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Ebusia moralesi n. gen. nov. sp, a new endemic caprine (Bovidae, Mammalia) from the Neogene of Eivissa Island (Balearic Islands, Western Mediterranean): evolutionary implications

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ABSTRACT

We describe the first endemic large mammal from the Neogene of the Island Eivissa (Balearic Islands, Spain), a new genus and species of an endemic insular bovid, *Ebusia* n. gen. *moralesi* n. sp. (Artiodactyla, Caprini). This new taxon is the smallest caprine currently described and shows primitive, continental-like complete dentition. It has a long and complex lower p2 and upper P2 and P3, long premolar series, non-hypsodont incisors and a moderate degree of hypsodonty of the check teeth. The long bones (in particular the tibia) are rather slender, similar to those of continental bovids. However, the metapodials show an intermediate degree of shortening between continental bovids and *Myotragus* species and other insular ruminants. The few derived insular adaptations of *Ebusia* n. gen. suggest that this taxon probably represents the first phase of isolation. The morphology of the dentition and postcranial is characteristic of Caprini and similar to that of the *Myotragus/Nesogoral* group. This suggests that *E. moralesi* would be close to the ancestral continental pattern of the endemic Neogene-Quaternary caprine lineage that colonised the western Mediterranean Islands during the Messinian salinity crisis.

Introduction

The Balearic Islands (Spain) form a small archipelago of continental Islands located in the Western Mediterranean sea, off the coast of the Iberian Peninsula (Figure 1). This archipelago comprises two groups of Islands, the Gymnesics (Mallorca and Menorca) and the Pytiusic Islands (Eivissa and Formentera). A general consensus exists that these Islands were settled by continental taxa, developing into endemic insular taxa, on at least two occasions during the Miocene. The first was in the Middle Miocene (Langhian–Serravalian) (Mein and Adrover 1982; Adrover et al. 1985) and the second during the Messinian salinity crisis at the end of the Miocene (Moyà-Solà et al. 1985; Bover et al. 2007, 2008; Mas et al. 2018). However, our knowledge on Balearic Islands faunal diversity is unbalanced. Although we have an important fossil record from the Gymnesic Islands (Moyà-Solà and Pons-Moyà 1979; Alcover et al. 1985; Agusti and Moyà-Solà 1990; Bover et al. 2007, 2014), the fossil records of the Pytiusic Islands are very scarce, including only those of some small mammals, birds and lower vertebrates (Moyà-Solà et al. 1984; Bover et al. 2008; Torres-Roig 2020).

The oldest episode of Miocene insular fauna has been identified only on the Islands of Mallorca and Menorca. Several lacustrine localities on Mallorca provided evidence of an unbalanced fauna composed of a lagomorph (*Gymnesicolagus gelaberti*) and three glirids (*Carbomys sacaresi, Margaritamys llulli* and *Peridiromys ordinasi*) (Mein and Adrover 1982). The presence of larger mammals is only testified by indeterminable bone fragments. On Menorca Island this episode is represented by one karstic locality containing the lagomorph *Gymnesicolagus* and the glirid *Margaritamys* (as well as other lower vertebrates (Bailón et al. 2002; Quintana and Agustí 2007).

The last episode is more recent and its origin is usually associated with the Messinian salinity crisis (Moyà-Solà et al. 1985; Bover et al. 2007, 2008; Mas et al. 2018). This faunal complex, which is well documented on Mallorca and Menorca, contains the typical Plio-Pleistocene taxa including the bovid *Myotragus*, the dormouse *Hypnomys* and the shrew *Nesiotites* (Alcover et al. 1985; Moyà-Solà et al. 1985; Bover et al. 2008). The fossil record of this faunal complex is well known for the Island of Mallorca (Alcover et al. 1985). From the Late Miocene–Lower Pliocene site of Caló den Rafalino (Bover et al. 2007, 2010, 2008, 2014) and Na Burgessa-1 (Bover et al. 2014) to the Holocene, hundreds of fossil sites covering the Plio-Pleistocene provide an extraordinary and complete fossil record that allows us to follow the evolutionary lineages of the endemic Plio-Pleistocene mammal genera *Myotragus, Hypnomys* and *Nesiotites*. The evidence from the oldest localities of Caló den Rafalino (Bover et al. 2007) and Na Burgessa-1 (Bover et al. 2014) (Late Miocene–Lower Pliocene) shows that the palaeobiodiversity during the first phase of insularity of the Balearic Islands was higher than that recorded for the classical Plio-Pleistocene fauna consisting of only three mammalian taxa. The record of this faunal complex on the Island of Menorca is less complete and seems to begin more recently in the Late Pliocene/Early Pleistocene (Moyà-Solà and Pons-Moyà 1980; Pons-Moya et al. 1981; Bover et al. 2007; Moyà-Solà et al. 2007; Quintana and Agustí 2019). However, the Messinian–Lower Pliocene of Menorca contains a different faunal complex, which is apparently older than the classical fauna including *Myotragus* (Quintana and Agusti 2019). Several localities on this Island yielded a new faunal complex composed of the giant land tortoise *Cheirogaster gymnesica*, the giant rabbit *Nuralagus rex*, the glirid
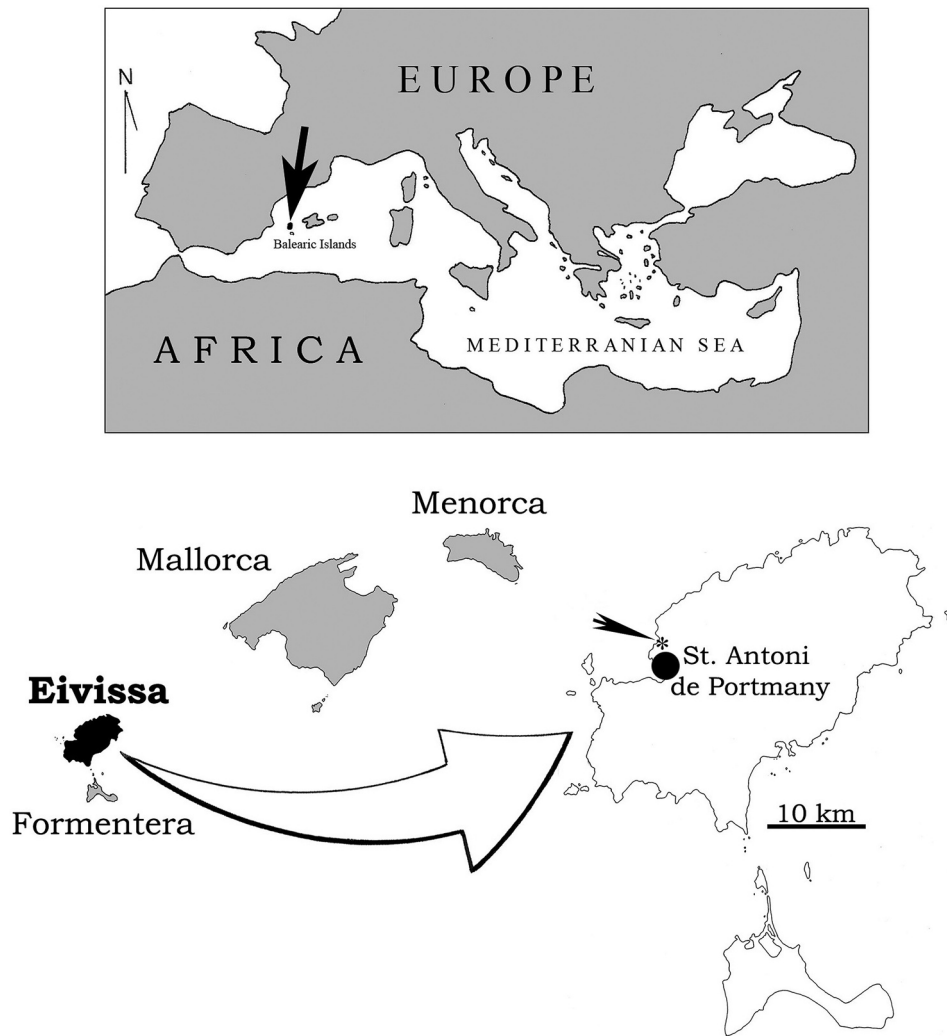
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Figure 1. Location map of the palaeontological site of Ses Fontanelles (Sant Antoni de Portmany, Eivissa, Pytiusic Islands).

Muscardinus cyclopeus and the chiropter *Rhinolophus* cf *grivensis*, as well as some small reptiles (Pons-Moya et al. 1981; Agusti et al. 1982; Quintana 1998, 2006).

In contrast to Mallorca and Menorca, the Eivissa (Pytiusic Islands) Neogene faunal composition is still poorly known. Three different endemic vertebrate faunal associations have been documented there. The oldest faunal complex is represented by the site of Ses Fontanelles (SF; St. Antoni de Portmany, Eivissa). In the preliminary description of the fauna (Moyà-Solà et al. 1984), two bovids, two rodents (a gerbillid, closely related to *Protatera* sp., and a glirid, *Eliomys* sp.), a leporid (*Alilepus* sp.), and some reptiles (a lizard and a tortoise) were recorded. The presence of cf. *Protatera* and cf. *Alilepus* (currently assigned to *Hypolagus*, Quintana et al. 2010; Quintana and Moncunill-Solé 2014) suggested that the age of this site is close to the Late Miocene or Lower Pliocene (Moyà-Solà et al. 1984; Agusti and Moyà-Solà 1990). The bovid material was assigned to two different taxa, the most abundant to a member of Antilopini indet. of small size and, on the basis of the larger size of some postcranial bones and the relatively short metapodials, a possible second taxon was proposed (Moyà-Solà et al. 1984). The second faunal complex, attributed to the Pliocene by some authors (Bover et al. 2007), is represented by a single site, Cova de Ca Na Reia (Santa Eulària des Riu, Moyà-Solà et al. 1984; Alcover and Agustí 1985; Bover et al. 2007). This karst deposit provided remains of two glirids (*Eivissa canariensis* and *Hypnomys* sp.) (Alcover and Agustí 1985),

a tortoise (*Cheirogaster* sp.), a lizard (*Podarcis* sp.), some bats and birds (Moyà-Solà et al. 1984; Bover et al. 2007). A Late Pleistocene vertebrate faunal complex composed exclusively of birds was identified at several fossil sites on Eivissa (Seguí 1998; Seguí and Alcover 1999; McMinn et al. 2005). Recent findings have added new lower vertebrate taxa to this complex (Torres-Roig 2020). In spite of the poor record, the faunal composition of the Pytiusic Islands seems to differ from that of the Balearic Islands, suggesting different biogeographic dynamics (Moyà-Solà et al. 1984, 1999; Bover et al. 2007; Torres-Roig 2020).

In this paper, we describe the bovid material from the SF site (Eivissa, Pytiusic Islands, Spain; Figure 1), which is the only Neogene macromammal fossil discovered on these Islands until now. Detailed analysis of its dental morphology and postcranial bones is presented, and its taxonomic placement is discussed. The new analysis suggests the presence of a single taxon with the basic caprine morphological pattern, close to that of the *Myotragus/Nesogoral* group. Bovidae (Mammalia) are not frequent members of the Plio-Pleistocene faunal assemblages of Mediterranean Islands. Only caprines (Caprini) are present in the fossil record of some Islands in the western Mediterranean, of which several endemic taxa have been described. The genus *Myotragus* is known from the Balearic Islands (Mallorca and Menorca) (Bate 1909; Pons-Moyà 1977; Moyà-Solà and Pons-Moyà 1980); two genera, *Nesogoral* and *Aselotragus* are endemic to Sardinia (Gliozzi and Malatesta 1980; Palombo et al. 2006; Palombo et al. 2013);
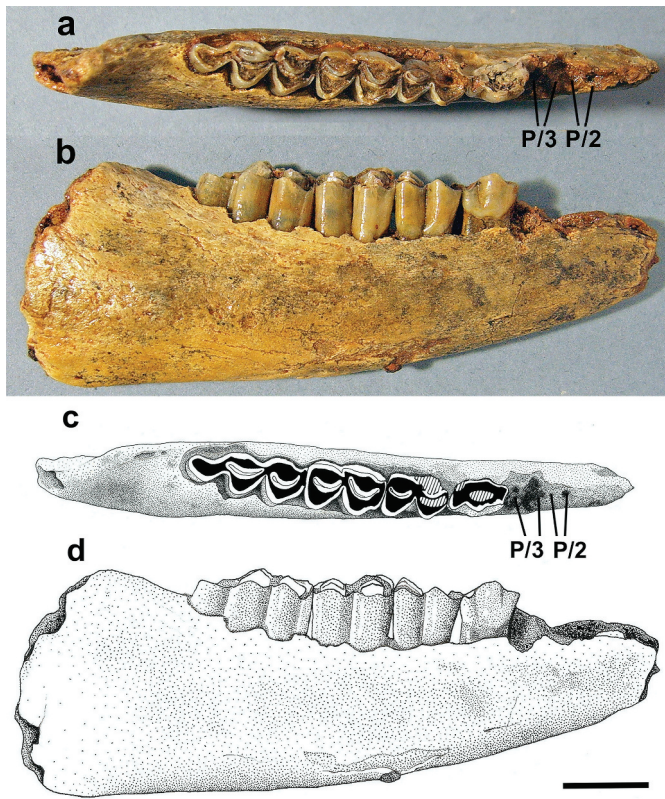
and some bovid remains have been discovered on the Island of Eivissa at the Ses Fontanelles site (Moyà-Solà et al. 1984). The morphological characteristics of the material have allowed the erection of a new genus and species that shares various features with the members of the endemic insular Plio-Pleistocene caprines of the western Mediterranean Islands. We further discuss the phylogenetic implications of these findings.

