Sifón-Pista (Fig. 13). This new estimate contradicts the Late Pliocene correlation previously proposed, which was based on planktonic foraminifera recovered from the marine deposits beneath the continental levels of Sant Nofre-Campredó (Magné 1978; Martinell & Domènech 1984). The Ruscinian age of Sant Nofre-Campredó was originally proposed after the first rodent studies (Agustí et al. 1983; Agustí & Gibert 1985), so that in subsequent publications the underlying marine deposits were already considered Early Pliocene in age (Martinell 1988; Aguirre et al. 2014).

The chronologic range of *Paraethomys baeticus* can be useful to estimate a numerical age for the site. As noted above, the oldest specimens of *Paraethomys baeticus* are recorded in Sifón-Pista, a level correlated by magnetostratigraphy to 4.6 Ma (Garcés et al. 2001; Agustí et al. 2006; Piñero & Agustí 2019). Its last appearance before *Paraethomys baeticus* evolved into *Paraethomys abaigari* is at Gorafe-1 (Guadix-Baza Basin), a site magnetostratigraphically correlated to 4.3 Ma (Piñero et al. 2018b). Therefore, the age of Sant Nofre-Campredó can be restricted to between ca. 4.6 and 4.3 Ma, and more likely closer to 4.6 Ma based on the presence of plesiomorphic traits in the *Paraethomys baeticus* assemblage (Fig. 13).

Hilgen et al. (2012) placed the transition between MN14 and MN15 at 5.0 Ma. Consequently, following these authors, there appears to be a discrepancy between the numerical age of the studied site and its assignment to MN unit. This apparent incongruity arises from the variability in the timing of appearance of marker species used for biostratigraphic correlation across different regions. Regarding the onset of MN15, this is marked by the appearance of *Mimomys* (Opdyke et al. 1997; Fejfar et al. 1998; Agustí et al. 2001; Hordijk & De Bruijn 2009). However, there is a chronological disparity between the arrival of *Mimomys* in southeastern and southwestern Europe. In Greece, Hordijk & De Bruijn (2009) correlated the shift from MN14 to MN15 to the upper part of chron C3n.3r, at approximately 4.95 Ma, based on the entry of *Mimomys* in the Ptolemais Basin. This age estimate was followed by Hilgen et al. (2012). Conversely, the MN14–MN15 transition occurred significantly later in Spain, where the first occurrence of *Mimomys* is documented at the top of chron C3n.1n, around 4.19 Ma, as indicated by records from the Teruel and Guadix-Baza basins (Opdyke et al. 1997; Oms et al. 1999; Agustí et al. 2001). In this work, we support the latter age calibration for the onset of MN15 due to geographical context.

