Hypolagus balearicus Quintana, Bover, Alcover, Agustí & Bailon, 2010 (Mammalia: Leporidae): new data from the Neogene of Eivissa (Balearic Islands, Western Mediterranean)

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ABSTRACT

New remains of *Hypolagus balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 from Ses Fontanelles (Eivissa) gives new information concerning this Early Pliocene endemic leporid from Eivissa and Mallorca (Balearic Islands, Western Mediterranean sea). The body mass estimated for *H. balearicus* ranges from 1.3 to 2.7 kg, which is small in comparison to other species of the same genus. The cranium of *H. balearicus* is proportionally short and has relatively smaller orbits than *Oryctolagus cuniculus* (Linnaeus, 1758). Remarkable in the usually conservative (in leporids) postcranial skeleton is the particular morphology of the elbow (with crests and pits with a soft outline) and its length in relation to the length and the transversal diameter of the humerus, which yields similar proportions to those of the Amami rabbit *Pentalagus furnessi* (Stone, 1900) from Amami-Ohshima Island and Tokuno-Shima Island (Japan). In contrast, the diaphysis of the ulna shows a robustness comparable to that observed in some mainland leporids of the genus *Pronolagus* Lyon, 1904 or *Caprolagus* Blyth, 1845. In light of the rather small size of the sample and the information yielded, two alternative hypotheses are proposed to explain the particular traits of the forelimb of *H. balearicus*: a) it is a leporid evolved under conditions of insularity; or b) the traits reflect an adaptation to particular ecological conditions, not necessarily linked to an island in the classical sense of the word. The observed differences between this species (morphology of p3 as well as particular traits of the forelimb) and other species of the genus *Hypolagus* Dice, 1917 are likely indicative of the particular taxonomical position of this taxon.

KEYWORDS
Messinian regressive episode,
Early Pliocene,
early insular faunas,
karstic deposit,
colonization process,
biogeographic model.

RÉSUMÉ

Hypolagus balearicus *Quintana, Bover, Alcover, Agustí & Bailon, 2010 (Mammalia: Leporidae): nouvelles données du Néogène d'Eivissa (Îles Baléares: Méditerranée occidentale).*

Les nouveaux restes d'*Hypolagus balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 provenant de Ses Fontanelles (Ibiza) fournissent de nouvelles informations concernant ce léporidé du Pliocène inférieur endémique de Majorque et d'Ibiza (îles Baléares, ouest de la Méditerranée). La masse corporelle de *H. balearicus* s'étend de 1.3 à 2,7 kg., ce qui est faible comparé à d'autres espèces du même genre. Le crâne d'*H. balearicus* est proportionnellement court et présente des orbitaux plus petits que ceux d'*Oryctolagus cuniculus* (Linnaeus, 1758). Sur le squelette postcrânien, usuellement conservateur chez les léporidés, la morphologie particulière du coude est remarquable (avec des crêtes et des fosses à profil doux) et sa longueur en relation avec le diamètre transversal et avec la longueur du humérus ; cela donne des proportions similaires à celles du lapin Amami *Pentalagus furnessi* (Stone, 1900) des îles Amami-Oshima et Tokuno-Shima (Japon). En revanche , la diaphyse du cube montre une robustesse comparable à celle observée chez quelques léporidés continentaux des genres *Pronolagus* Lyon, 1904 et *Caprolagus* Blyth, 1845. En raison de la plutôt petite taille de l'échantillon et de l'information donnée, nous proposons deux hypothèses alternatives pour expliquer les traits caractéristiques de l'avant membre d'*H. balearicus* : a) il s'agit d'un léporidé évolué sous conditions d'insularité ; ou b) les traits sont le résultat d'une adaptation à des conditions écologiques particulières, et pas nécessairement à une île au sens classique du mot. Les différences observées entre cette espèce (la morphologie du p3 et aussi les traits caractéristiques de l'avant membre) et d'autres espèces du genre *Hypolagus* Dice, 1917 sont probablement indicatives de la position taxonomique particulière de ce taxon.

MOTS CLÉS
Épisode régressif du Messinien,
Pliocène inférieur,
faunes insulaires précoces,
dépôt karstique,
processus de colonisation,
modèle biogéographique.

INTRODUCTION

The Neogene fauna of terrestrial fossil mammals (Chiroptera excluded) from Eivissa (Official Catalan name = Ibiza, Spanish name) is the less studied in the Balearic archipelago. This is due to both the scarcity of sites and the generally poor preservation of the few remains (Moyà-Solà *et al.* 1984b). We also have to keep in mind that, in contrast to Mallorca and Menorca, the record of mammals from Eivissa seems to be limited to the earliest Neogene sites, because these remains have not been found at the Pleistocene sites, which are dominated by peculiar ornithological assemblages (Alcover 1989; Alcover & McMinn 1992; Alcover & Bover 2002; McMinn *et al.* 2005).

Broadly speaking, the terrestrial vertebrate fauna from Eivissa is characterized by a progressive impoverishment and the disappearance of most of the taxa between Early Pliocene and the arrival of the first human population on the island, especially important during the first stage (Alcover *et al.* 2001).

In Eivissa, large mammals appear only at the Ses Fontanelles site (Sant Antoni de Portmany; Fig. 1), which yielded a bovid with short metapodials and a dwarf antelope, both with an uncertain taxonomic position. Besides these bovids, and together with the rests of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010, the small mammalian fauna of consists of a soricid, a gerbillid and a glirid (*Eliomys* sp.) (Moyà-Solà *et al.* 1984a, b; Agustí & Moyà-Solà 1990; Alcover 2000; Bover *et al.* 2008).