Material and methods

The studied fossil specimens are curated in two different institutions: the Catalan Institute of Palaeontology M. Crusafont (ICPMC, Sabadell, Barcelona, Spain) and the 'J. Pons' collection, curated at the Institut Mediterrani d'Estudis Avançats (IMEDEA, Esporles, Mallorca, Spain). The comparative material used in this work is curated at the ICPMC. Material from other institutions also has been included in our analysis, in particular the material of endemic bovids from the Miocene sites of Tuscany, curated at the Basel Museum of Natural History, the Museo Nacional de Ciencias Naturales (MNCNM, Madrid, Spain) and the Obussier Collection at the Zoological Museum of Hamburg (Köhler et al. 2008). All measurements are given in millimetres (mm). Dental nomenclature follows Bärmanna and Rössner (2011); lower case indicates lower dentition; upper case indicates upper dentition. The anatomical terminology used in the description of the skeleton sticks to that of Köhler (1993). We follow the bovid classification proposed by Groves and Grubb (2011).

The new names published here are nomenclaturally available according to the requirements of the amended International Code of Zoological Nomenclature, including registration of the work in ZooBank (http://zoobank.org) with the following Life Science Identifier: urn:lsid:zoobank.org:act:CBBC820B-99CE-49D1-AFC5-4F5C6883772E.

The site and its fauna

The locality of SF is situated on the western coast of the Island of Eivissa, on the road to Cala Salada from Sant Antoni de Portmany (Figure 1). The fossil site is a karstic deposit filling a fissure in Mesozoic (Middle–Late Jurassic) limestones that cross the anteriorly mentioned way. The highly calcified breccia containing the fossil bones is a phreatic gallery infilled by fine-grained sediments (sand–lime and microconglomerate) with abundant limonite and other ferruginous minerals. It was dissolved using acetic acid in order to recover the fossil specimens.

In addition to the bovid material described in this paper, the locality of SF has provided fossil material of two rodents, a gerbillid (*Protatera* sp.) and a glirid (*Eliomys* sp.), a leporid (*Hypolagus balearicus*) (Moyà-Solà et al. 1984; Bover et al. 2010; Quintana and Moncunill-Solé 2014) and some fragmentary remains of reptiles, in particular a lizard and a tortoise (Moyà-Solà et al. 1984, 1999). Considering the karstic nature of the deposit, without stratigraphic context and the insular condition of this fauna, it is difficult to establish its age. However, the presence of the gerbillid and *Hypolagus* (Quintana et al. 2010; Quintana and Moncunill-Solé 2014) in the Miocene–Pliocene transition in the continental deposits of the Iberian Peninsula (Agusti and Moyà-Solà 1990; Agustí et al. 2006) suggests a similar age for this insular locality. Some authors consider this fauna to be chronologically close to the oldest post-Messinian faunas of the Mallorca archipelago at the Caló den Rafelino and Na Burgesa-1 (Mallorca) sites (Quintana et al. 2010; Bover et al. 2014; Quintana and Moncunill-Solé 2014) or at the Punta Nati site on Menorca (Pons-Moya et al. 1981; Quintana 2005; Quintana et al. 2005).

Results

Systematic palaeontology

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Family BOVIDAE Gray, 1821
Subfamily CAPRINI Gray, 1821
Ebusia new genus
1984 Antilopini indet. Moyà-Solà et al. p.33
1984 Bovidae indet. Moyà-Solà et al. p.33

Type Species: E. moralesis sp. nov

Diagnosis
A small caprine with primitive, complete dentition as in continental bovids, with c1?; i 03; pP 3/3 and mM 3/3. It shows long and complex lower p2 and upper P2 and P3, long premolar series, non-hypsodont incisors, and a moderate degree of hypsodonty with a reduced size discrepancy between the incisiviform elements. *Ebusia* n. gen. lacks a bicuspid third lobe (absence of entoconulid) and ectostylids; it presents short third lobes in lower m3. Upper molars show simple outlines of central fossettes, a caprine fold in the lower molars and the upper M3, well-developed mesostylids and metastylids, and absence of basal pillars (entostyle) on the molars. The long bones display a low degree of robusticity and there is moderate shortening of the metacarpals and metatarsals. In this respect, *E. moralesi* occupies an intermediate position between the degree of limb gracility of continental bovids and the insular pattern of high robusticity observed in the limb bones of *Myotragus* lineage, with the possible exception of *M. palomboi*.

Etymology: From *Ebusia*, the Roman name of Eivissa (Latinisation of the Punic name Ibosim).

Ebusia moralesis sp. nov

Holotype: Right mandible with m3-m2 series, the labial parts of m1 and p4 and the alveoli of p3 and p2 (IPS-26569), Figure 2(a–d).

Paratypes: Lower dentition: m3 (IPS-26551-10, IPS-26551, IPS-26551-9, IPS-26551, IPS-26551, IPS-26551, IPS-26551, IPS-26551, IPS-26551, IPS-26559, IMEDEA-58296, IMEDEA-58294, IMEDEA-59101); M1-2 (IMEDEA-58285, IPS-26553-1, IPS-26553-2, IPS-26553-3, IPS-26553-4, IPS-26553-5, IPS-26553-6, IPS-26553-7, IPS-26553-8, IPS-58285; p4 (IPS-26559, p3 (IPS-26550); p2 (IPS-26588); IPS-26597-1 I2?, IPS-26597-2 IPS-26597-3 I3? (Figures 3 and 4). Upper dentition: M3 IPS-26595, M1-2 (IPS-26554-5, IPS-26554-4, IPS-26554-3, IPS-26554-2, IPS-26554-1 IPS-26554, IMEDEA-58298, IMEDEA-58299, IMEDEA-58293, IMEDEA-58297), P4 (IPS-26559-1, IPS-26559-2), P3 (IPS-26555), P2 (IPS-26559-3), DP4 (IPS-26596) (Figures 4 and 5). Postcranial: IPS-26679 femur; tibia (IPS-26560, IPS-26551, IPS-26566, IMEDEA58288, IMEDEA58289); metatarsal (IPS-26580, IPS-26561, IPS-26582-1, IPS-26582-2, IPS-26609); cubonavicular (IPS-26679); humerus (IPS-26604, IPS-26577 – 1, IPS-26577 – 2, IPS-26577 – 3, IPS-26567); radius (IPS-26571, IPS-26572, IPS-26564, IPS-26570); metacarpal (IMEDEA58286, IMEDEA58287, IPS-26581, IPS-26561); intermediate phalanx (IPS-26562) (Figures 6–8).

Diagnosis
– The genus is presently monospecific, so the descriptive diagnosis given for the genus also applies to the species.

Type locality: Ses Fontanelles, Sant Antoni de Portmany (Eivissa, Balearic Islands, Spain).

Figure 2. Lower mandible with m3, m2, m1, p4 and the alveolus of p3 and p2 (Holotype, IPS-26559) of Ebusia n.gen. moralesi n. sp. 2a, c: occlusal view; 2b, d: labial view (Graphic scale 1 cm).

Age and distribution: Only known from the type locality (Late Neogene).

Etymology: The species is dedicated to Prof. J. Morales, a great friend, and in recognition to his outstanding contributions to the knowledge of the Neogene faunas of the Iberian Peninsula.

Description and comparisons

Lower dentition

The most complete specimen of *Ebusia* n.gen. *moralesi* n. sp. (Holotype IPS-26559) is a right mandible with m3-m2, m1 and p4 missing some parts and the alveoli of p3 and p2. This specimen allows inference of the molar/premolar length proportions. Continental extant and fossil members of Caprini show two basic patterns in respect of the molar/premolar proportions (Figure 9). There is a group with a longer premolar series in respect to the molars, represented by the Miocene fossil taxa *Norbertia helenica* (Köhler et al. 1995) and *Aragoral mudejar* (Alcalá and Morales 1997), the Villafranquain caprine *Gallogoral meneguini* (Guerin 1965) and the extant Asian taxa *Nemorhaedus* and *Capricornis* (Figure 9). Another group, consisting of extant *Oreamnos* and *Ammotragus* species, and the fossil and extant members of the genus *Hemitragus*, *Capra*, *Ovis* and *Rupicapra* (Figure 9), has shorter premolar rows than the previous group. The western Mediterranean insular caprines show a clear tendency towards short premolar rows. *Nesogoral melonii* from Capo Figari (Sardinia) and the primitive species of *Myotragus* (*M. pepgonellae*, *M. antiquus*) fit well with the last group (Figure 9). Furthermore, more recent *Myotragus* species (*M. kopperi*, *M. batei* and *M. balearicus*) show a progressive tendency towards shortening of the premolar and lengthening of the molar series, with *M. balearicus* losing the p2 and p3 (Moyà-Solà and Pons-
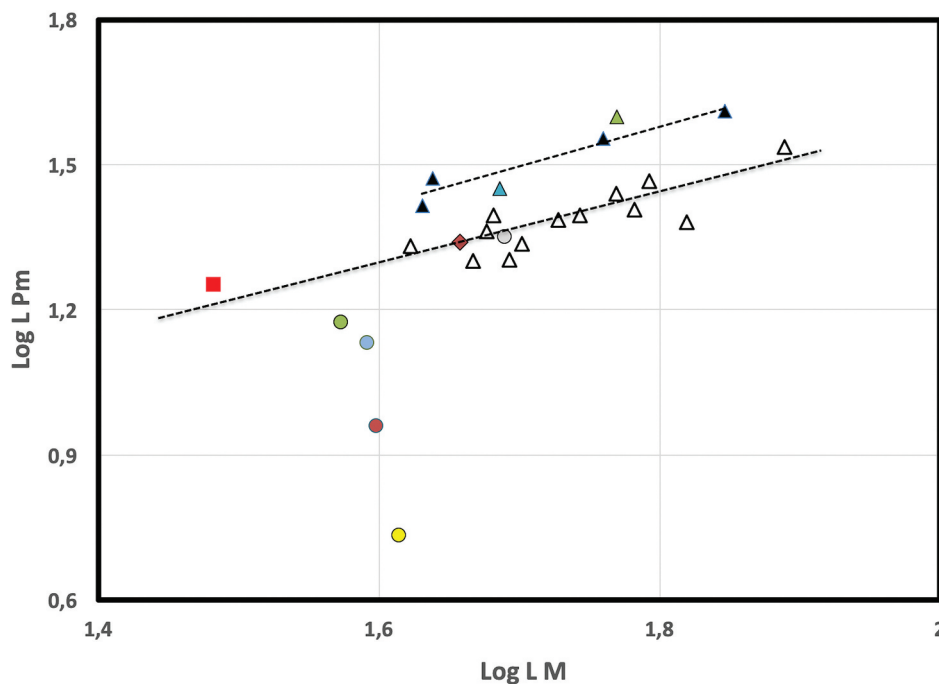
Figure 3. Scatterplot of log-transformed length of the molar and log-transformed length of the premolar row (y) in insular and continental Caprini. Black triangles: includes *Nemorhaedus goral, N. cryspus, Capricornis sumatraensis* and the fossil taxon *Gallogoral meneginii*); green triangles: *Aragoral mudejar*; blue triangles *Norbertia helenica*; empty triangles includes: *Hemitragus jemlaicus, Ovis ammonantiqua* (Pleistocene, Grotte de l'Arago, France), several *Ovis* sps., *Capra hircus, Capra ibex,* Lower Pleistocene Capra alba (Venta Micena, Granada, Spain); brown diamond: *Nesogoral meloni*; red square: *Ebusia* n.gen. *morales*i n.sp.; black triangle: *M. pepgonellae* (Lower Pliocene, Cala Morlanda, Mallorca); green triangle: *M. antiquus* (Lower Pleistocene, Cova des Fum, Mallorca); brown triangle: *M. antiquus* (Lower Pleistocene, Cap Ferrutx, Mallorca); blue triangle: *M. kopperi* (Lower Pleistocene, Pedrera de S'Onix, Mallorca); grey triangle: *M. batei* (LowerPleistocene, Pedrera de Gènova, Mallorca); Orange triangle: *M. balearicus* (Middle-Late Pleistocene several Pleistocene. The temporal trend in reduction of the premolar row teeth number during the evolution of the genus *Myotragus* is clearly observable. Data from Guérin (1965); Rivals (2004); Crégut- Bonnoure (1979); Salari et alli (2014); Pons-Moyà (1977), Moyà-Solà (1987), Moyà-Solà and Pons-Moyà 1980, 1981, 1982), Alcala and Morales (1997), Köhler et al. (1995), Gliozi and Malatesta (1980) and own data.
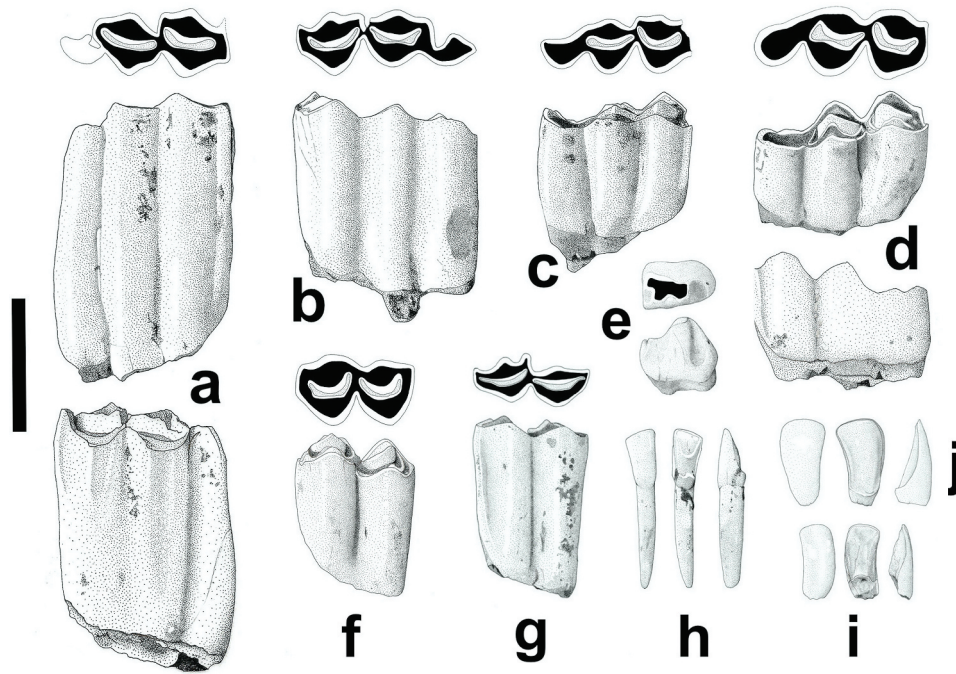
Figure 4. Lower dentition (isolated specimens) of *Ebusia* n.gen. *moralesi* n.sp. a: m3 (IPS-26551-1) in occlusal, labial and lingual views; b: m3 (IPS-26551-2) in occlusal and labial views; c: m3 (IPS-26551-3) in occlusal and labial views; d: m3 (IPS-26594) in occlusal, labial and lingual views; e: p2 (IPS-26588) in occlusal and lingual views; f: (IPS-26553-1) m2 in occlusal and labial views; g: m1 (IPS-26553-2) in occlusal and labial views; h: i1 (IPS-26597-1) in left to right: anterior, posterior and labial views; i: i2 (IPS-26597-2) in left to right: anterior, posterior and labial views; j: i3 (IPS-26597-3) in left to right: anterior, posterior and labial views (Graphic scale 1 cm).
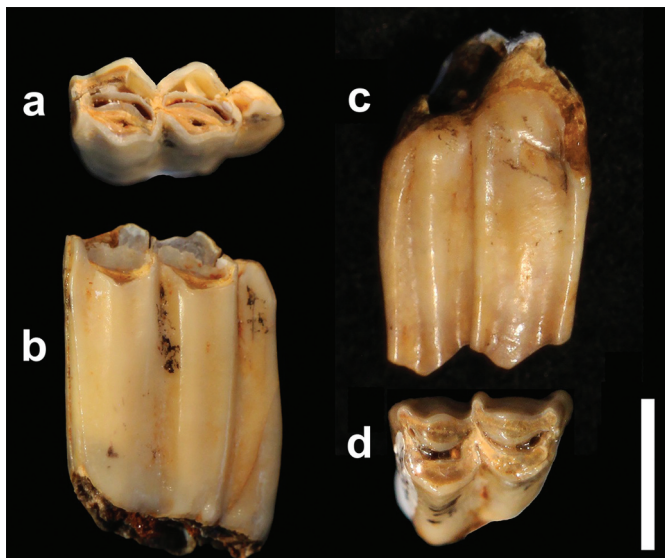
Figure 5. Lower m3 (IPS-26551-1). a: occlusal view, b: Lingual view; Upper M3 (IPS-26595). c: Labial view, d: occlusal view (Graphic scale 1 cm).