PALAEOENVIRONMENT

Remarks on Palynology

The marine blue clays of the Sant Nofre section, underlying the vertebrate site (Figs 1, 3), were deposited in a shallow coastal bay, and have yielded an abundant malacofauna (Martinell & Domènech 1984; Aguirre et al. 2014) accompanied by echinoid and decapod remains, ostracods, and foraminifera. In addition, approximately 20 rich pollen samples collected from this part of the section provide a detailed palaeoenvironmental picture (Solé de Porta & Valle 1986; Bessais & Cravatte 1988). These record over 80 different taxa and are overwhelmingly dominated by *Pinus* (pine), which is known to be overrepresented in marine coastal sediments and is generally excluded from analyses (see Fauquette et al. 1999). Amongst arboreal pollen, Taxodioideae (swamp cypresses), *Cedrus* (cedar), Cupressaceae (cypresses and allied), and deciduous *Quercus* (oaks) are abundant, whereas Ulmaceae (elms) are also relatively common. Extant Mediterranean xerophytic taxa, such as *Olea* and *Phillyrea* (olive trees), *Pistacia* (lentisks), and particularly evergreen oaks of the *Quercus ilex-coccifera* type represent a significant component of the pollen assemblage. Herbaceous pollen (Poaceae, Amaranthaceae-Chenopodiaceae, Asteraceae) are well represented in all samples, accounting for 30–40% of the recovered pollen. In addition, some herbaceous taxa characteristic of subdesertic Mediterranean regions such as *Lygeum*, *Nitraria,* and *Calligonum* are also present. Overall, the vegetation of Sant Nofre is very similar to that found in the longer, although approximately time-equivalent, Tarragona E2 section (Bessais & Cravatte 1988; Carrión et al. 2022). Both are characterized by the predominance of herbs, a significant proportion of extant Mediterranean xerophytes, and the occurrence of herbs that grow in very warm and dry conditions. Indeed, the pollen assemblages resemble the modern thermo-Mediterranean formation, so that the environment may have been warmer and more arid than today, likely corresponding to a xerophytic woodland/scrubland (Bessais & Cravatte 1988; Fauquette et al. 1999; Jiménez-Moreno et al. 2010). It is noteworthy that Early Pliocene pollen data from slightly more northern areas of Catalonia (e.g., Garraf 1 and el Papiol, both near Barcelona) show marked differences, with a predominance of arboreal mega-mesothermal elements (*Taxodium*, *Engelhardia,* and others) and rare herbaceous pollen (Bessais & Cravatte 1988; Fauquette et al. 1999; Jiménez-Moreno et al. 2010). This indicates marked precipitation differences between northern and southern Catalonia at the time, which would have corresponded to different vegetation domains (Fauquette et al. 1999; Jiménez-Moreno et al. 2010). This environmental reconstruction seems to be somewhat drier than that provided by the vertebrate fauna recovered from slightly younger deposits in the same section.

Palaeoenvironmental interpretation of the vertebrate site

Vertebrates, and especially small vertebrates, have been widely used as palaeoclimatic and palaeoecological indicators. Amphibian and reptile species are particularly useful for palaeoenvironmental reconstructions (e.g., Blain et al. 2009, 2016; Sánchez-Bandera et al. 2020). Small mammal assemblages also provide interesting information on the past environmental and climatic conditions (e.g., Martín-Suárez et al. 2001; Minwer-Barakat et al. 2005; Montuire et al. 2006; Casanovas-Vilar & Agustí 2007; Furió et al. 2011; Piñero et al. 2016, 2024b). Determination of the ecological requirements of the extinct taxa can be established based on actualism, phylogenetic relationships with extant species, dental ecomorphology, and association with taxa whose ecological requirements are known (e.g., Martín-Suárez et al. 2001; García-Alix et al. 2008e; Gómez-Cano et al. 2013; Piñero et al. 2016). Here, we provide preliminary palaeoenviromental inferences based on the ecological requirements of the vertebrate fauna.

Van Dam (2006) and Van Dam & Utescher (2016) found a positive correlation between the relative diversity of arboreal and insectivorous small mammals (only considering rodents, lagomorphs, and eulipotyphlans) and palaeoprecipitation. In Sant Nofre-Campredó these groups are rare. Arboreal small mammals only include the glirid *Muscardinus* cf. *meridionalis* (see below), whereas insectivores are represented by two teeth belonging to two distinct soricids (*Plioblarinella dubia*, Soricidae indet.) and another tooth belonging to an erinaceid (*Parasorex* sp.). Despite the small sample of eulipotyphlans available, the occurrence of *Plioblarinella dubia* is considered indicative of moist environments.