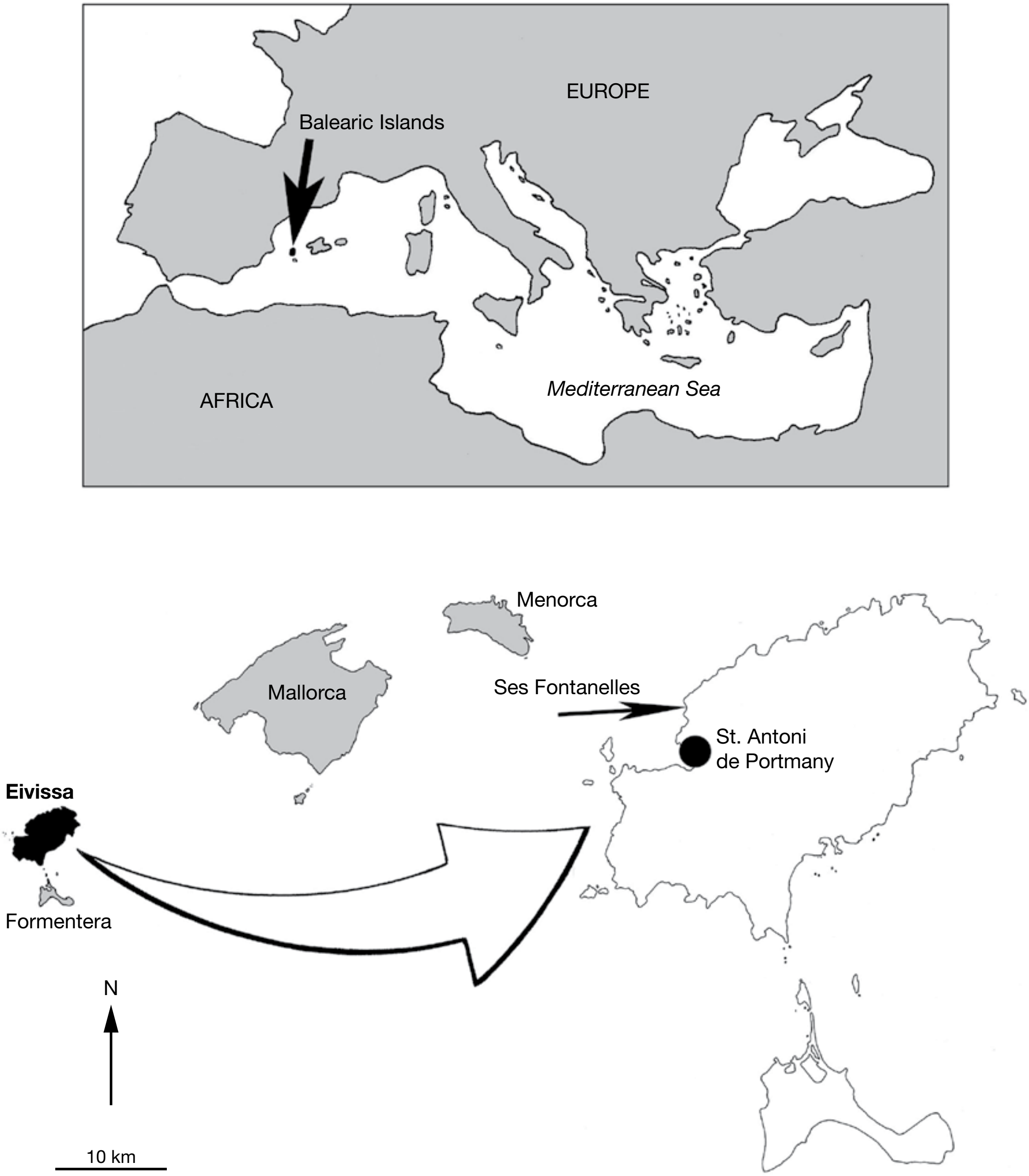

FIG. 1. — Geographical location of Ses Fontanelles (Eivissa, Balearic Islands).

Chronology and faunal context of Ses Fontanelles is comparable to the Caló den Rafelino site (Mallorca). Both sites include the so-called post-Messinian "Early Faunas", characterized by large chelonids (Bour 1985; Bover *et al.* 2008) and leporids (Alcover *et al.* 1981; Moyà-Solà *et al.* 1984b; Quintana *et al.* 2010). The chronological equivalent to these "Early Faunas" has not been discovered in Menorca yet. A slightly more modern faunal group is described from Menorca, characterized by a giant tortoise

(*Cheirogaster gymnesica* Bate, 1914) and a giant rabbit (*Nuralagus rex* Quintana, Köhler & Moyà-Solà, 2011), amongst other taxa (Agustí *et al.* 1982; Quintana 1995; Seguí 1998, 1999, 2002; Seguí *et al.* 2001; Bailon *et al.* 2002, 2005; García-Porta *et al.* 2002; Bailon 2004; Quintana *et al.* 2005).

At the Eivissa sites of Cova de Ca na Reia (Santa Eulària) (provisionally attributed to Pliocene or Early Pleistocene)(Alcover & Agustí 1985) and at the lower levels of Cova des Pouàs (Alcover *et al.* 2000), part of the terrestrial vertebrates of the "Early Faunas" have already disappeared. This fauna is only represented by a large chelonid, two glirids (*Eliomys* [*Eivissia*] *canarreiensis* Alcover & Agustí, 1985 and *Hypnomys* sp.) (Agustí & Moyà-Solà 1990) and one lacertid. As it is commented above, the Pleistocene and ancient Holocene faunas (prior of the human colonization) are characterized by a total lack of terrestrial mammals and the presence of one lacertid, apparently the only survivor of the ancient Pliocene faunas from Eivissa.

Although the leporids of Balearic Neogene are known since the beginning of the eighties of the past century (Pons-Moyà *et al.* 1981; Moyà-Solà *et al.* 1984b), in-depth studies of these taxa has been done in recent times (Quintana *et al.* 2010, 2011). Thus, the detailed study of the rests of *H. balearicus* found in Ses Fontanelles provides new information about this species and the colonization process of the Balearic Islands (and the Western Mediterranean) during the Messinian regression. It further adds to our knowledge about the evolution of leporids in insular ecosystems, because it allows comparisons of relatively little modified species (*H. balearicus*) with typically insular ones (*N. rex*).

HISTORICAL PRECEDENTS

The first reference about Neogene fossil vertebrate from Eivissa Island belongs to Petit (1963). This author cites *Hypnomys* Bate, 1918 and *Lagomys* Cuvier, 1800 in Cova d'en Marçà, in the locality of Sant Miquel de Balansat. However, posterior explorations of the site did not support the existence of these two taxa (Alcover & Agustí 1985).

Subsequently, Alcover *et al.* (1981) published preliminary results from explorations on Eivissa in September of the same year. These authors cited the presence of a leporid slightly larger than extant hares at the site of Ses Fontanelles (Sant Antoni de Portmany). Moyà-Solà *et al.* (1984b) confirmed the existence of a fossil leporid (Leporidae indet.). Posterior studies considered the systematic position of the Ses Fontanelles leporid, including it either in the genus *Trichizolagus* Radulesco & Samson, 1967 (Moyà-Solà *et al.* 1984a; Agustí & Moyà-Solà 1990) or in the genus *Alilepus* Dice, 1931 (Alcover 2000; Bover *et al.* 2008). In 2010, Quintana *et al.* (2010) consider the leporid of Ses Fontanelles as belonging to the genus *Hypolagus* Dice, 1917. These authors figured only one p3 of the fossil leporid from Eivissa.