Moyà 1982; Moyà-Solà et al. 2007). In contrast, the premolar row of *Ebusia* n.gen. *moralesi* n. sp. is longer than that in any species of *Myotragus* and *Nesogoral*, intermediate between the primitive Miocene Caprini *Aragoral* and *Norbertia*, as well as the extant *Capricornis* and *Nemorhaedus* and the shorter premolars group of extant and fossil continental caprines (Figure 9). In respect of this feature, *Ebusia* n.gen. *moralesi* n. sp. is the most primitive insular caprine of the western Mediterranean.

p2. A single left lower second premolar, with moderate wear, is known (IPS-26588) (Figure 3e; Table 1) and the holotype mandible shows the alveolus of this tooth (Figure 2). The most notable

Table 1. Lower dentition of *Ebusia* n.gen. *moralesi* n. sp. from Ses Fontanelles (Eivissa, Pityusic Islands). 1,2: The tooth has minimal wear and the measure of the crown high, although approximate, it's a good estimation; 3: wear only affect the posterior lobe; 4: the measure of the crown high is approximate. (Measures in mm).

CATALOGUE N°	TEETH	L	W	LPM	LM	H	Notes
IPS-26551-10	m3	13,54	5,54	-	-	21,6	1
IPS-26551	m3	13,89	6,68	-	-	-	
IPS-26551-9	m3	14,70	5,32	-	-	20,0	2
IPS-26551	m3	11,48	4,70	-	-	-	
IPS-26551	m3	14,79	5,06	-	-	-	
IPS-26551	m3	13,12	5,41	-	-	-	
IPS-26551	m3	12,64	5,33	-	-	-	
IPS-26551	m3	14,13	5,68	-	-	-	
IPS-26551	m3	13,80	6,08	-	-	-	
IPS-26559	m3	13,40	5,72	29,9	17,8	-	
IMEDEA-58296	m3	15,65	6,08	-	-	-	
IMEDEA-58294	m3	15,85	6,52	-	-	-	
IMEDEA-59101	m3	12,41	5,41	-	-	-	
IMEDEA-58285	m1-2	9,50	5,70	-	-	18,5	3
IPS-26553-1	m1-2	10,04	4,85	-	-	-	
IPS-26553-2	m1-2	11,09	6,16	-	-	-	
IPS-26553-3	m1-2	8,83	5,37	-	-	-	
IPS-26553-4	m1-2	8,90	5,63	-	-	-	
IPS-26553-5	m1-2	10,06	5,16	-	-	-	
IPS-26553-6	m1-2	9,85	4,84	-	-	-	
IPS-26553-7	m1-2	10,60	6,57	-	-	-	
IPS-26553-8	m1-2	8,80	4,90	-	-	-	
IPS-26559	m1-2	7,70	-	-	-	-	
IPS-58285	m1-2	9,56	6,00	-	-	22	4
IPS-26559	p4	6,50	6,16	-	-	-	
IPS-26550	P3	7,90	6,81	-	-	-	
IPS-26588	p2	5,78	3,32	-	-	-	

characteristic of this specimen is its large size relative to the general size of the dentition, and its elongated shape, with a rectangular outline and a low crwn. The tooth has two roots, apparently partially fused, at least in their upper part. The tooth's morphology is complex. The protoconid is the central and highest cusp; anteriorly there is a clear protoconulid that
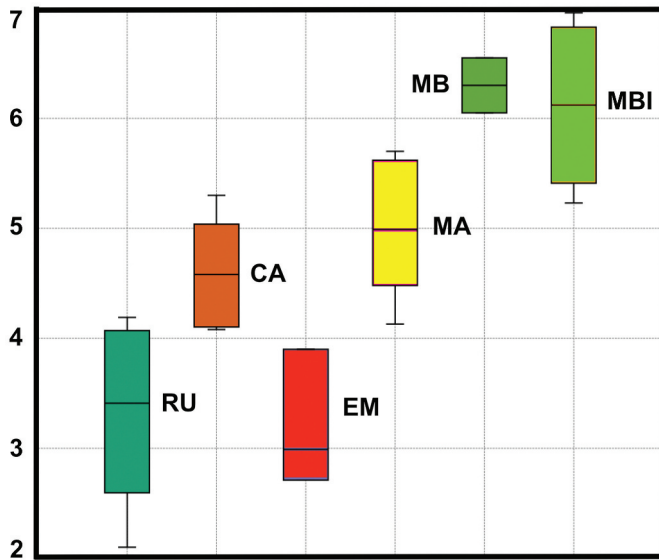
Figure 6. Box-and-whisker plots depicting the index of hypsodonty (We calculated the hypsodont index (IH) dividing M3 height by M3 width; Janis 1988). The height of the crown was measured on the metaconid and only unworn or slightly worn M3were used. Horizontal lines denote the median, boxes the interquartile range (25 -75% quartiles), and whiskers the maximum and minimum values; percentile ranks are computed by linear interpolation between the two nearest ranks. We dividedthe Caprini in two groups, RU containing the taxa previously included in the old tribe Rupicaprini, (*Nemorhaedus goral, Capricornis sumatraensis, Oreamnos americanus, Rupicapra rupicapra, Capricornis crispus, Budorcas taxicolor*) and CA including the rest of the Caprini (*Ammotragus lervia, Capra ibex, Hemitragus jemlahicus, Ovis canadensis, O. dalli, Pseudois nayaur*). EM: *Ebusia* n.gen. *moralesi* n.sp; MA: *Myotragus antiquus* (Cova des Fum, Mallorca); MB: *M. batei* (Genova, Mallorca); MBl: *M. balearicus* (Several Pleistocene localities, Mallorca), (Caprini data are from Janis(1988); *Myotragus* data are from Moyà-Solà and Pons-Moyà (1980, 1981, 1982) and own data.

Figure 7. M3 size scatterplot of log-transformed length (x) and log-transformed width of the lower m3 (y) in *Ebusia* n.gen. *moralesi* n. sp. (Eivissa) and Myotragus species(Mallorca). Red square: *Ebusia* n.gen. *moralesi* n.sp.; empty dot: M. pepgo-nellae (Cala Morlanda, Mallorca), yellow dot: M. antiquus (Cova des Fum, Mallorca); blue dot: *M. antiquus* (Cap Ferrutx, Mallorca), Orange dot: *M. kopperi* (Pedrera de s'Onix, Mallorca); violet dot: *M. batei* (Pedrera de Gènova, Mallorca); grey dot: *M. balearicus* (several Pleistocene sites). Data are from Moyà-Solà and Pons-Moyà (1980, 1981, 1982) and own data.

is connected to the protoconid by means of a preprotocristid that curves anteriorly. An anterior valley is clearly visible between the protoconid and the protoconulid in the lingual part. A clear talon is also well developed in the posterior part of the tooth. A entoconid is clearly present, separated by an anterior and a posterior valley.

This pattern strongly contrasts with the p2 morphology of the oldest *Myotragus* species. *M. palomboi, M. pepgonellae* and *M. antiquus* show more reduced lower second premolars, especially the latter taxon. The p2 of *M. palomboi* has a higher crown with a reduced anterior part, without a clear individualised protoconulid, and also shows a reduced posterior region, without an individualised entoconid and medial and posterior valleys. The outline is subtriangular, but this taxon possesses two roots that are fused proximally (Bover et al. 2010). *M. pepgonellae* also have a p2, but this is only known from the single alveolus present in specimen JPC 10 (Moyà-Solà and Pons-Moyà 1982). Despite the doubt expressed by Bover et al. (2010) that the anterior alveolus present in front of the p3 belongs to a p2, suggesting that it could belong to

Figure 8. Upper dentition of Ebusia n.gen. moralesi n.sp. From down to top, lingual,occlusal and in a and b, lingual views. a: P2 (IPS-26559-3); b: P4 (IPS-26559-2); c: P3(IPS-26555); d: M1-2 (IPS-26554-2); e: M3 (IPS-26595) (Graphic scale 1 cm).

preserved lacking some parts, the modern caprine molariform p4 is observable, with the anterior, medial and posterior valleys closed (Figure 2).

Lower molars. Apart from the holotype lower mandible that has the three molars, ten isolated m3 and 13 m1-2 are known. The lower molars are moderately hypsodont and narrow, with caprine folds and well-developed mesostylids and metastylids, and lack basal pillars. The mandibular ramus is slightly higher below the m3, but it does not show the strong increase in height observed in *Myotragus*, especially the most recent forms such as *M. balearicus*. Thirteen lower m3 specimens have been recovered, showing different degrees of wear (Figure 3(a–d); Figure 4(a,b); Table 1). Three of these indicate no or only slight wear, allowing calculation of the hypsodonty index. Following Janis (1988), we calculated the hypsodonty index (IH) by dividing m3 height by m3 width (Janis 1988). The alternative use of the length would be misleading, considering that in certain taxa (as is the case in *Myotragus balearicus*) the length of the last molar is also increased, a fact that may distort the real index of hypsodonty in these taxa (Janis 1988). The degree of hypsodonty in *Ebusia* n.gen. *moralesi* n. sp. is similar to that of extant rupicaprines (Figure 10), the group of caprines that have relatively low-crowned teeth compared with extant and fossil Caprini (Figure 10).