The rodent fauna from Sant Nofre-Campredó includes the cricetine *Apocricetus* cf. *barrieri*, which is closely related to extant taxa inhabiting steppe environments (*Cricetus*, *Mesocricetus*, *Phodopus*), so that open habitat preferences are generally inferred for this taxon (García-Alix et al. 2008e). Xerinae squirrels, also found at Sant Nofre-Campredó, include both arboreal and terrestrial species, although terrestrial forms are far more common in the Pliocene European record. The single specimen recovered at Sant Nofre-Campredó does not allow for a taxonomic assignment even at the genus rank, but shows greater affinities with xerin ground squirrels such as *Heteroxerus*. Murines, particularly *Apodemus gorafensis*, dominate the rodent assemblage. Unfortunately, the ecological preferences of Pliocene murines are hotly debated. Different methods, ranging from ecomorphology (Van Dam 1997; Renaud & Van Dam 2002; Hernández-Fernández & Peláez-Campomanes 2003; Gómez-Cano et al. 2017), to microwear analysis (Gomes Rodrigues et al. 2013) and continental-marine correlations with known eustatic sea-level and climatic curves (Martín-Suárez et al. 2001), have been used, often yielding conflicting results. Most studies (but see for example García-Alix et al. 2008e) agree in considering that murines inhabiting more arid environments are characterized by broader molars than those inhabiting more forested environments (Van Dam 1997; Renaud et al. 1999; Renaud & Van Dam 2002; Casanovas-Vilar et al. 2011). The stephanodonty (development of crests connecting molar cusps) present in some extinct murines, particularly *Stephanomys* and, to a lesser extent, *Occitanomys*, is also associated with broader molars and has been interpreted as a specialization to consume fibrous vegetal material such as grasses (Van Dam 1997; Renaud & Van Dam 2002; Casanovas-Vilar et al. 2011), which is apparently supported by microwear analyses (Gomes Rodrigues et al. 2013). Therefore, in the Sant Nofre-Campredó assemblage, *Occitanomys alcalai*, *Occitanomys brailloni* and *Stephanomys* sp. would have inhabited relatively open and arid environments, likely grasslands or open woodlands. All these genera account for 10% of the recovered rodent remains, which is a significant proportion, but the assemblage is clearly dominated by *Apodemus gorafensis* (50%). Its molar morphology is markedly different, more generalized, and with narrower and slenderer molars, which are better suited for an omnivorous diet as in extant species of this genus. García-Alix et al. (2008e) inferred that *Apodemus gorafensis* preferred warm and wet environments based on a purported ancestor-descendant relationship with *Apodemus gudrunae*. In contrast, Piñero & Agustí (2020) considered that ecological preferences for this taxon are unknown, further pointing out that it might be an immigrant into the Iberian Peninsula rather than a descendant of *Apodemus gudrunae*.

In Sant Nofre-Campredó, taxa inhabiting humid and/or forested areas include the glirid *Muscardinus*, the castorid *Castor fiber*, and possibly the murines *Paraethomys baeticus* and *Apodemus atavus*, which together account for almost 30% of the rodent sample. The only extant representative of *Muscardinus* is *Muscardinus avellanarius*. It is a nocturnal arboreal species, mainly associated with the presence of hazelnut bushes or trees, occurring in a broad range of wooded habitats (García-Ibaibarriaga et al. 2015). *Muscardinus meridionalis* presents a similar dental morphology with a low molar crown and flat occlusal surface consisting of multiple narrow ridges (for a simple ecomorphological characterization of the cheek teeth of extinct and extant glirids see Van der Meulen & De Bruijn, 1982), so we infer that it presented a similar diet and habitat. Therefore, a similar habitat is assumed for *Muscardinus meridionalis*. The presence of *Castor fiber* unambiguously indicates the existence of permanent freshwater bodies, such as rivers or lakes, surrounded by woodland (Batbold et al. 2021). The ecological preferences of the extinct *Paraethomys baeticus* remain unknown. However, this species clearly dominates the rodent assemblage from Baza-1 (almost 40%) (Piñero et al. 2017a). Based on previous macromammalian dental ecometric analyses, the mean annual precipitation in Baza-1 was estimated at 873 mm, consistent with the dominance of forests (Saarinen et al. 2021). In addition, this species exhibits the morphology typical of a murid that does not inhabit open environments, such as a relatively narrow upper molars and alternate, non-straight lamellae (e.g., Casanovas-Vilar et al. 2011). Consequently, woodlands are the expected habitat for *Paraethomys baeticus*. On the other hand, *Apodemus atavus* is considered by some authors to be a direct ancestor of the living *Apodemus sylvaticus* (Rietschel & Storch 1974; Fejfar & Storch 1990; Martín-Suárez & Mein 1998; Piñero et al. 2022). The latter species prefers areas with rich shrub or tree cover, although its density decreases in homogeneous, densely-forested landscapes, where it prefers marginal areas (Spagnesi & De Marinis 2002). Therefore, it may be assumed that *Apodemus atavus* mainly lived in forest margins.