METHODS

The extraction of skeletal remains included in the rock matrix from Ses Fontanelles was done plunging the samples in acetic acid solution with a concentration of 10%, following López-Martínez (1989) and Quintana (2005). Once dry and free of residues, the bones were consolidated with Paraloid B-67. All the remains of *H. balearicus* from Eivissa are housed in the ICP (Institut Català de Paleontologia Miquel Crusafont, Sabadell, Barcelona; acronym IPS). The measurements of the extant leporids and *N. rex* of the Tables 1 and 4-11 are from Quintana (2005: appendix III). Measurements of depth of the hypoflexid and the protoflexid of the p3 were obtained from photographs, following White (1988) criteria. The description of the teeth morphology was done using the nomenclature of López-Martínez (1989). The classification of the Central European species of *Hypolagus* genus was done following the nomenclatural criteria of Čermák (2009). To estimate the body mass of *H. balearicus*, the slope and intercept values are obtained from the model performed by Quintana (2005), which predicts the body mass of extinct lagomorphs (*log body mass* = 2.67 + 3.6865 *log toothrow length*). To predict, the toothrow length is obtained from two different mandibles (IPS-41727 and IPS-26590).

GEOLOGICAL CONTEXT

The area in which the cave of Ses Fontanelles is located is formed of Middle-Late Jurassic limestone and Early Cretaceous dolostone and limestone (Rangheard 1971). The lithology of the infilling red microconglomerates with the vertebrate remains is unknown. Moyà-Solà *et al.* (1984b) described the Ses Fontanelles site as "a phreatic gallery filled by fine grain sediment, with a size matrix of sand-lime and carbonated cement". During the process of recuperation of the vertebrate remains with acetic acid, it could be observed that the matrix includes heterometric, more or less rolled boulders of grey limestone, ferruginous nodules, some small limonisitated Ammonoidea and hematoide quartz, some of them very rolled.

None of these traits offer some clue about the possible age of the site. According to Moyà-Solà *et al.* (1984b), the presence of one gerbillid permits to situate the site of Ses Fontanelles between the Late Miocene and Early Pliocene, period in which the presence of gerbillids in the southeastern part of Iberian Peninsula is documented (Agustí *et al.* 2006).

SYSTEMATIC PALEONTOLOGY

Order LAGOMORPHA Brandt, 1855
Family LEPORIDAE Gray, 1821
Subfamily ARCHAEOLAGINAE Dice, 1929
Genus *Hypolagus* Dice, 1917

Hypolagus balearicus
Quintana, Bover, Alcover,
Agustí & Bailon, 2010

DESCRIPTION

Cranium (IPS-41726; Fig. 2; Tables 1, 2)

Relatively small, badly preserved, without teeth. The body of maxilla is partially preserved. The two maxillas show the alveolus of P2, P3, P4 and M1. The M2 alveolus is only partially preserved. Only the facial tubercles of the two zygomatic arches are preserved. The maximum distance between the ventral surface of the facial tubercle and the dental alveolus is very small. The two major palatine foramina are situated very close to the anterior side of the choana. The posterior side of the palatine fissure is situated at the same level as the mean length of P2. The frontal bones are partially preserved. The supraorbital caudal notch appears shallow.

TABLE 1. — Cranial measurements (mm) of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010.

P2-M1 length	9.76
Width of palate	9.61
Distance between facial tubers	29.0
Width of the choanae (anterior margin)	5.18
Distance between the major palatine foramina and the choanae	0.6-0.8
Distance between the two palatine foramina	6.17
Width of the palatine fissure (posterior side	5.44
Minimum distance between the choanae and the palatine fissure	6.67
Width between caudal supraorbital incisures	13.47

The posterior zone of the zygomatic process (and the supraorbital caudal notch) is only little developed, which is likely due to the poor preservation of this part of the cranium.

Though both orbits are badly preserved, the distance between the zygomatic process of the frontal bone and the dorsal side of the facial tubercle suggests that the orbits of *H. balearicus* are proportionally smaller than those of *Oryctolagus cuniculus* (Linnaeus, 1758).

Left incisor I1 (IPS-61674; Fig. 3H)

The linguoventral and medioventral margins show a well rounded outline. The central part of the ventral margin is slightly concave. The dorsal face is crossed by a rather wide V-shaped groove. It shows a depth of 18% in relation to the dorso-ventral width of tooth. Labial lobule with a well rounded outline, wider than the lingual lobule, which is acuter and narrower. The enamel is only present on the dorsal half of the tooth.

Left premolar P2 (IPS-61601; Fig. 3D)

The paraflexus has a depth equivalent to the 36% of the anteroposterior tooth length. The lagiocone is formed by two lobes with similar contour, separated by a mesoflexus that shows a depth that equals 1/3 of the paraflexus length and 12% of the anteroposterior length. The metaflexus forms a very slight concavity. The hypercone antero-lingual contour is genuinely rounded, without hypoflexus.

TABLE 2. — Length (in mm) of the superior toothrow of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 compared with other leporids. Data sources: **0**, Quintana (2005); **1**, Fostowicz-Frelik (2007a); **2**, Fostowicz-Frelik (2003); **3**, Sych (1965); **4**, White & Morgan (1995); **5**, Averianov *et al.* (2000).

Taxon	n	Max.-min.	Mean	SD	Source
Hypolagus furlongi Gazin, 1934	–	–	11.50	–	4
Hypolagus edensis Frick, 1921	1	–	11.70	–	4
Sylvilagus audubonii (Baird, 1858)	18	13.58-10.66	12.04	0.79	0
Sylvilagus nuttallii (Bachman, 1837)	2	12.39-11.79	12.09	0.42	0
Sylvilagus floridanus (J. A. Allen, 1890)	1	–	12.31	–	0
Bunolagus monticularis (Thomas, 1903)	2	13.03-11.75	12.39	0.90	0
Hypolagus balearicus	1	–	13.35	–	–
Oryctolagus cuniculus (Linnaeus, 1758)	17	16.95-11.92	13.84	1.27	0
Sylvilagus brasiliensis (Linnaeus, 1758)	2	14.24-13.66	13.95	0.41	0
Lepus saxatilis F. Cuvier, 1823	5	19.23-13.69	15.27	2.24	0
Nesolagus netscheri (Schlegel, 1880)	1	–	15.54	–	0
Lepus capensis Linnaeus, 1758	1	–	15.67	–	0
Lepus californicus Gray, 1837	6	16.63-15.11	15.91	0.68	0
Hypolagus gidleyi White, 1988	6	16.60-15.20	16.00	0.56	4
Nesolagus timminsi Averiánov, Abrámow & Tikhonov, 2000	–	–	16.10	–	5
Pronolagus crassicaudatus (I. Geoffroy, 1832)	1	–	16.17	–	0
Lepus granatensis Rosenhauer, 1856	2	18.39-14.58	16.19	1.97	0
Hypolagus balearicus	1	–	16.20	–	–
Lepus castroviejoi Palacios, 1976	2	16.85-16.43	16.64	0.30	0
Hypolagus brachygnathus (Petényi, 1864)	1	–	16.80	–	3
Hypolagus brachygnathus	7	18.90-16.80	16.93	–	3
Hypolagus brachygnathus	2	–	17.25	–	3
Hypolagus beremendensis (Petényi, 1864)	5	18.00-16.90	17.30	0.43	2
Hypolagus schreuderae Teilhard de Chardin, 1940	5	18.00-17.00	17.30	0.44	2
Hypolagus schreuderae	5	18.00-17.00	17.30	–	3
Hypolagus petenyii Čermák & Fladerer *in* Čermák, 2009	1	–	17.40	–	1
Hypolagus brachygnathus	6	18.80-17.10	17.40	–	3
Hypolagus brachygnathus	2	–	17.40	–	3
Hypolagus brachygnathus	8	18.70-16.90	17.51	–	3
Hypolagus beremendensis	18	18.60-16.60	17.63	0.61	2
Hypolagus petenyii	12	–	17.70	0.70	1
Hypolagus petenyii	7	–	17.70	0.80	1
Hypolagus petenyii	3	–	17.70	–	1
Hypolagus petenyii	1	–	18.00	–	1
Hypolagus brachygnathus	2	–	18.40	–	1
Hypolagus beremendensis	2	–	18.40	–	2
Hypolagus brachygnathus	2	–	18.40	–	3
Pentalagus furnessi (Stone, 1900)	–	–	18.47	–	0
Hypolagus gromovi Gureev, 1964	4	19.60-18.90	19.20	–	2
Hypolagus gromovi	5	20.10-19.00	19.60	–	3
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	20	25.85-18.81	23.60	2.03	0