Figure 9. Bones of the forelimb of Ebusia n.gen. moralesi n.sp. a: Left distal half ofthe humerus (IPS-26577) in anterior view; b: distal part of the humerus ofM. balearicus; c: metacarpal IPS 26561 in anterior view and the section at themidshaft; Intermediate phalanx (IPS-26562) in d: lateral, e: anterior, f: posterior, g:distal, h: proximal views. i: Distal part of the metacarpal (IPS-26581) in posteriorview; j: metacarpal (IMEDEA 58286) in anterior view (Graphic scale 1 cm).

a milk p2. However, the fact that the m3, the p3 and the p4 are completely erupted and show significant wear, rules out this possibility. A similar situation can be observed in *M. antiquus* (Pons-Moyà 1977). This species shows a single-rooted, high-crowned p2 that is short and subtriangular in outline, with a single cusp (protoconid) in non-worn specimens. Indeed, the p2 of *Ebusia* n.gen. *moralesi* n. sp. is more similar in shape to that in continental primitive caprines than in insular ones. The continental Miocene caprines *Aragoral* and *Norbertia* (Köhler et al. 1995; Alcalá and Morales 2007) exhibit a long, low-crowned and morphologically complex p2, more similar to that of *Ebusia* n.gen. *moralesi* n. sp. In this respect, the p2 of *Ebusia* n.gen. *moralesi* n. sp. is similar in shape and complexity to the homologous tooth of *Nesogoral* sp. from the Lower Pliocene site of Capu Manu (Sardinia) (van der Made 1999). However, it is worth noting that the p2 from SF is more brachyodont than the specimen from Capu Manu (van der Made 1999); (Figure 3e).

p3-p4. Only the alveolus of the p3 is visible on the IPS-26559 holotype specimen (Figure 2; Table 1). Only the p4 of the holotype specimen is known. In spite that the lingual wall is not well
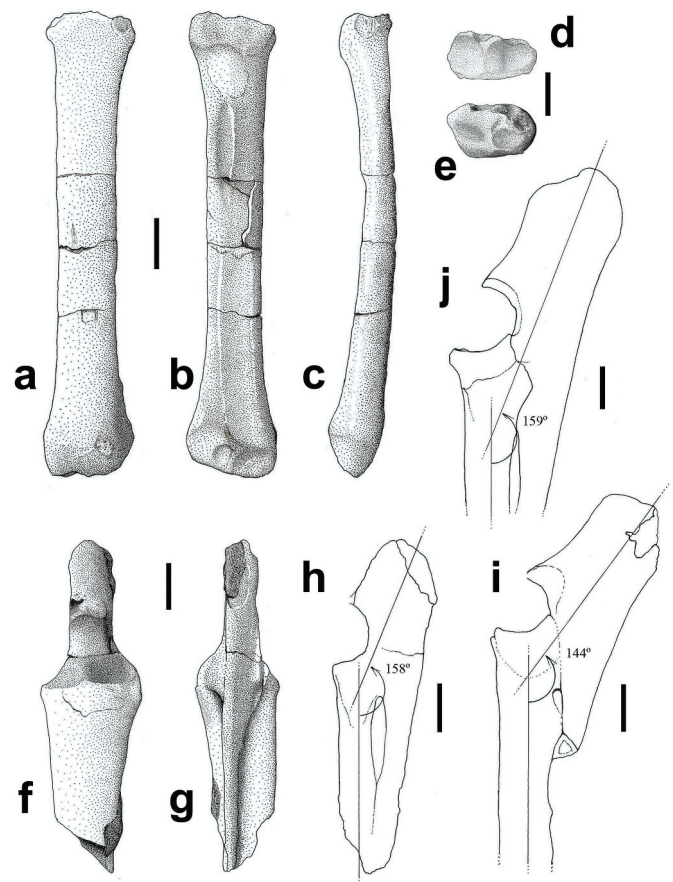

Figure 10. Radius-ulna of *Ebusia* n.gen. *moralesi* n.sp. Left radius (IPS-26571) in a: anterior, b: posterior and c: lateral views; d: proximal view of the proximal epiphysis: distal view of the distal epiphysis; proximal half of left radio-ulna (IPS-26572) f: anterior, g: posterior views. Lateral view of the radius-ulna of h: *Ebusia* n.gen. *moralesi* n.sp., i: *Myotragus balearicus*, j: *Ovis aries* showing the degree of inclination of the ulna over the radius axis (Graphic scale 1 cm).

The m3 of *Ebusia* n. gen. is small (Figure 11) and shows the typical caprine pattern. A clear caprine fold is observable on the labial aspect of the preprotocristid and is visible along the height of the crown, but it is not strongly developed, particularly at the base of the crown (Figure 3; Table 1). Strong mesostylids, metastylids and entostylids are present in the lingual wall that become less marked towards the base of the crown. The metaconid and the entoconid are also marked on the upper part of the crown. Ectostylids are absent at the base of the crown. In specimens with significant wear, the lingual wall becomes smoother. The m1-2 specimens show the same general pattern as the m3. Considering the size of the m3 (Figure 11), *Ebusia* n. gen. is clearly smaller than in all *Myotragus* species. The length/width ratio of the lower m3 of *Ebusia* n. gen. is close to that of the more primitive species of *Myotragus*, such as *M. pepgoneallae, M. antiquus* and *M. kopperi*, but the more recent *Myotragus* species (*M. batei* and *M. balearicus*) show longer m3 in respect to its width (Figure 11).

Incisiviform teeth. Three isolated lower incisiviform teeth have been recovered from the SF site (IPS-26597-1; IPS-26597-2; IPS-26597-3) (Figure 3(h–j); Table 2). Caprine, and bovid deciduous (primary) incisiviform teeth (canines and incisors) in general, are smaller, shorter and wider than their adult (secondary) counterparts. Considering this, the three teeth found at the SF site are of the secondary dentition. The IPS-26597-1 specimen is probably a left crown of an I1 with the root broken and without wear. It is moderately spatulate (crown length: 7,6; width: 4,2) and shows the distal continuous cingulum as a prolongation of the medial and lateral margins of the tooth. The posterior half shows a clear central elevation on the occlusal surface. The IPS-26597-2 specimen is narrower and slightly more elongated than the IPS-26597-1 specimen, and probably is an I3. It shows moderate wear in the apical region and lacks the proximal part of the crown (the cingulum region) and the root. IPS-26597-3 is a right specimen with preserved crown and root, showing significant wear. In spite of this, the crown is moderately wide in the apical zone, a fact that suggests this specimen could be an I2. It also shows a well-developed cingulum on the posterior occlusal surface. The root is straight and the crown deviation from the root edge is low. All specimens are brachyodont and minimally elongated, a pattern they share with the primitive bovids. In this respect, *Ebusia* n.gen. is more similar to primitive rupicaprines like *Naemorhedus crispus* (Natsume et al. 2004) than to the members of the Caprini, *Ovis* or *Capra*, that show more elongated incisiviform teeth. Obviously, the brachyodont pattern of the incisiviform dentition of *Ebusia* n.gen. *moralesi* n. sp. strongly contrasts with the tendency to increase in hypsodonty and the subsequent reduction in number of the incisors and canines during the evolution of *Myotragus* (Moyà-Solà and Pons-Moyà 1980, 1981; Moyà-Solà et al. 2007). This pattern of increasing hypsodonty can be observed in the most primitive species of *Myotragus*, such as *M. palomboi* (Bover et al. 2010).

Upper dentition

All the upper dental specimens recovered from SF are isolated specimens (Figure 5), a fact that makes it difficult to discriminate between M1 and M2. For this reason, these molars will be described together. *Ebusia* n.gen. shows the primitive condition of Bovidae having three premolars, with a single lobed P4, an elongated P3 and a more elongated, bilobulated P2.

P2. One single specimen (IPS-265599-3) (Figure 5a; Table 3), from the right side, is known. It shows a low degree of wear and lacks the lingual enamel, but the dentine is well preserved and the general shape is perfectly visible. This specimen is characterised by its mesiodistal elongation and relative narrowness (length: 7.20; width: 6.20), being longer than broad (Table 3). Two lobes, clearly separated by an indentation, are visible, separating the protocone from the hypocone; in occlusal view, and thanks to the small wear, it is possible to observe the presence of two separate fossae in the central region of the tooth – one deeper, located in the mesial part, labial to the protocone, and another, located in the distal part, labial to the hypocone. Both are separated by an irregular ridge. The crown is not particularly high, in spite of the low degree of wear. The labial wall is long. The paracone and metacone are widely separated by a wide and well-marked vertical groove, mesial to the paracone. A strong parastyle is placed well anteriorly to the paracone and separated from it by a deep vertical groove, a pattern that gives this P2 its elongated shape.

This tooth strongly differs from that of *Myotragus*, especially in its relatively low crown, bilobed, long and narrow shape, and the elongated and well-defined anterior part, where the parastyle and a long preparacrista conforms an anterior mesial projection of the tooth. In fact, in the oldest species of *Myotragus* (*M. palomboi, M. pepgonella, M. antiquus* and *M. batei*) that still have P2, it is a much more reduced tooth, with a single lobe, lacking the anterior one. Only remnants of a small parastyle placed close to the paracones can be observed in some specimens of the oldest taxa (*M. palomboi; M. pepgonella*). In fact, all species of *Myotragus*, as well as recent continental Caprini such as *Ovis* and *Capra*, have occlusal dimensions that are wider than long (ratio length/width < 1) (Bover et al. 2010). *Myotragus* and recent Caprini species also show higher crowns than the SF specimen. Accordingly, the general shape of the IPS-26598 looks primitive for Bovidae, being elongated and relatively narrow, bilobed, not very high crowned and with an anterior projecting preparacrista and

Table 2. Upper dentition of *Ebusia* n.gen. *moralesi* n. sp. from Ses Fontanelles (Eivissa, Pityusic Islands). 1: The tooth has minimal wear and the measure of the crown high, although approximate, it's a good estimation; 2: No wear; 3: No wear. (Measures in mm).

CATALOGUE N°	TEETH	L	W	H	Notes
IPS-26595	M3	9,74	5,94	13,02	1
IPS-26554-5	M1-2	8,93	6,50	-	
IPS-26554-4	M1-2	9,09	7,06	-	
IPS-26554-3	M1-2	9,89	6,67	-	
IPS-26554-2	M1-2	*10,52*	*8,13*	-	
IPS-26554-1	M1-2	10,25	6,75	16,1	2
IPS-26554	M1-2	9,05	6,82	-	
IMEDEA-58298	M1-2	12,15	6,40	19,6	3
IMEDEA-58299	M	9,60	8,20	-	
IMEDEA-58293	M(M3)?	11,49	8,45	-	
IMEDEA-58297	M	10,44	7,78	-	
IPS-26559-1	P4	6,96	5,90	-	
IPS-26559-2	P4	6,50	7,16	-	
IPS-26555	P3	8,55	7,70	-	
IPS-26559-3	P2	7,20	6,20	-	
IPS-26596	DP4	9,53	5,80	-	

Table 3. Incisiviform teeth of *Ebusia* n.gen. *moralesi* n. sp. from Ses Fontanelles (Eivissa, Pityusic Islands). 1: No wear; 2: moderate wear; 3: No wear. (Measures in mm).