Taken as a whole, the rodent fauna agrees with the presence of woodland and woodland-margin areas (*Muscardinus*, *Apodemus atavus*, and *Paraethomys baeticus*). Furthermore, the murines *Stephanomys* and *Occitanomys*, the cricetine *Apocricetus* and an indeterminate xerine ground squirrel may be indicative of grassland habitats, which is also supported by the likely occurrence of caprins. The most abundant rodent, *Apodemus gorafensis*, may have been a generalist that was able to thrive in both open and more forested or humid environments. Permanent water bodies also occurred nearby, as indicated by the presence of beavers.

As far as amphibians and reptiles are concerned, despite the open nomenclature of many taxa, interesting paleoclimatic and paleoenvironmental inferences can be made. As a whole, both associations suggest a permanent water area with surrounding wetland forests, under a warm and probably humid climate. Extant *Tylototriton* is today generally found in southeastern Asian forests, where it seeks humid areas with dense vegetation, and extinct *Chelotriton* has been suggested to have had similar habits (Estes 1981). The only extant pleurodeline newt in the Iberian Peninsula is *Pleurodeles waltl*, which tends to dwell in aquatic habitats more than many other European tailed amphibians. It prefers cool, calm, and deep waters and does not show a particular preference for vegetative cover. Similarly, the extant *Latonia nigriventer* is currently found in the marshy environment of the Hula Valley (Israel), where remnants of the swampy Hula Lake are surrounded by swamps, springs, and streams (Biton et al. 2013, 2016; Perl et al. 2017) under Mediterranean climate conditions characterized by hot, dry summers and cool, rainy winters (Biton et al. 2016). The *Latonia*-bearing localities of the Vallès-Penedès Basin are also indicative of warm and humid conditions (see Villa et al. 2019). Indeterminate terrapins (Geoemydidae or Emydidae) may also indicate the presence of freshwater bodies such as rivers or swamps, while the occurrence of a natricid snake (cf. *Natrix* sp.) is certainly indicative of proximity to water-edge environments. More terrestrial taxa are also represented in the assemblages with indeterminate lizards (Lacertidae or Scincidae) and snakes (Colubridae or Psammophiidae), an anguid lizard (cf. *Ophisaurus* sp.), and a spadefoot toad (*Pelobates* sp.). The terrestrial environments typically inhabited by spadefoot toads are characterized by sandy soils, with ponds, seasonal streams, or marshes nearby. Even though it is considered the Iberian amphibian best adapted to arid conditions, the spadefoot toad requires water sources of a certain volume, typically still with a prolonged hydroperiod and containing aquatic vegetation. This is due to the size of its tadpoles and the extended period required for metamorphosis (Lizana 1997). Finally, large anguid lizards are primarily associated with warm and locally humid subtropical environments. A good vegetational cover also appears to be an essential requirement for the genus *Ophisaurus*. The Moroccan Koelliker's glass lizard (*Ophisaurus koellikeri*) lives in evergreen oak (*Quercus ilex* and *Q. suber*) forests (Escoriza & Comas 2015), in the sub-humid bioclimatic zone (Bons & Geniez 1996). Climatically, these forests experience very hot, dry summers, with relatively wet, mild winters.