P3-M2 (IPS-61661, 61662, 61665 [Fig. 3E]; IPS-61663 [Fig. 3F]; IPS-61664, 61666)

Variable hypoflexus morphology, but with no more than three lobules on the anterior margin. The hypoflexus enters up to half of the tooth approximately. Posterior side of the hypoflexus only slightly undulated.

Mandible

- IPS-26592A: mandibular fragment with p4, m1 and m2 (Fig. 3C);
- IPS-26592B: left/right mandibular fragment;
- IPS-41727: incomplete right mandible (Fig. 4);
- IPS-26590: incomplete left mandible;
- IPS-26591: left mandibular fragment (Table 4).

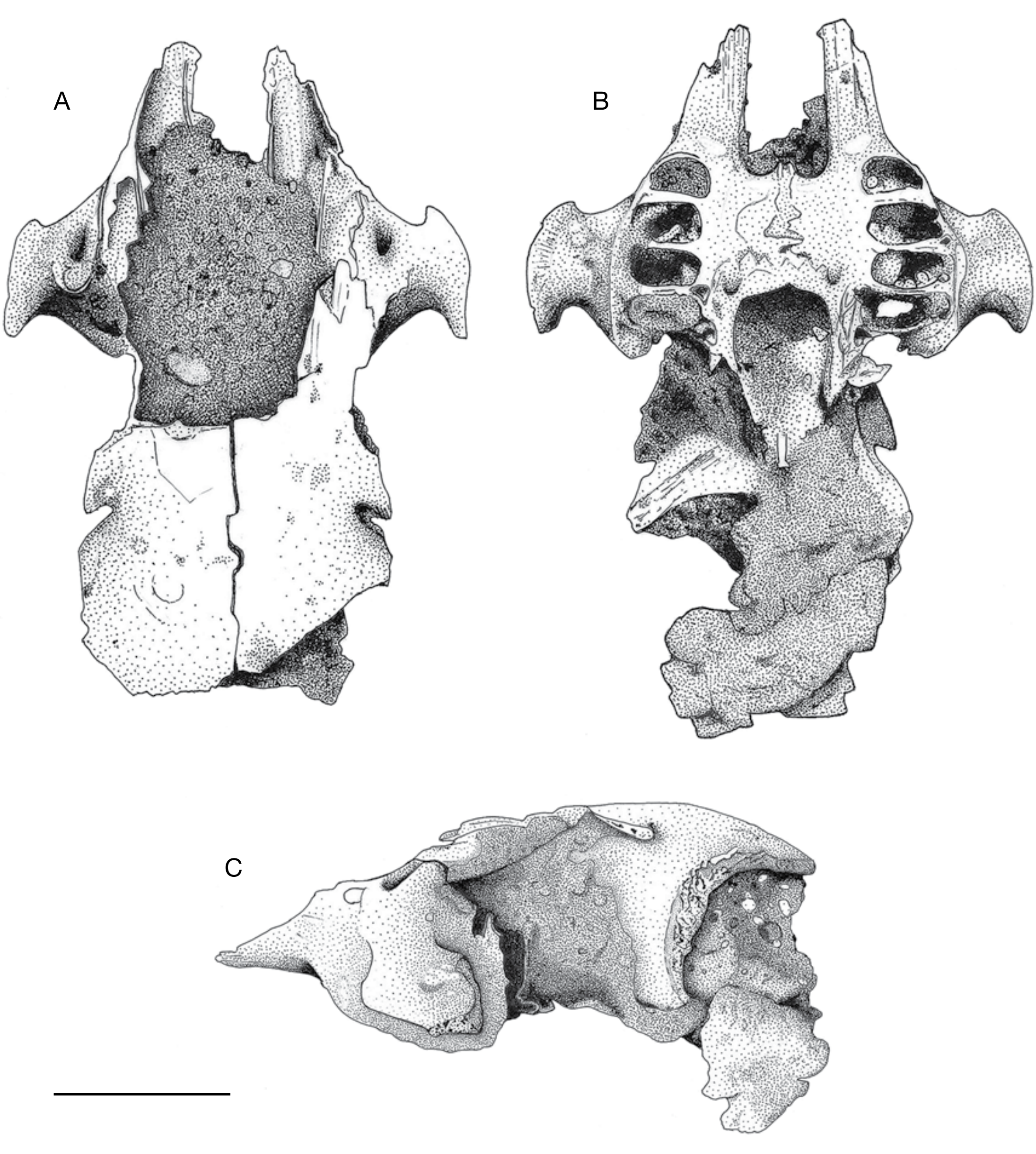

FIG. 2. — Skull of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 from Ses Fontanelles (IPS-41726) in dorsal (**A**), ventral (**B**) and lateral views (**C**). Scale bar: 10 mm.

The retroalveolar foramen is small with an elliptic outline. The mandibular ramus is 134° inclined in relation to the dorsal side of the mandibular body (Table 3). The posterior side of the mental foramen is in line with the anterior side of p3.

Remarks. The inclination of the mandibular ramus appears to be related to the cranium length. The inclination is similar in *H. balearicus* and other leporids with a proportionally short skull (Table 3).