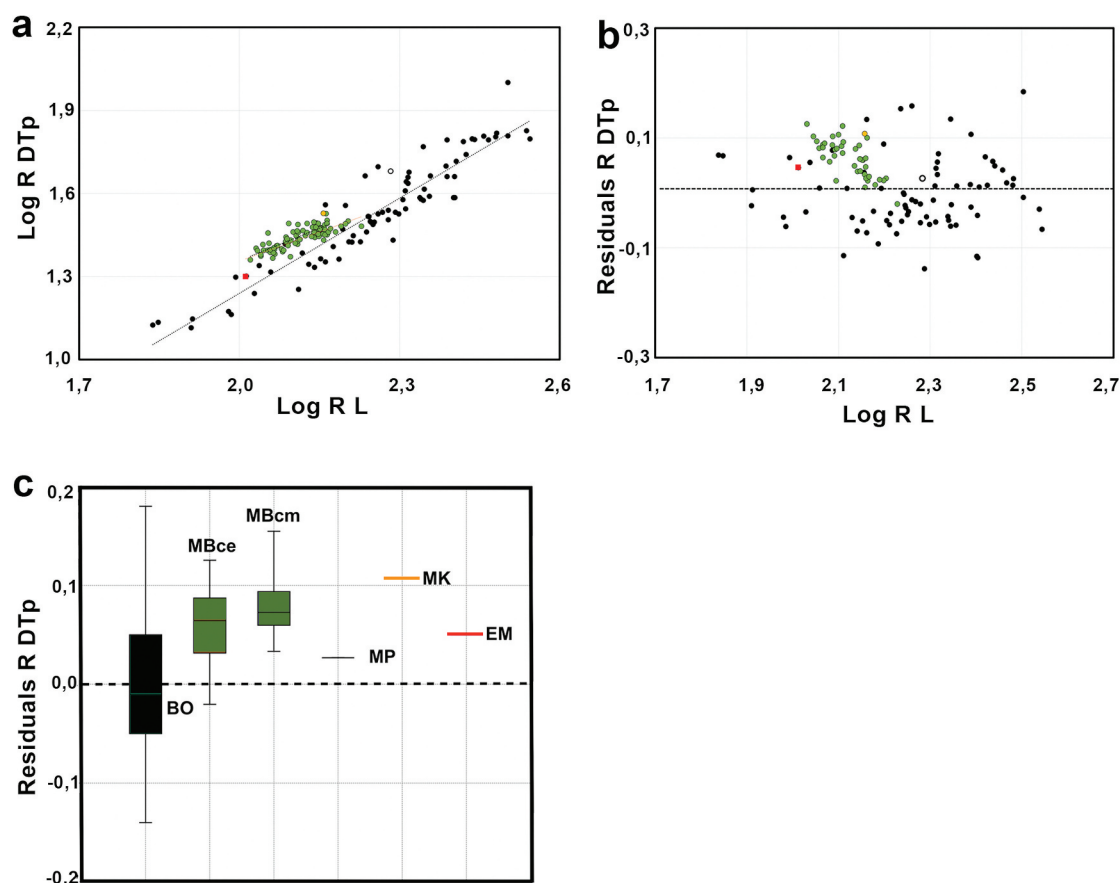| CATALOGUE N°	TEETH	L	W	Notes
IPS-26597-1	I2?	4,20	7,60	1
IPS-26597-2	I3?	3,40	-	
IPS-26597-3	I3?	2,92	-	

Figure 11. Scatterplot of log-transformed length (x) and log-transformed DT of the proximal epiphysis of the radius (y) in insular and continental Caprini, *Ebusia* n.gen. *moralesi* n.sp. (Eivissa) and *Myotragus* species (Mallorca). Black dots: Continental bovidae (Includes: *Cephalophus natalensis, C. montícola, Sylvicapra grimmia*, M*adoqua kirki Nesotragus moschatus, Ourebia ourebi, Oreotragus oreotragus, Raphicerus campestris, Redunca fulvorufula, Redunca redunca, Redunca arundinum, Kobus kob,* K. (*Onototragus*) *leche, K. ellipsiprymnus, Damaliscus dorcas, Alcelaphus buselaphus, Connochaetes gnou, C. taurinus, Tragelaphus strepsiceros, T. scriptus, T. angasi, T. buxtoni, T. spekei, Syncerus caffer, Anoa depressicornis, Oryx dammah, O. gazelle, Addax nasomaculatus, Aepyceros melampus, Antidorcas marsupialis, Gazella dorcas, G. thomsoni, G. rufifrons, G. granti, G. dama, Pelea capreolus, Lithocranius walleri, Antilope cervicapra, Hemitragus jemlahicus, Nemorhaedus goral, Rupicapra rupicapra, Capra hircus*; Red square: *Ebusia* n. gen. *moralesi* n.sp.; Empty dot: *M. pepgonellae* (Cala Morlanda, Mallorca); Orange dot: *M. kopperi* (Pedrera de S'Onix, Mallorca; green dots: *M. balearicus* (Cova Estreta and Cova des Moro, Mallorca, Balearic Islands). b: Radius Residual distribution of the DT of the proximal epiphysis against radius length in log10 (y = 0,9849x - 0,8341, R2 = 0,5717) in insular and continental Bovidae, *Ebusia* n.gen. *moralesi* n. sp. (Eivissa) and *Myotragus* species (Mallorca). c: Box-and-whisker plots depicting the residuals of the DT of the proximal epiphysis against radius length BO: Bovidae; MBce: *M. balearicus* (Cova Estreta, Mallorca); MB cm: *M. balearicus* (Cova des Moro, Mallorca); MP: *M. pepgonellae* (Cala Morlanda, Mallorca); MK: *M. kopperi* (Pedrera de S'Onix, Mallorca); EM: *Ebusia* n.gen. n. *moralesi* n.gen. Anova results indicates that the radius of *M. balearicus* is more robust (shorter length in respect to the distal DAP) than continental bovidae (F: 37,87; p = 3,936E-14E-45; Kruskal-Wallistest: H:54,95, p 1,144E-12, Dunn's P values highly significant, showing that there are significant differences between continental bovids and Myotragus balearicus sample medians). The radius of primitive species of *Myotragus* as *M. pepgonellae* and *M. kopperi*, as well as Ebusia n.gen. moralesi n. sp. has similar proportions than *M. balearicus*. Horizontal lines denote the median, boxes the interquartile range (25 -75% quartiles), and whiskers the maximum and minimum values; percentile ranks are computed by linear interpolation between the two nearest ranks. Continental bovidae data are from Köhler et al. (2008); *Myotragus* data are from Moyà-Solà and Pons-Moyà (1980, 1981, 1982) and own data.

parastyle, similar in this respect to primitive Miocene Caprini such as *Norbertia helenica* (Köhler et al. 1995) and *Aragoral mudejar* (Alcalà and Morales 1997).

P3. One single specimen (IPS-26650) (Figure 5c; Table 3), of the right side is known. It shows a moderate degree of wear, with the central fossa still visible. Considering the moderate wear, the crown seems to be not very high. In agreement with the P2, the P3 is relatively elongated in respect to its width, and shows a groove on the lingual wall that separates the protocone and hypocone, giving a bilobed aspect to the tooth (Table 3). The labial wall shows strong parastyle and metastyle, which diverge upwards; a strong pillar is visible in the centre of the labial wall that, towards the base, cover SF ges with the parastyle. The parastyle and protocone pillar diverge upwards. The P3 of the SF specimen also strongly differ from those of extant Caprini and the Mallorca species of *Myotragus*, especially by its relatively low crown, the bilobed, long and narrow shape, and the upward divergence of the protocone pillar, parastyle and

metastyle. The P3 from the SF specimen is more primitive than that in all known species of *Myotragus*, and more similar to continental primitive Caprines like *Norbertia helenica* (Köhler et al. 1995) and *Aragoral mudejar* (Alcalà and Morales 1997). However, these forms are larger and more brachyodont than in the *Ebusia* n.gen.

P4. Two complete left and two partial P4 have been recovered from SF (IPS-26555-1 and 2) (Figure 5b; Table 3). The first shows a moderate degree of wear and the second shows significant wear. The occlusal profile is subquadrangular, being more elongated in the specimen with lower wear. All specimens show strong and upwardly diverging parastyles and metastyles, and a moderately expressed labial pillar.

Upper molars – Only six upper molars have been recovered from the SF site (IPS-26596 M1-2; IPS-26595 M3; IMEDEA-58293M1-2; IMEDEA-58298 M1-2; IMEDEA-58299 M1-2; IMEDEA-58287M1-2) (Table 3). The most outstanding

morphological characteristics of the upper molars are their small size, moderate degree of hypsodonty and relative narrowness (Figure 4(c,d); Figure 5(d,e)). The labial styles are strongly developed; the metastyle, as occurs in the extant genus *Capra*, shows a basal slightly posterior extension known as a caprine fold. The pillar of the paracone on the labial wall is very strong and more marked than the same structure on the metacone. Basal pillars between the protocone and hypocone are completely absent.

Postcranial

The postcranial bones recovered at the SF site are scarce, fragmented and not well preserved. The presence of limonite deposited on the postcranial bone surface made the correct preservation of the cortical bone of some specimens difficult. This fact, combined with the significant size variation between the specimens, was the main reason for suggesting the presence of two different bovid taxa (Moyà-Solà et al. 1984). Some fragmentary bones are of a larger size than the great majority of the postcranial elements recovered; in particular, they consist of a large diaphysis of a femur (IPS-26578), a fragmentary proximal diaphysis and partial epiphysis (IPS-26566), and a proximal shaft of humerus (IPS-26567). Although the scarcity of material makes it difficult to evaluate these differences in size, the homogeneity in size and morphology of the dentition, and the significant degree of variability in size in insular endemic ruminants (van der Geer 2008), suggest that a single taxon is present at this site.

Fore limbs. Six partial humeri have been preserved and these show significant variation in size. A partial proximal shaft lacking articulation of a right humerus is preserved. It is of a large size compared with the rest of the humeri specimens of the same locality, but the partiality of the specimen makes a correct comparison difficult. It looks more gracile than the humerus of *Myotragus* species; the deltoid tuberosity is less marked and the teres major insertion area is not visible, whereas in *Myotragus* both are strongly expressed. Five distal humeri specimens (Figure 6a) (Table 4) share a relatively small size compared with the previously discussed specimen. The distal articulation is preserved in four specimens (IPS-26577-3 and 4); in another two (IPS-26577-1 and 2) a large part of the shaft is preserved. As in the previous specimen, they are more gracile than in *Myotragus* (Figure 6(a,b)), the deltoid tuberosity is less marked and the teres major insertion area is not visible. In contrast with *Myotragus, Ebusia* n.gen. *moralesi* n. sp. exhibit a higher and less mediolaterally extended trochlea with a more marked medial ridge and a higher capitulum. In these features, *Ebusia* n.gen. *moralesi* n. sp. is more similar to continental caprines than to *Myotragus*. However, its distal articular surface is strongly laterally tilted and its lateral proximodistal high is relatively small compared with the medial part of the distal articular surface. In this respect, *Ebusia* n. gen. is more similar to *Myotragus* than to continental caprines (Figure 6(a,b)).

A complete radius has been recovered (IPS-26570) (Figure 7(a–e)) two proximal parts including the epiphysis (IPS-26572 and 26564) and another one with a preserved, fused proximal ulna (Figure 7(f,g); Table 4). The scatterplot of log-transformed length and log-transformed transversal diameter of the proximal epiphysis of the radius of a large sample of continental bovidae (Figure 12a) shows that the complete specimen (IPS-26570) of *Ebusia* n.gen. *moralesi* n.sp. shows a moderate degree of robusticity, but within the variation of continental bovids. *Myotragus* species (Mallorca) shows a tendency to a major degree of robusticity. This is confirmed by the analysis of residuals (Figure 12(b,c)). The proximal ulna preserved in the IPS-26571 specimen is relatively short compared with the tendency in continental caprines to has longer olecranon

CATALOGUE N°	BONE	L	Midshaft		Proximal		Distal	
			TD	APD	TD	APD	TD	APD
IPS-26679	Femur	-	17,74	18,70	-	-	-	-
IPS-26560	Tibia (a)	113,7	9,83	8,91	-	-	21,6	10,5
IPS-26551	Tibia	-	-	-	-	-	18,53	13,02
IPS-26566	Tibia	-	17,14	16,11	-	-	-	-
IMEDEA58288	Tibia	-	12,40	10,90	-	-	-	-
IMEDEA58289	Tibia	-	16,79	15,00	-	-	-	-
IPS-26580	Metatarsal	83,03	15,08	-	-	15,86	-	9,19
IPS-26561	Metatarsal (b)	73,00	12,50	7,79	13,64	14,77	-	-
IPS-26582-1	Metatarsal		1135	9,52	14,85	13,60	-	-
IPS-26582-2	Metatarsal		-	-	14,29	12,59	-	-
IPS-26609	Metatarsal		-	-	17,85	14,53	-	
IPS-26679	Cubonavicular		9,50	24,50				
IPS-26604	Humerus	-	-	-	-	-	23,98	-
IPS-26577 – 1	Humerus	-	12,24	14,15	-	-	19,91	-
IPS-26577 – 2	Humerus	-	10,12	13,70	-	-	19,91	-
IPS-26577 – 3	Humerus	-	-	-	-	-	21,56	11,93
IPS-26567	Humerus	-	15,30	20,4	-	-	-	-
IPS-26571	Radius	102,79	12,50	7,79	19,95	10,90	20,25	12,19
IPS-26572	Radius	-	-	-	19,82	10,82	-	-
IPS-26564	Radius	-	-	-	18,95	10,12	-	-
IPS-26570	Radius	-	-	-	19,39	-	-	-
IMEDEA58286	Metacarpal	85,00	22,40	13,00	-	-	25,7	-
IMEDEA58287	Metacarpal	-	8,80	4,90	-	-	20,78	-
IPS-26581	Metacarpal						22,50	9,50
IPS-26561	Metacarpal(c)	75?	11,90	9,13	-	-		
IPS-26562	Int.phalanx	13,11	6,29	7,93	7,70	8,45	6,43	8,88

(Figure 7j). In this respect, *Ebusia* n. gen. is more similar to *Myotragus*. However, *M. balearicus* shows a strong posterior inclination of the olecranon (Figure 7i), that is less marked in *Ebusia* n. gen and continental caprines (Figure 7(h,j)).