Overall, the ecological affinities of the identified vertebrates suggest the presence of a landscape dominated by forests in the surroundings of the mouth of the Ebro River approximately 4.6 Ma, with presence of grasslands under humid and warm environmental conditions. Proximity to the ancient Ebro River is attested by the high diversity of semiaquatic freshwater vertebrates. In contrast, the underlying marine deposits that yielded pollen samples seem to suggest a more arid and xerophytic woodland/scrubland. We interpret that the globally lower temperatures that implied sea-level regression, as recorded in the Sant Nofre-Campredó section, favoured the expansion of more humid and forested landscapes by 4.6 Ma.

CONCLUSIONS

The microvertebrate assemblage from Sant Nofre-Campredó is diverse, encompassing up to 22 vertebrate taxa. This identifies it as a key site for the faunas of the Early Pliocene in southwestern Europe. However, large mammals are underrepresented, with only two taxa, possibly due to taphonomic or sampling biases. Amphibians are represented by Pleurodelinae indet., *Latonia* sp., and *Pelobates* sp. Among reptiles, Geoemydidae vel Emydidae indet., Lacertidae vel Scincidae indet., cf. *Ophisaurus* sp., cf. *Natrix* sp., and Colubridae vel Psammophiidae indet. have been identified. The small mammal assemblage comprises Soricinae indet., *Plioblarinella dubia*, *Parasorex* sp., *Stephanomys* sp., *Apodemus gorafensis*, *Apodemus atavus*, *Paraethomys baeticus*, *Occitanomys alcalai*, *Occitanomys brailloni*, *Apocricetus* cf. *barrierei*, Xerinae indet., *Muscardinus* cf. *meridionalis*, and *Prolagus* sp. The large mammal association includes *Castor fiber*, *Propotamochoerus provincialis*, and cf. Caprini indet.

The rodent assemblage indicates an early Ruscinian age, later part of the MN14 unit, at about 4.6 Ma. The ecological requirements of the small mammals and herpetofauna suggest the dominance of forested environments with presence of open grassy areas and permanent water bodies, under warm and humid conditions during the Early Pliocene in the Baix Ebre Basin. According to the Lower Pliocene sedimentological succession of the Baix Ebre, the continental deposits in which the site is located represent the first continentalization of the shallow bay at the mouth of the Ebro River after the Zanclean reflooding at 5.3 Ma.

The Sant Nofre-Campredó assemblage stands out as the most abundant and diversified collection of small vertebrates from the Pliocene documented thus far in the northeast of the Iberian Peninsula, enhancing our understanding of the regional biostratigraphic sequence during the Neogene. The genera *Castor* and *Latonia* extend their known chronological range in the Iberian Peninsula to the Early Pliocene, with their oldest and youngest records identified in Sant Nofre-Campredó, respectively. This site also probably records the earliest Iberian occurrence of the genus *Natrix*.

This study sheds new light on the Lower Pliocene mammal faunas of the northeastern Iberian Peninsula, which have been poorly documented thus far. Continental Pliocene deposits are not that rare in the region, occurring in other major basins such as the Empordà Basin, but have not been sampled or studied in detail. Ongoing work will focus in the characterization of the mammal faunas of this region with particular emphasis on faunal and environmental dynamics.

Author's contributions: The study is based on fieldwork by JA, with the contribution of all co-authors. CLL and AAT contributed to the section of geology. The systematic study of herpetofauna was carried out by HAB, ALM, and RMB; the study of insectivores by MF; the study of rodents by PP, JA, and ICV; the study of lago-

morphs by CA; and the study of artiodactyls by DMA. Biochronological interpretation was developed from discussions by PP, whereas palaeoecological interpretations are based on discussions between ICV, PP, and HAB. The manuscript was prepared by PP with contributions from all co-authors.

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