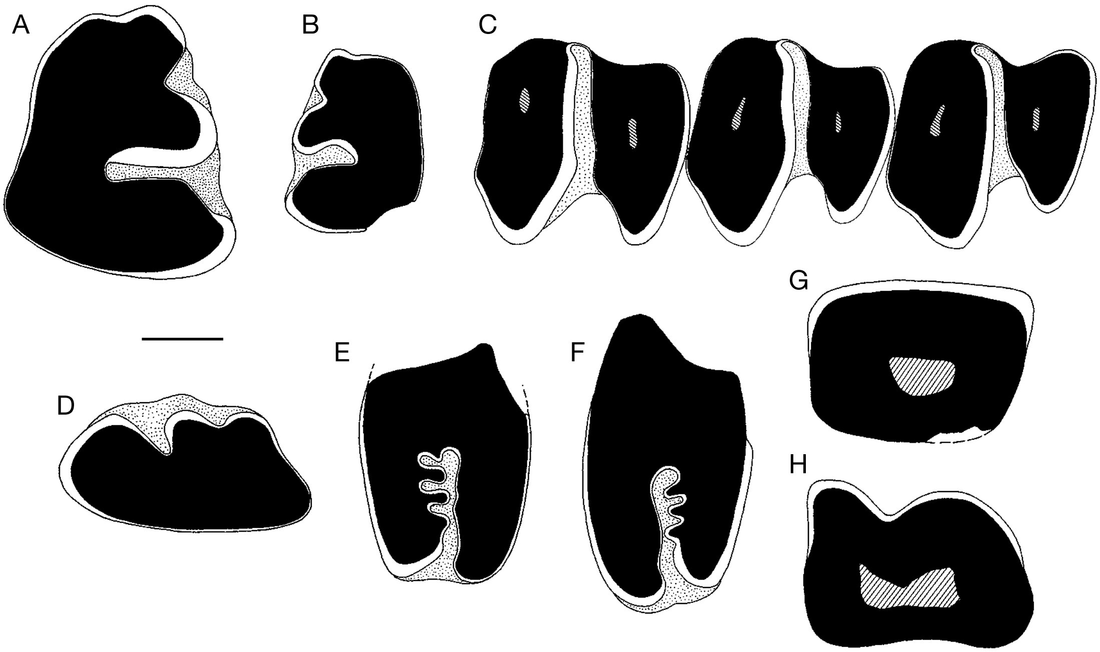

Fig. 3. — Dentition of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010: **A**, right p3 (IPS-61602); **B**, left p3 (IPS-61603); **C**, p4-m2 (left mandible IPS-26592A); **D**, left P2 (IPS-26583); **E**, right P3-M2 (IPS-61665); **F**, left P3-M2 (IPS-61663); **G**, left i1 (IPS-61675); **H**, left I1 (IPS-61674). Scale bar: 1 mm.

Table 3. — Inclination of the mandibular ramus of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 in relation to other leporids.

Taxon	n	Max.-min.	Mean	SD
Pentalagus furnessi (Stone, 1900)	1	–	130°	–
Nesolagus netscheri (Schlegel, 1880)	1	–	132°	–
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	1	–	134°	–
Hypolagus balearicus	1	–	134°	–
Poelagus marjorita (St. Leger, 1932)	1	–	135°	–
Oryctolagus cuniculus (Linnaeus, 1758)	6	143°-136°	139°	3.14
Lepus capensis Linnaeus, 1758	1	–	143°	–
Lepus saxatilis F. Cuvier, 1823	1	–	145°	–
Bunolagus monticularis (Thomas, 1903)	1	–	150°	–

Left incisor i1 (IPS-61675; Fig. 3G)
Tooth with a rounded trapezoidal outline. The enamel only covers the ventral side of the tooth.

Right premolar p3 (IPS-61602; Fig. 3A)
and left premolar p3 (IPS-61603; Fig. 3B)
Tooth with trapezoidal outline. Little pronounced or shallow anteroflexid and absent paraflexid. The anteroconid shows a rounded, slightly sharpened outline. V-shaped protoflexid, with a depth equal to 13.5%-16% of the total width of the tooth. The hypoflexid relative depth is about 48%-52%; undulation of the flexid is not observed; the mesial side of the hypoflexid shows, sometimes, a marked convexity; distal and mesial walls run almost parallel. Lingual side with rounded outline, slightly wider (anteroposterior direction) than the medial zone of the hypoflexid; labial anteroconid with trapezoidal outline. Lingual anteroconid with straight or convex contour.

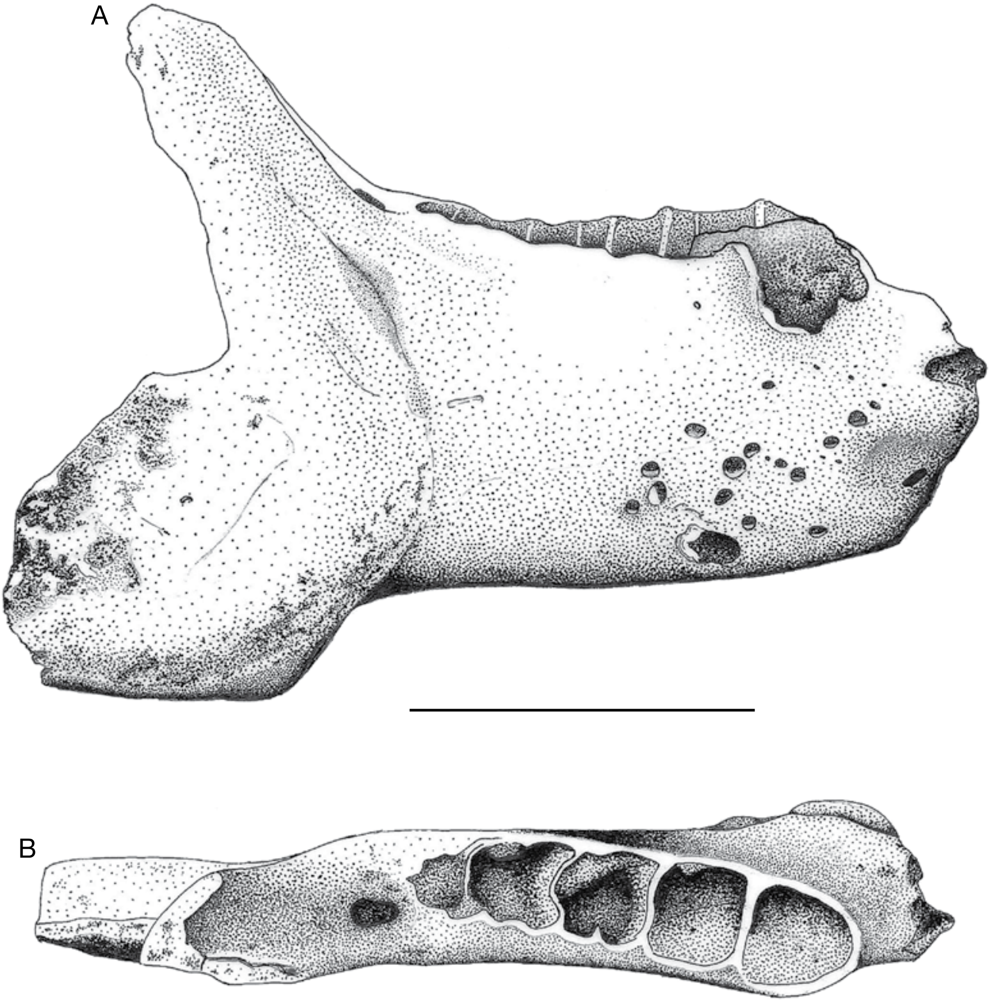

Fig. 4. — Right mandible of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 (IPS-41727) in lateral (**A**) and dorsal views (**B**). Scale bar: 10 mm.