Four fragmentary metacarpals are preserved (Table 4). The only metacarpal that is relatively complete is IMEDEA-58286 (Figure 6j). The proximal epiphysis is partially damaged, but the cast preserved in the breccia has facilitated the reconstruction of the proximal articulation (Table 4). The cortical is eroded in several parts. The left distal articular surface is missing, but the right is preserved, allowing correct measuring of the length of the specimen. The Mc is short, robust, with parallel lateral and medial margins; it is highly anteroposteriorly compressed. When comparing the length and the transversal diameter of the mid-shaft however, *Ebusia* n.gen. *moralesi* n. sp. shows an intermediate degree of robusticity between the species of the genus *Myotragus* of Mallorca and extant and fossil continental caprines (Figure 13(a–c)). IPS 26561 is a partially preserved metacarpal laking proximal and distal epiphysis. In spite of this it can be asserted that the bone is relatively gracile compared with that of the *Myotragus* species (Figure 6c). IMEDEA-58292 is a complete Mc of a young individual, without fused distal epiphysis. It is also robust and anteroposteriorly compressed; in contrast with the adult individual IMEDEA-58286, the mid-shaft transversal diameter is narrower than the proximal and distal shaft portions. IMEDEA-58287 is a distal part of a Mc preserving the distal articulation (Figure 6i); it also shows a high degree of anteroposterior compression and robusticity of the shaft. IPS-26581 is another distal metacarpal part, with a preserved left articular surface, and is also highly anteroposterior-compressed (Figure 6i). The sample of Mc specimens shows that the distal forelimb segment of *Ebusia* n. gen. is short and robust compared with continental caprines, demonstrating the characteristic adaptations of insular ruminants (Sondaar 1977). However, the degree of
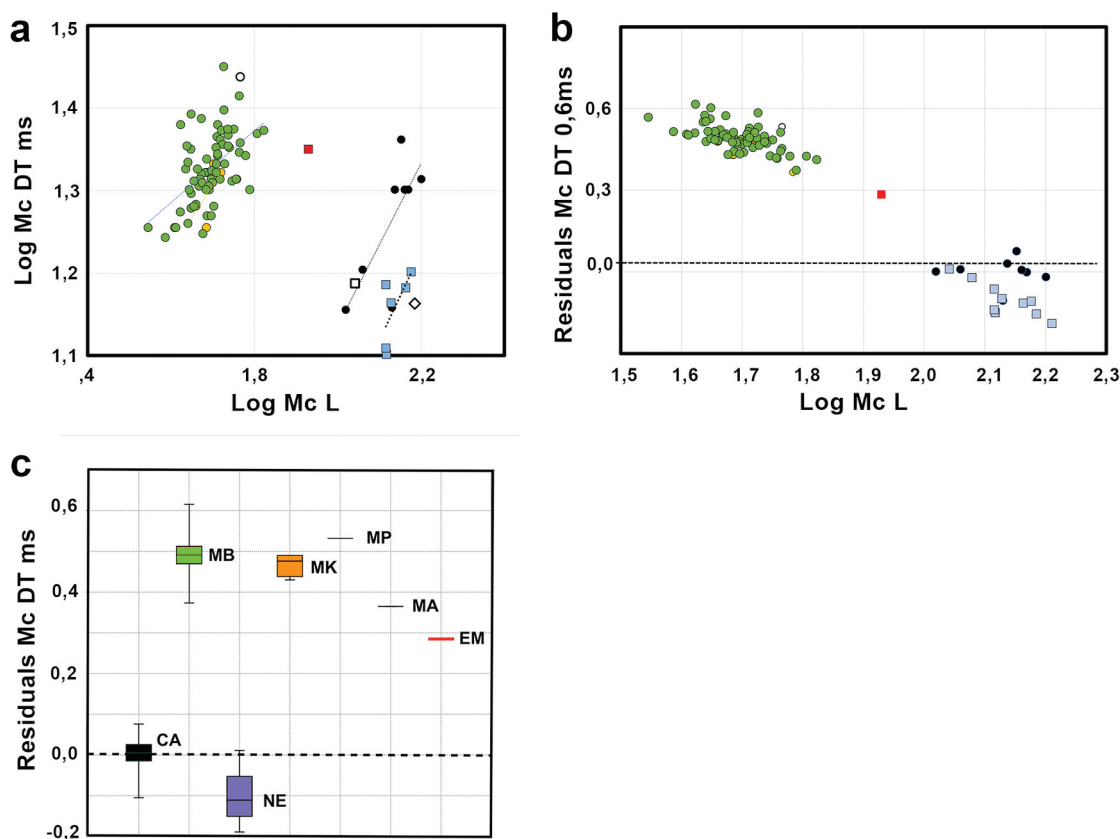
Figure 12. A: Scatterplot of log-transformed length (x) and log-transformed transversal diameter of the proximal epiphysis of the metacarpal (y) in insular andcontinental Caprini, *Ebusia n.gen. moralesi n. sp.* (Eivissa) and Myotragus species (Mallorca). Red square: *Ebusia n. gen. moralesi n.sp.*; Empty dot: *M. pepgonellae* (Cala Morlanda, Mallorca); Orange dot: *M. kopperi* (Pedrera de S'Onix, Mallorca; green dots: *M. balearicus* from Cova Estreta (Mallorca, Balearic Islands); blue dots: *M. balearicus* from C2 Cave (Menorca, Balearic Islands). Black dots: Continental caprini (Includes: *Capra alba, Hemitragus jemlaicus, Nemorhaedus goral, Rupicapra rupicapra*, Capra *hircus, Capricornis sumatraensis and Ammotragus lervia);* Blue square: Nesogoral (Monte Tutavista, Sardinia); empty diamond: *Nesogoral cenisae*, (Campisano, Sardinia); empty square: *Nesogoral melonii* (Capo Figari, Sardinia). b: Residual distribution of the DT of the proximal epiphysis of the metacarpal (y) against length in log10 (y = 0,9849x - 0,8341, R2 = 0,5717 for continental Caprini) in insular and continental Caprini, *Ebusia n.gen. moralesi n.sp.* (Eivissa) and *Myotragus* species (Mallorca). c: Box-and-whisker plots depicting the residuals of the DT of theproximal epiphysis against metacarpal length. Anova results indicates that the metatarsal of *M. balearicus* is more robust (shorter length in respect to the proximal DAP) than continental caprini (F: 621,5; p = 1,096E-57, Kruskal-Wallis test: H:43,98, p. 1,526E-09, Dunn's P values shows that there are significant differences between sample medians between *M. balearicus* and continental caprines. *Nesogoral ssp.*does not differ significantly from continental caprines and *M. kopperi* from *M. balearicus. Ebusia n.gen.* moralesi n. sp. have an intermediate position, between continental caprines and *M. balearicus, M. kopperi*. Horizontal lines denote the median, boxes the interquartile range (25 -75% quartiles), and whiskers the maximum and minimum values; percentile ranks are computed by linear interpolation between the two nearest ranks. Continental bovidae data are from Köhler et al. (2008); *Myotragus* data are from Moyà-Solà and Pons-Moyà (1980, 1981, 1982) and own data; *Nesogoral* data are from Palombo et al. (2013), Van der Made (2005), Gliozzi and Malatesta (1980).

shortening of the Mc is intermediate between that in continental caprines and *Myotragus* species from the Plio-Pleistocene of Mallorca. In this context, the endemic Caprini *Nesogoral* from Sardinia shows an Mc robusticity pattern similar to that of continental caprines (Figure 13(a–c)).

A complete, but eroded, intermediate anterior phalanx (IPS-26562) showing a significant degree of robusticity (Figure 6(d–h)), and a proximal part of a proximal (IPS-26610), are the only evidence of the phalanges of *Ebusia* n. gen. The proximal articulation of the intermediate phalanx does not show the characteristic ligamentary pits present in *Myotragus* species (Köhler and Moyà-Solà 2001).

Hind limbs. A femoral shaft is the single evidence of this bone from the SF site. The IPS-26578 specimen is a nearly complete femoral shaft lacking both epiphyses. Its size is larger compared with the other bones from the site (Figure 8).

One nearly complete tibia is preserved (IPS-26560) (Figure 8a), together with four distal fragments (IPS-26603-1; IMEDEA-58289; IPS-26613; IPS-26576) and four proximal parts (IPS-26603-2; IPS-

26563; IPS-26574; IPP-26566). The IPS-26560 specimen is nearly complete, lacking only the proximal articular surface. For this reason, we have estimated the total length to evaluate its degree of gracility, compared with that in *Myotragus* and continental caprines. The scatterplot of log-transformed length and anteroposterior diameter of the distal epiphysis of the tibia of a large sample of continental bovidae (Figure 14a) shows that the complete specimen (IPS-26560) of *Ebusia* n.gen. *moralesi* n.sp. shows a similar degree of robusticity then continental bovidae. In contrast, *Myotragus* species (Mallorca) shows a higher degree of robusticity. This is confirmed by the analysis of residuals and by the statistical analysis (Figures 14(b,c)). Another fact worth mentioning, as for other postcranial elements described, is the relatively significant size variability, a frequent phenomenon in insular taxa (Figure 15 (a–c); Table 4).

The only, more or less complete metatarsal recovered is IPS-26580 (Figure 8d). The proximal and distal articular surfaces are preserved in this specimen, but the cortical in some parts of the bone is eroded making it difficult to take any measurement.
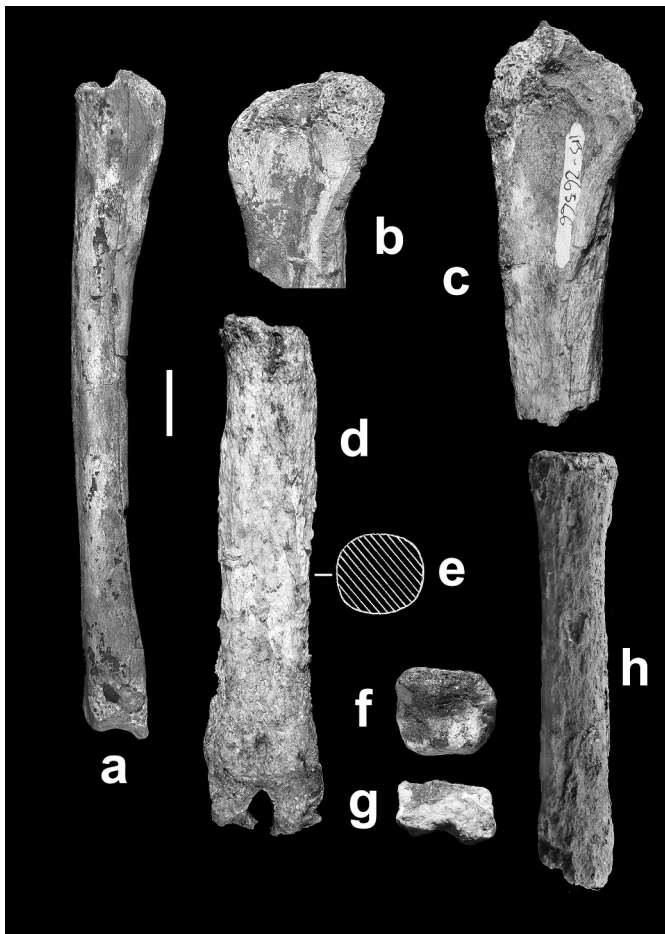
Figure 13. Hind limb bones of *Ebusia* n.gen. *moralesi* n.sp. a: right tibia (IPS-26560) in medial view; b and c: proximal epiphysis of tibia in lateral views (IPS-26603 y IPS-26566); d: right metatarsal (IPS-26580) in anterior view; e: mid-shaft section; f: cubonavicular (IPS-26556) in proximal view; g: the same specimen in anterior view; h: metatarsal lacking distal epiphysis in anterior view (IPS-28582-1) (Graphic scale 1 cm).

Fortunately, the length and proximal anteroposterior diameter of the specimen can be measured with confidence (Table 4). The specimen is short and robust with parallel medial and lateral margins. The poor preservation of the cortical of the bone makes it difficult to inspect the morphology of the articular surfaces. Specimen IPS-26581 is a left metatarsal lacking the most distal epiphysis. It shows a high degree of gracility, even higher than that of the anterior specimen. Proximally it has similar anteroposterior and transversal diameters, but the degree of anteroposterior compression increases distally. An estimation of the total length of the specimen is possible considering that only the distal articulation is lacking (Table 4). As the anterior specimen, it shows a considerably lower degree of robusticity than in the *Myotragus* species from Mallorca (Figure 14a). Similar proportions have the more incomplete specimen IPS-28582-1, (Figure 8h). Comparing the length and the proximal anteroposterior diameter, *Ebusia* n.gen. *moralesi* n. sp. occupies again an intermediate position between the *Myotragus* species of Mallorca and extant and fossil continental caprines (Figure 14a). Analysis of residuals confirms this fact (Figure 14(b,c)). Only the oldest and more primitive Mallorcan *Myotragus* species, *M. palomboi* (Bover et al., 2010), has a lower degree of robusticity than more recent *Myotragus* species (Figure 14a). Other metatarsal specimens are incomplete, which makes it difficult to obtain adequate measurements. IMEDEA-

58291 is a metatarsal shaft without proximal and distal epiphyses; the most proximal part shows a transversal section with moderate anteroposterior compression that increases distally. Compared with the characteristic condition of bones of *Myotragus* species, it is relatively gracile. Two proximal metatarsal parts are also preserved in IPS-26582-1 and IPS-26582-2, differing only in size, IPS-26582-2 being considerably larger and showing a similarly significant degree of size variation as observed in the postcranial skeleton of this taxon. Two other metatarsal shafts, without epiphyses, are preserved in IPS-26565 and IPS-26561. The first one has retained a small portion of the proximal articulation and both have a high degree of gracility compared with *Myotragus*. In spite of the metacarpal of *Ebusia* n. gen. being less massive and robust than that of *Myotragus* species, it is still short when compared with that of continental caprines, or even considering the high degree of gracility of *Nesogoral* species from Sardinia (Gliozzi and Malatesta 1980; van der Made 1999).