Remarks. The two p3 from Eivissa differ in size and in the morphology of the hypoflexid. There are considerable differences in size between the Eivissa p3 and that of Caló d'en Rafelino (Mallorca) (Quintana *et al.* 2010: fig. 3). However, the morphological differences between the p3 of the two island populations are little significant, and consist basically in the absence of undulation on the hypoflexids of the p3 from Eivissa.

p4-m2 (IPS-61667-61673; Fig. 3C)

Hypoflexid with smooth or slightly undulated anterior and posterior margins. The lingual extreme of the hypoflexid is curved towards the anterior margin of the tooth. This curvature increases progressively from p4 to m2. The enamel of the posterior margin of the hypoflexid is extremely thin, similar to that on the anterior margin of the trigonid. The enamel disappears on the lingual face on both trigonid and talonid.

TABLE 4. — Mandible height (in mm) of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 compared with other leporids. Data sources: **0**, Quintana (2005); **1**, Fostowicz-Frelik (2003); **2**, Fostowicz-Frelik (2007a); **3**, Sych (1965); **4**, Fladerer & Fiore (2002).

Taxon	n	Max.-min.	Mean	SD	Source
Oryctolagus cuniculus (Linnaeus, 1758)	5	13.30-11.01	12.02	0.85	0
Hypolagus balearicus	2	13.90-11.84	12.87	1.45	
Hypolagus brachygnathus (Petényi, 1864)	1	–	13.20	–	2
Lepus granatensis Rosenhauer, 1856	1	–	13.58	–	0
Hypolagus peregrinus Fladerer & Fiore, 2003	6	14.60-12.50	13.60	–	4
Hypolagus brachygnathus	4	14.40-14.20	14.33	–	3
Hypolagus brachygnathus	13	16.30-14.00	14.49	–	3
Hypolagus petenyii Čermák & Fladerer *in* Čermák, 2009	1	–	14.50	–	2
Hypolagus petenyii	24	–	14.50	0.90	2
Hypolagus petenyii	13	–	14.50	0.60	2
Hypolagus beremendensis (Petényi, 1864)	16	15.90-13.00	14.60	0.90	1
Hypolagus petenyii	68	–	14.60	0.90	2
Hypolagus beremendensis	14	16.20-14.00	14.82	0.74	1
Hypolagus brachygnathus	14	15.70-14.60	14.90	–	3
Hypolagus beremendensis	1	–	15.00	–	2
Hypolagus brachygnathus	4	–	15.00	0.40	2
Hypolagus brachygnathus	1	–	15.10	–	3
Hypolagus brachygnathus	9	15.30-14.90	15.12	–	3
Lepus europaeus Pallas, 1778	32	16.70-14.00	15.18	–	3
Hypolagus brachygnathus	14	15.90-14.80	15.21	–	3
Hypolagus beremendensis	3	15.61-14.55	15.24	–	1
Hypolagus brachygnathus	5	15.80-14.80	15.40	–	3
Hypolagus beremendensis	2	15.90-15.00	15.45	–	1
Hypolagus petenyii	2	16.70-14.30	15.50	–	2
Hypolagus brachygnathus	2	–	15.70	–	3
Hypolagus schreuderae Teilhard de Chardin, 1940	5	16.50-15.50	15.90	0.42	1
Hypolagus gromovi Gureev, 1964	1	–	15.91	–	1
Hypolagus petenyii	1	–	16.57	–	2
Hypolagus gromovi	7	18.50-15.10	17.07	–	3
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	6	18.40-15.58	17.17	1.10	0

Humerus (IPS-41728, left incomplete humerus, see Table 5; IPS-61604, distal epiphysis fragment of left humerus, see Fig. 5)

The head of the humerus shows, from a lateral view, a very rounded outline. The lateral and medial faces of the proximal epiphysis are largely worn. The crests of the trochlea show a slightly sharp outline (Fig. 5) and are quite separated.

Remarks. The trochlea of the distal epiphysis is relatively wide (Fig. 6B) and the crests show a light acute outline in comparison to the other species included in the genus *Hypolagus* (Dawson 1958: fig. 30C; Fladerer 1984; Fladerer & Fiore 2003: pl. 2, fig. 2; Fostowicz-Frelik 2007b: figs 24-30). We exclude the possibility that the particular morphology of the IPS-61604 distal epiphysis is caused by abrasion due to taphonomic processes.

In leporids, the development and separation of the crests and pits on the elbow articulation are likely related to the speed attained during running and leaping. Species better adapted to high speeds are those with more acute crests, whereas the non-running species have lower crests and the distal epiphysis is wider transversally, as it happens in *N. rex* (Quintana 2005: fig. 56) or, to a lesser extent, in *Pentalagus furnessi* (Stone, 1900).

Radius (IPS-61605, left proximal epiphysis)

The fovea is shallow and the surface portion of the articulation situated on the lateral side is bended 42° in relation to the diaphysis.

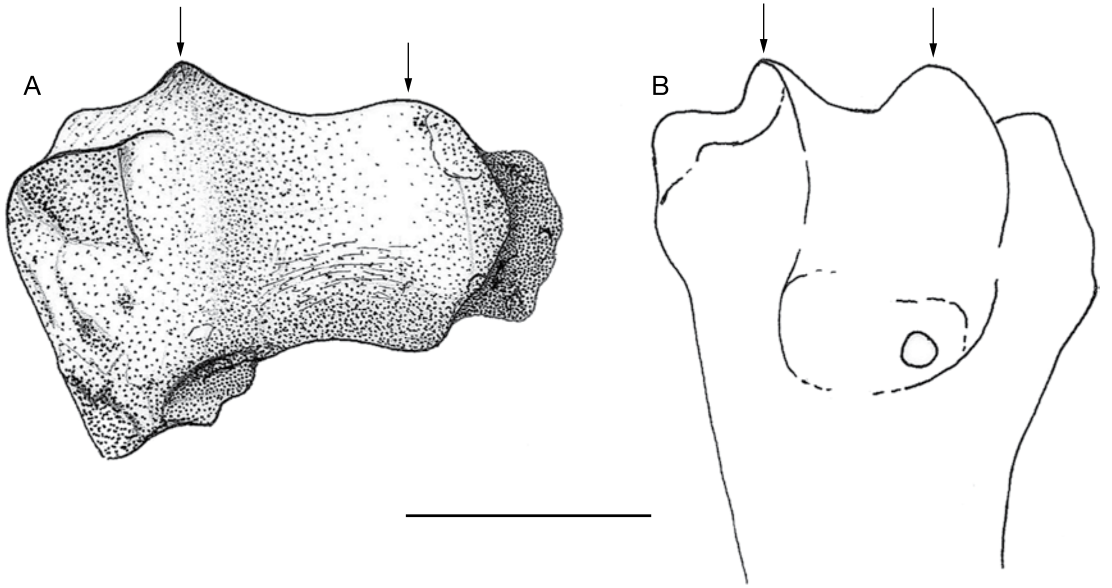

FIG. 5. — Distal epyphysis of the left humerus of: **A**, *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 (IPS-61604); **B**, *O. cuniculus* (Linnaeus, 1758). Dorsal views. Arrows shows the different development of the crests of the trochlea in both cases. Scale bar: 5 mm.

Remarks. The craniocaudal diameter of the proximal radius from Eivissa is larger than that of its Mallorcan homologue, and the lateral margin is substantially lower (Quintana *et al.* 2011: fig. 8) (Table 6). On *H. balearicus* the fovea is less concave than *H. beremendensis* (Petényi, 1864) (Fladerer 1984: abb. 5, figs 1, 2) and *Hypolagus petenyii* Čermák & Fladerer *in* Čermák, 2009 (Fostowicz-Frelik 2007a: figs 32, 34). The poor depth of the fovea is related to the low sharp outline of the lateral crest of the distal humeral epiphysis.

Ulna (IPS-41733, right ulna without distal epiphysis, see Fig. 7; IPS-61606, left proximal epiphysis)

From an anterior view, the anconeal process shows a well-rounded outline. The diaphysis is wide, both transversally and anteroposteriorly. (Fig. 8; Table 7).

Remarks. The rounded outline of the anconeal process suggests that the trochlea on the distal epiphysis of the humerus forms an arch with an opened outline, even more than in *N. rex* (Quintana 2005: fig. 56a). Both, this trait and the morphology of the proximal radius in *H. balearicus* from Mallorca (Quintana *et al.* 2010: fig. 8), suggest that the crests and the elbow articulation pits in *H. balearicus* have a low acute contour.

The ulna proximal epiphysis of *H. balearicus* shows an aspect considerably more robust than *H. beremendensis* (Fladerer 1984: abb. 6, fig. 1). In lateral view, the trochlear incisure of *H. balearicus* forms a similar arch than *N. rex* (Quintana 2005: fig. 72) and slight more open than *H. beremendensis.*

Second metacarpal (IPS-61607, right proximal epiphysis, see Fig. 9B and Table 8; IPS-61608, right proximal epiphysis)

From cranial view, the epiphysis shows a quadrangular outline. The trapezoid fossa forms an arch slightly open in mediolateral direction. The lateral crest (dorsal view) forms an angle of 75°. The medial crest is proportionally lower and rounded. The capitatum facet is bended more or less 40° in relation to the longitudinal axis of the diaphysis. From a lateral view, this facet shows a V-form outline, rather open and symmetric. The crest, which separates the facets for the capitatum and the third metacarpal, as well as the pit for the third meta-

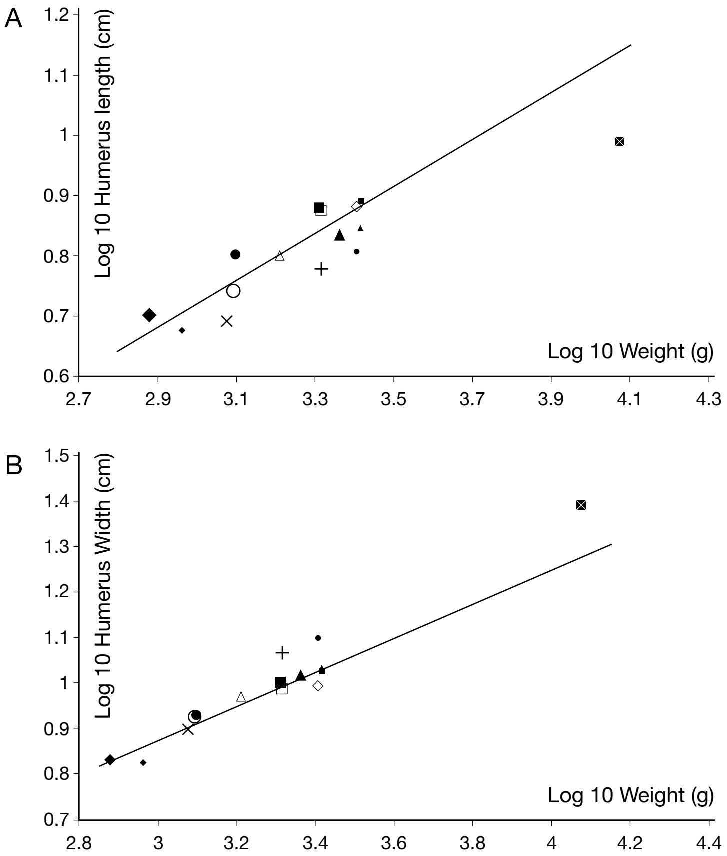

Fig. 6. — Allometric representation of the humeral length (**A**) and transversal diameter of the humerus distal epiphysis (**B**) of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 in relation to other extant and fossil leporids. The allometric relationships are defined by the equations: **A**, *log body mass* = 0.3916 *log humerus length* – 0.4552 (r^2 = 0.8317); **B**, *log body mass* = 0.3748 *log transversal diameter of humerus distal epiphysis* – 0.2506 (r^2 = 0.9388). Symbols: +, *Hypolagus balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010; •, *Pentalagus furnessi* (Stone, 1900); ⊠, *Nuralagus rex* Quintana, Köhler & Moyà-Solà, 2011; ▲, *Pronolagus randensis* Jameson, 1907; ▴, *Pronolagus crassicaudatus* (I. Geoffroy, 1832); △, *Pronolagus rupestris* (A. Smith, 1834); ×, *Sylvilagus floridanus* (J. A. Allen, 1890); ◆, *Sylvilagus nuttallii* (Bachman, 1837); ⬩, *Sylvilagus audubonii* (Baird, 1858); ○, *Oryctolagus cuniculus* (Linnaeus, 1758); ●, *Bunolagus monticularis* (Thomas, 1903); ■, *Lepus capensis* Linnaeus, 1758; □, *Lepus granatensis* Rosenhauer, 1856; ◇, *Lepus californicus* Gray, 1837; ▪, *Lepus saxatilis* F. Cuvier, 1823.

carpal form a gentle arch. On the first metacarpal facet, the ventral extreme is missed. It presents an elongated surface in dorsoventral direction, slightly irregular and concave in anteroposterior direction.