One single cubonavicular specimen has been recovered (IPS-26556; Figure 8(f,g)). It shows the generalised ruminant pattern. However, it is worth mentioning that, in contrast to that of *Myotragus*, it is proximodistally short and not fused with the cuneiform and proximal metatarsal as is usual in *Myotragus* (Sondaar 1977; Alcover et al. 1985).

Discussion

Comparisons, taxonomic and phylogenetic relationships

The preliminary attribution of the dentition to Antilopini indet. (Moyà-Solà et al. 1984) was based on the small size of the specimens and the moderate degree of hypsodonty. Some superficial similarities with the small bovid *Tyrrenotragus* from the classic Late Miocene localities of Tuscany and Sardinia (Weithofer 1888; Thomas 1984; Abbazzi et al. 2008) suggested this possibility (Moyà-Solà et al. 1984). However, a close inspection of the specimens and direct comparison with extant and fossil antilopines allows this attribution to be dismissed. Antilopini and Neotragini (Antilopinae) share dental features that clearly are not present in the SF dental specimens. Antilopinae are usually smaller, but some taxa are of a similar size to that of the material from SF. Nevertheless, Antilopini usually possess, apart from the crescent hypoconulid, a secondary cuspid (entoconulid) on the lingual aspect of the M3 tooth, conforming a bicuspid third lobe. This is the pattern that can be observed in *Gazella* species or in most Neotragini (*Raphicerus, Neotragus* and *Oreotragus*, but not in *Madoqua* or *Ourebia*). Ectostylids are also usually present in Antilopini and Neotraguini. In contrast, these features are not present in *Ebusia* n. gen. or in fossil or extant Caprini. Furthermore, in Antilopini the lingual wall of the lower molars is flatter than in caprines, with less-marked pillars and stylids. Antilopini and Neotragini also tend to have long third lobes in the lower m3, in comparison with Caprini. The only exception is the extant *Ourebia*. Similar observations can be made on fossil antilopines, and in particular the peculiar insular bovids of the Miocene Tusco-Sardinian palaeobioprovince (Thomas 1984; Abbazzi et al. 2008). *Tyrrhenotragus gracillimus* and *Neotragini* gen. et sp. from the Fiumesanto locality (Late Miocene, Tuscany and Sardinia, Italy) are of a similar size to *Ebusia* n. gen. In spite of this, they have basal pillars on the lower molars (a variable feature), they are less hypsodont (Abbazzi et al. 2008), the hypoconulid is larger with respect to the median and anterior lobe compared with *Ebusia* n. gen., they have flat lingual walls with weak lingual stylids, and lack caprine folds. Furthermore, the lower premolars are not molarised in Antilopini, but show a high degree of molarisation in
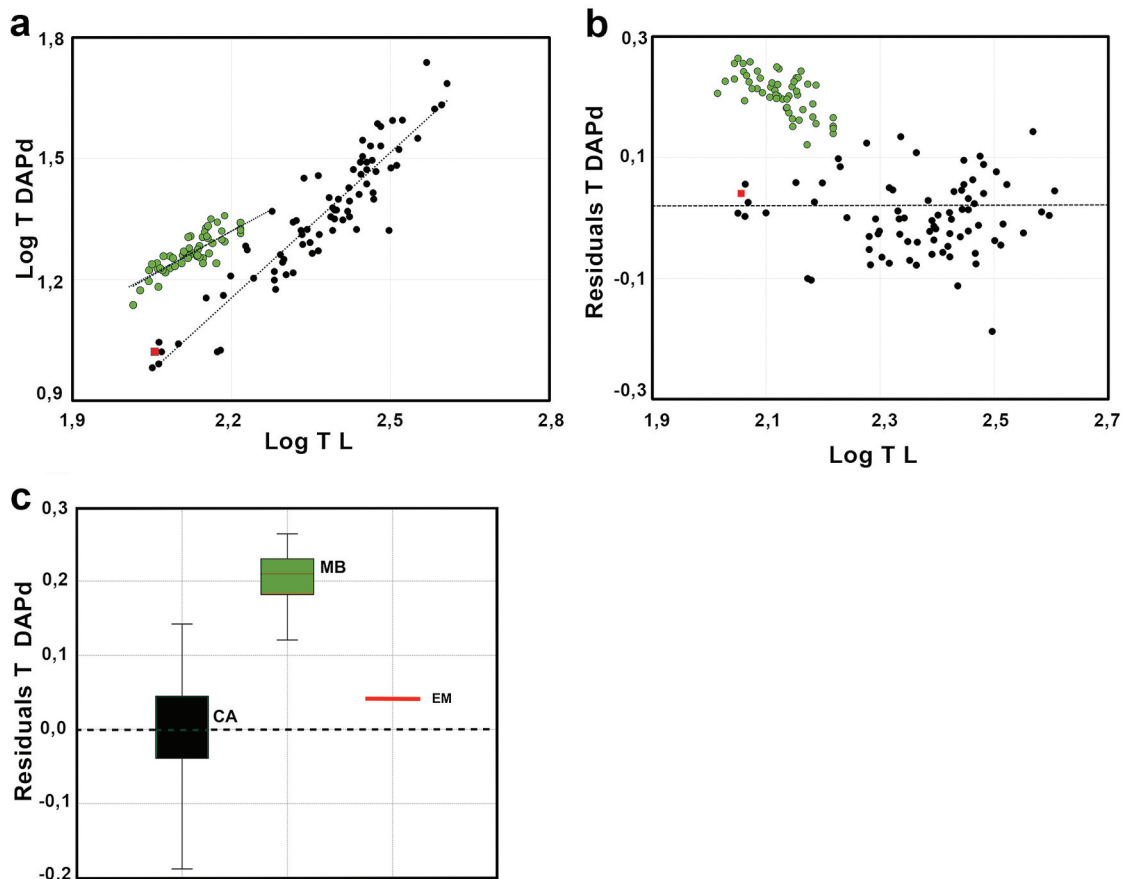
Figure 14. A: Scatter plot of log-transformed length (x) and log-transformed DAP of the distal epiphysis of the tibia (y) in insular and continental Caprini, *Ebusia* n.gen.*moralesi* n.sp. (Eivissa) and *Myotragus* species (Mallorca). Black dots: Continental bovidae (Taxa included as in Figure 12a). Includes: Red square: *Ebusia* n. gen. *moralesi* n.sp.; Empty dot: *M. pepgonellae* (Cala Morlanda, Mallorca); Orange dot: *M. kopperi* (Pedrera de S'Onix, Mallorca; green dots: *M. balearicus* (Cova Estreta and Cova des Moro,Mallorca, Balearic Islands). b: Residual distribution of the tibia DAP of the distal epiphysis against length in log10 (y = 1,2005x − 1,4861, R2 = 0,86,365) in insular andcontinental Caprini, *Ebusia n. gen. moralesi* n. sp. (Eivissa) and *Myotragus* species (Mallorca). c: Box-and-whisker plots depicting the Residual distribution of the tibia DAP ofthe distal epiphysis against length in insular and continental Caprini, *Ebusia n.gen. moralesi n. sp.* (Eivissa) and *Myotragus* species (Mallorca). Anova results indicates thatthe tibia of *M. balearicus* is more robust (shorter length in respect to the proximal DAP) than continental caprini (F: 484,3; p = 1E-05, Kruskal-Wallis test: H:93,09, p. 4,992E-22, Dunn's P values shows that there are significant differences between sample medians between *M. balearicus* and continental caprines. *Ebusia n.gen. moralesi n. sp*. shows the same proportions than continental bovids. Continental bovidae data are from Köhler et al. (2008); *Myotragus* data are from Moyà-Solà and Pons-Moyà (1980,1981, 1982) and own data.

Caprini, where the anterolingual cristid of the mesolingual conid closes the anterior basin, connecting with the anterior conid. In *Ebusia* n. gen. the only lower p4 (holotype) is a molarised Caprini-like tooth. Finally, the shape of the incisiviform specimens from SF is clearly different from that of Antilopinae, showing a very spatulate i1 associated with a set of narrow i2-c1.

In contrast, *Ebusia* n. gen. share the basic set of features that define the Caprini family including a simple outline of central fossettes on the upper molars, the presence of a caprine fold in the lower molars and the upper M3, well-developed mesostylids and metastylids, and an absence of basal pillars on the molars (Gentry 1992; Köhler et al. 1995; Alcala and Morales 1997; Gentry et al. 1999). As in Caprini, *Ebusia* n. gen. shows less of a size discrepancy between the incisiviform elements. The presence of these features in the material from SF, together with the absence of Antilopinae features in the postcranial and dental remains, indicates that the material belongs to the Caprini family. This hypothesis is confirmed by the general morphology of the postcranial remains from Ses Fontanelles. In particular, the relatively short, dorsopalmar compression of the metacarpals and metatarsals is also characteristic of the members of the Caprini (Gentry 1992; Gentry et al. 1999). However, this last argument should be viewed with

caution, considering that shortening of the metapodials is a common feature of insular ruminants, irrespective of the taxonomical placement of the taxa (Sondaar 1977). For instance, short metapodials are present in the Bovidae indet. of the Baccinello fauna in Tuscany (Italy) (Abbazzi et al. 2008) that are members of different bovid taxonomic groups.

The general morphology of the dentition of *Ebusia* n. gen. *moralesi* n. sp. is similar to that of the oldest species of *Myotragus* from the nearby Island of Mallorca. Obviously, the most relevant similarities are found with the primitive *Myotragus* species that still show no reduction in the number of premolars (*M. palomboi* and *M. pepgonellae*). The number of anterior premolars has reduced in the more recent *Myotragus* species (Bate 1909). However, apart from the same set of caprine dental features, a considerable number of differences are worth mentioning. *Ebusia* n. gen. shows a more primitive dentition compared with that of the *Myotragus* species. The primitive pattern of the dentition in *Ebusia* n. gen. suggests that the ancestral taxon of the *Myotragus* group of species, and probably of the endemic caprines of the Mediterranean Islands, is not like that of extant caprines (the genera *Capra, Ovis* and *Rupicapra*), but that in some dental features it is more similar to Miocene forms such as *Aragoral* or *Norbertia*, or extant primitive forms such as
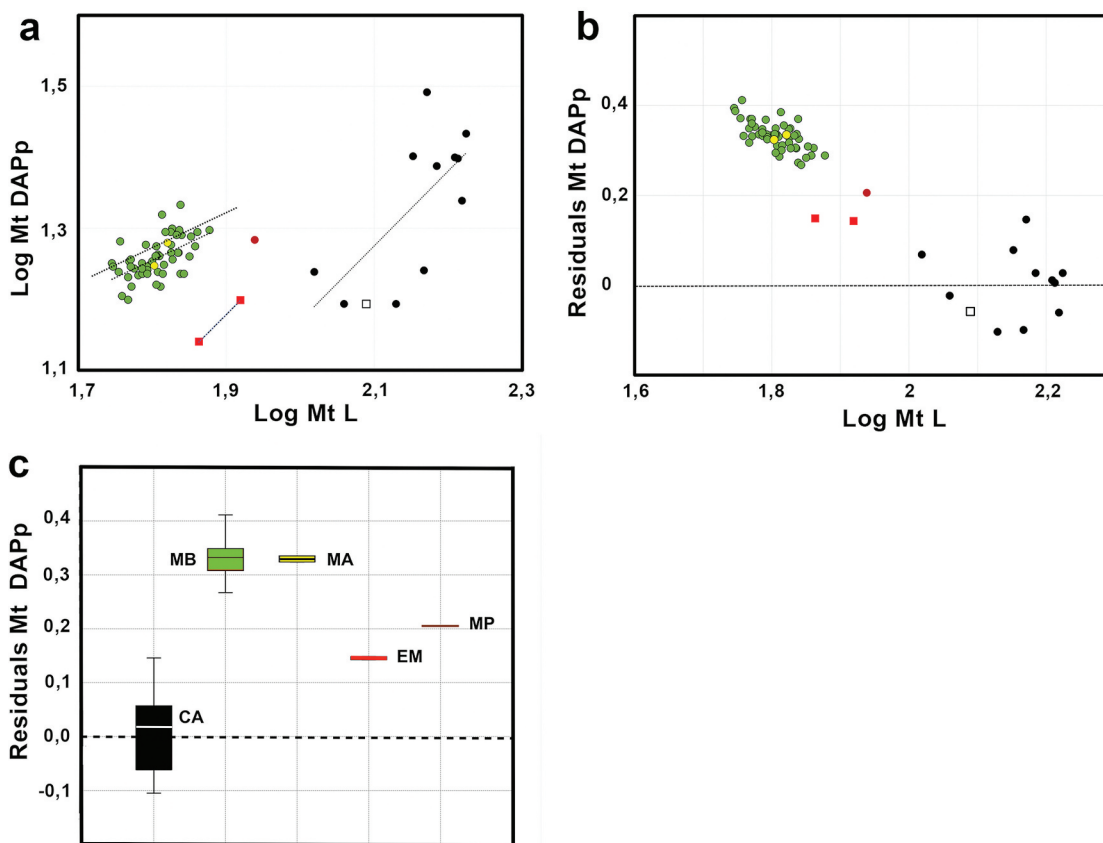
Figure 15. a: Scatterplot of log-transformed length (x) and log-transformed width of the proximal epiphysis of the metatarsal (y) in insular and continental Caprini, *Ebusian.gen. moralesi n. sp.* (Eivissa) and Myotragus species (Mallorca). Red square: Ebusia nov. gen. moralesi nov.sp.; yellow dot: M. antiquus (Cova des Fum, Mallorca; grey dots: *M. balearicus* from Cova de Muleta (Mallorca, Balearic Islands). Black dots: Continental caprini (Includes: Capra alba, *Hemitragus jemlaicus, Nemorhaedus goral, Rupicaprarupicapra, Capra hircus, Capricornis sumatraensis and Ammotragus lervia)*; Orange diamond: *Aragoral mudejar* (Teruel); empty square: *Nesogoral melonii* (Capo Figari,Sardinia). b: Residual distribution of the width of the proximal epiphysis of the metatarsal (y) against length in log10 (y = 1,0579x − 0,9465, R2 = 0,46,197: continentalCaprini) in insular and continental Caprini, *Ebusia n.gen. n. moralesi n.gen.* (Eivissa) and *Myotragus* species (Mallorca). c: Box-and-whisker plots depicting the residuals ofthe DAP of the proximal epiphysis against metatarsal length. Anova results indicates that the metatarsal of *M. balearicus* is more robust (shorter length in respect to theproximal DAP) than continental caprini (F: 206,9; p = 1,461E-32; Kruskal-Wallis test: H:32,93, p. 3,337E-07, Dunn's P values shows that there are significant differencesbetween sample medians between *M. balearicus* and continental caprines). *E. moralesi* and *M. palomboi* have an intermediate position, between both groups, but thedifferences with continentals caprines are not significant, considering Raw p values (uncorrected significance) of Dunn's test. *M. antiquus* from Cova des Fum (Mallorca)shows similar proportions than *M. balearicus*. Horizontal lines denote the median, boxes the interquartile range (25–75% quartiles), and whiskers the maximum andminimum values; percentile ranks are computed by linear interpolation between the two nearest ranks. Continental bovidae data are from Köhler et al. (2008); *Myotragus* data are from Moyà-Solà and Pons-Moyà (1980, 1981, 1982) and own data; *Nesogoral* data are from Gliozzi and Malatesta (1980); Aragoral data are from Alcala and Morales (1997).

Capricornis or *Nemorhaedus*. The complex morphology of the lower p2 of *Nesogoral* species from the Lower Pliocene site of Capu Manu (Sardinia) (van der Made 1999) confirms this view.

Ebusia n. gen. *moralesi* n. sp. seems to be more derived in its dentition than the two known Miocene continental caprines from Europe, *Aragoral* and *Norbertia*. Both taxa are larger, with a more brachyodont dentition, in particular the molars; the anterior valley of the lower p4, between the paraconid and metaconid, is open as occurs in primitive bovid groups in *Aragoral* (Alcala and Morales 1997), but it is closed in some specimens of *Norbertia* (Köhler et al.1995). In the holotype mandible of *Ebusia* n. gen, despite the p4 lingual wall being damaged, it is possible to observe that the anterior valley is closed by an anterior expansion of the metaconid, as occurs in modern caprines such as *Capra* and *Ovis*, or in rupi-caprines. In this respect, the western Mediterranean insular rupi-caprines demonstrate the same modern pattern of anterior closure of the p4. Considering the current evidence on the dentition of this group, no data permits us to establish any phylogenetic relationship between *Ebusia* n.gen. *moralesi* n. sp. and continental Miocene caprines. The only possible exception could be *Norertia hellenica*, considering the presence of molarised p4 teeth in some individuals

(Köhler et al. 1995). Even so, this taxon still has a more brachyodont dentition and wider upper molars than *Ebusia*, thereby retaining a more primitive pattern than insular taxa. Instead, the insular taxa seem to share a more derived pattern, including increased hypso-donty, narrow upper molars and a full modern caprine p4 with a closed anterior valley. Considering the current continental fossil record, no convincing sister taxa for the insular caprines can be envisaged.

The dental morphological similarities between *Ebusia* n. gen., *Myotragus* ssp. and *Nesogoral* ssp. strongly suggest close phylogenetic relationships between these taxa, and a close continental ancestor is highly probable. *Ebusia* n.gen. shows the most primitive dental pattern of the insular taxa, which leads us to suggest that this taxon could be morphologically close to the theoretical sister taxon of the insular forms. *Norbertia hellenica*, from the Mio-Pliocene transition locality of Maramena (Greece) (Köhler et al. 1995), is currently the only known continental species sharing some derived features (including the tendency towards molarisation of the lower p4) with *Ebusia* n.gen. *moralesi* n. sp. Likewise, some authors suggested similarities of *Nesogoral* with the *Protoryx/Skoufotragus* group (Palombo et al. 2013). However, these taxa still retain a more

primitive dental pattern and their horn core morphology is more similar to that of the Capra-Hemitragus group than to the simple conical pattern present in the *Nemorhaedus- Capricornis group*, as to be considered sister taxa of the insular forms. Establishing a more complete continental record of the Caprini would be necessary to resolve this question.

Apart from the scarce continental fossil record, the difficulties in analysing the phylogenetic relationships between insular and continental forms lie in the frequent and extreme morphological, parallel adaptations of insular taxa. The western Mediterranean caprines share a set of features, in special hypsodont dentition, that differentiates these taxa from any known Miocene continental caprine. The question is whether this increase in hypsodonty is a derived feature shared with the continental ancestor or a parallel acquisition as a consequence of the insular adaptation.

Adaptations to the insular ecosystem

Evolving traits in repeated and predictable way is the most pervasive phenomenon in the evolution of species on isolated Islands (Foster 1964; van Valen 1973; Sondaar 1977; Lomolino 1985, 2005). Island ecosystem characteristics drive predictable trends in the evolution of Island organisms (Carlquist 1974; Benitez-Lopez et al., 2021). In this context, each finding of a new fossil of an insular taxon provides a new case of insular evolution that approaches this phenomenon of repeatable natural experiments in the ecology and evolution of species. In this context, insular taxa show recurrent patterns in the evolution of morphological characteristics (Foster 1964; van Valen 1973; Sondaar 1977; Lomolino 1985, 2005) as well as in life-history patterns (Köhler and Moyà-Solà 2009) that allow them to be identified as insular endemisms.

A paradigmatic change occurring on Islands is a change in body size. Dwarfism and gigantism are pervasive trends on Islands that define the Island rule (Foster 1964; van Valen 1973; Lomolino 1985, 2005). *Ebusia* n. gen. is the smaller member of the Plio-Pleistocene of the Mediterranean Islands' caprines. The oldest *Myotragus* species are relatively large (*M. palomboi* and *M. pepgonellae*) while the more recent species (from *M. antiquus* to *M. balearicus* the size is smaller) are smaller (Moyà-Solà and Pons-Moyà 1982). *Ebusia* n. gen. is smaller than the most recent *Myotragus* species (Figure 11), as well as the insular close relative from Sardinia, *Nesogoral* (Gliozzi and Malatesta 1980). Furthermore, taking into account that the known continental Miocene/Pliocene caprines, such as *Norbertia* (Köhler et al., 1995), *Aragoral* (Alcala and Morales 2007) or *Sinocapra* (Chen 1991) are considerably larger, it is probable than the small size of *Ebusia* n.gen. *moralesi* n. sp. is also an insular adaptation. Considering that body size in resource-limited environments is highly dependent on the size of the Island (McNab 2002; Jessop et al. 2006; Benítez-López et al. 2021), it is possible that the relatively small size of the Island of Eivissa (571 km^2) compared with Mallorca (3640 km^2) could be a determining factor for the selection of the small size of *Ebusia* n. gen.

The shortening with a concomitant increase in the degree of robusticity of the appendicular bones is another of the most frequent adaptations of the postcranial skeleton in insular ungulates. This pattern is usually associated with fusion of carpal and tarsal bones (Leinders and Sondaar 1974; Sondaar 1977) and the presence of intra-articular phalangeal ligaments (Köhler and Moyà-Solà 2001), features that are indicative of the reduction of cursorial capabilities, which is an adaptation associated with the absence of terrestrial predators in Island ecosystems (Leinders and Sondaar 1974; Moyà-Solà 1977; Sondaar 1977; Moyà-Solà et al. 1999; Köhler

and Moyà-Solà 2001; Abbazzi et al. 2008). In the case of the western Mediterranean Islands, this hypothesis is confirmed considering that on Sardinia, a large Island that still retains terrestrial predators (), the postcranial skeleton, and in particular Mc and Mt, of *Nesogoral* does not differ from the pattern of continental caprines (Figures 13 and 14). *Ebusia* n. gen. *moralesi* nov. sp. clearly combines the shortening of the distal limb elements (Mc and Mt) coupled with an increase in robusticity of the phalanges. The complete fossil record of *Myotragus* on the Island of Mallorca shows that the postcranial pattern was acquired rapidly during the first stages of insularity. This seems logical, considering the lack of predators on small- to medium-sized Islands is one of the factors determining these adaptations. This new locomotor pattern in *Myotragus* evolved in parallel to a reduction in the brain structures relating to locomotion (Köhler and Moyà-Solà 2004) as well as sense organs relating to vision (Köhler and Moyà-Solà 2004) and smell (Bover and Tolosa 2005). However, species of *Ebusia* n. gen. retain a degree of gracility of the proximal long bones similar to that in continental bovids that suggests that the postcranial adaptation to low-gear locomotion (Sondaar 1977) in the insular environment was at the initial stages. In contrast, all species of *Myotragus* from Mallorca, with the possible exception of *M. palomboi*, exhibit more derived robust postcranial limb bones. *Ebusia* n. gen. also displays an absence of fusion between the cubonavicular-cuneiforms and metatarsal, a pattern present in the genus *Myotragus* and other insular ungulates (Sondaar 1977; van der Geer 2008, 2014).

A second anatomical complex of ungulates that has been deeply modified under insular evolution is the masticatory system. Typical insular ruminants show a tendency to reduce the number of premolars, increase the length of the molar row and the degree of hypsodonty, coupled with a reduction of the number of incisiviform teeth, an increase in length (hypsodonty) of the remaining incisors and even an ever-growing pattern as occurs in *Myotragus* and *Maremmia* (Bate 1909; Moyà-Solà and Pons-Moyà 1980, 1981; Alcover et al. 1985; Hürzeler 1983; Abbazzi et al. 2008). The evolution of the dental adaptations of insular ungulates is a gradual phenomenon that has been thoroughly documented in the case of *Myotragus* on the Island of Mallorca (Moyà-Solà and Pons-Moyà 1980, 1982). In contrast with the postcranial and brain size, and reduction of size in sense organs, the dentition pattern was a gradual phenomenon that lasted the whole time of the isolation (from the Messinian to the extinction of *Myotragus* in the Holocene). The selection of this gradual anagenetic pattern was a consequence of the resource-limited environment intrinsic to small and medium-sized Islands coupled with the absence of terrestrial predators and the concomitant lack of control of the herbivore population density (Köhler and Moyà-Solà 2004, 2009). The increase in hypsodonty and posterior reduction of the incisors and canines, the reduced number of premolars and the increase of the molar row length presented a high adaptive advantage at times when denudation of the vegetation, caused by the lack of predators that control the overpopulation of herbivores, led to mass starvation (Sondaar 1977). These dental adaptations permitted *Myotragus* individuals to access and consume additional food resources and a diet shift towards a more generalistic browsing niche (Winkler et al. 2013), thereby increasing their survival probabilities (Köhler and Moyà-Solà 2004, 2009). These critical periods of devastation of the vegetation and mass mortality are highly selective and, like a bottle-neck mechanism, permit the survival of only a small portion of the population (Sondaar 1977; Coulson and Crawley 2004). Considering such overpopulation events are cyclical (Sondaar 1977; Coulson and Crawley 2004), cyclicality determines the gradual pattern of these features. This complex of anatomical adaptations in *Myotragus* has occurred in parallel with their slow and flexible

growth rates, attainment of somatic maturity extremely late at 12 years of age and an increase in longevity (Köhler and Moyà-Solà 2009; Jordana et al. 2012), reducing metabolic rates, and synchronising their metabolic requirements with fluctuating resource levels (Köhler and Moyà-Solà 2009).

Ebusia n. gen. have a complete, moderately hypsodont dentition, with brachyodont incisor crowns and long premolar series, similar to continental caprines. Considering that the evolution of the dental complex in insular ungulates is a gradual phenomenon, the plesiomorphic condition of *Ebusia* n. sp. clearly suggests that this taxon is temporally very close to the first stages of insularity, which is congruent with the previously discussed postcranial evidence. Unfortunately, the endemicity of the fauna of SF made it impossible to estimate an age for this locality and therefore to confirm its probable age close to the Messinian salinity crisis, the theoretically best epoch for Island–continent interchanges during the Mio-Pliocene in this area (Moyà-Solà et al. 1985; Mas et al. 2018). However, the presence of a gerbillid and *Hypolagus* (Moyà-Solà et al. 1984; Quintana et al. 2010) makes this hypothesis highly probable.

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