Remarks. The proximal epiphysis of the second metacarpal of *H. balearicus* differs from *O. cuniculus* and *Lepus granatensis* Rosenhauer, 1856 by a trapezoid fossa that is more open and wider in mediolateral direction and proportionally shorter in dorsoventral direction. The lateral crest is wider and less acute in *H. balearicus*. Cranial view, the proximal epiphysis of *H. balearicus* shows a quadrangular outline, while in *N. rex* and *H. beremendensis* is more elongated in dorsoventral direction (Quintana 2005: fig. 84; Fladerer 1984: abb. 19e).

Femur (IPS-26589, left proximal epiphysis, see Fig. 9C; IPS-41730, left proximal left epiphysis;
IPS-41729, right diaphysis from a juvenile individual)
From a dorsal view, the transversal section of the cranial face of the greater trochanter shows a rounded outline. The lesser trochanter is little

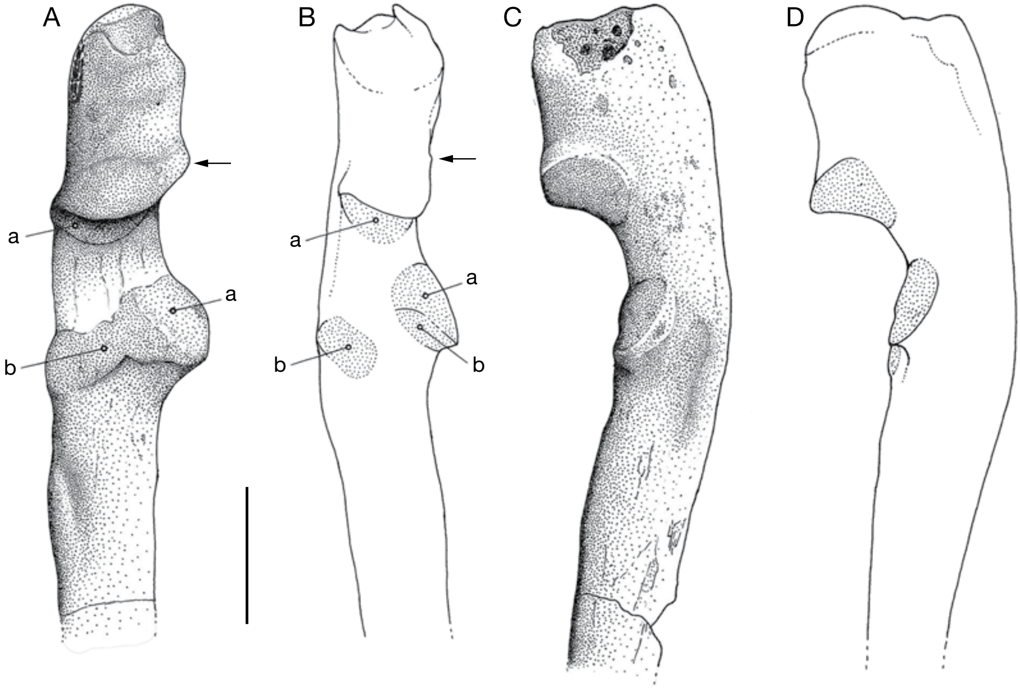

FIG. 7. — Proximal epiphysis of the right ulna of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 (IPS-41733) in cranial (**A**) and medial (**C**) views and of *O. cuniculus* (Linnaeus, 1758) in cranial (**B**) and medial (**D**) views. Abbreviations: **a**, humerus facet; **b**, radius facet. Arrows show the different development of the humerus facet in the medial surface. Scale bar: 5 mm.

elevated in mediolateral direction and in relation to the femoral neck. The dorsal margin of the femoral neck is short, so that the femoral head and the greater trochanter are close to each other. On the cranial face, the margin that separates the femoral head from the neck shows a low sharpened outline. The transversal section of the diaphysis has a circular outline.

Remarks. The lateral margin of the femoral head of *H. balearicus* is proportionally closer to the greater trochanter than in *O. cuniculus* and *H. petenyii* (Fostowicz-Frelik 2007b: fig. 4). From a cranial view, the femoral neck length is proportionally shorter than in *O. cuniculus* but longer than *H. petenyii.*

The minor trochanter is proportionally less developed in *H. balearicus*. The anteroposterior diameter of femoral head (Table 9) is intermediate between *Pronolagus rupestris* (A. Smith, 1834) and *H. petenyii.*

Tibia (IPS-61609, right distal epiphysis;
IPS-61658, left distal epiphysis;
IPS-61659, right distal epiphysis, see Fig. 9A)

The facet where the lateral margin of the astragalus is articulated shows a U-shaped outline. A groove, separating the lateral and medial face from this facet, is not observed. The cranial half of the calcaneus facet is wider than the caudal half and shows, in craniocaudal direction, a slightly concave outline. The area that separates the calcaneus and astaragalus facets shows an elliptic outline, with the principal axis pointing in craniocaudal direction.

Remarks. The lateral fossa that articulates with the astragalus shows a mediolateral outline similar to that of *L. granatensis* and slightly less acute and more open than the one of *O. cuniculus.* However, the facet for articulation with calcaneus of *H. balearicus* shows a concavity (in craniocaudal direction)

Table 5. — Length and transversal diameter (in mm) of the humerus diaphysis of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 in relation to other leporids.

		Length		
Taxon	**n**	**Max.-min.**	**Mean**	**SD**
Sylvilagus audubonii (Baird, 1858)	17	54.24-42.35	47.56	3.06
Sylvilagus nuttallii (Bachman, 1837)	2	50.92-49.92	50.42	0.70
Sylvilagus brasiliensis (Linnaeus, 1758)	2	52.97-48.67	51.36	2.34
Oryctolagus cuniculus (Linnaeus, 1758)	14	59.09-50.59	54.97	2.78
Sylvilagus floridanus (J. A. Allen, 1890)	6-5	62.44-48.67	56.95	5.18
Nesolagus netcheri (Schlegel, 1880)	1	–	57.17	–
Poelagus marjorita (St. Leger, 1932)	1	–	59.55	–
Caprolagus hispidus (Pearson, 1839)	1	–	59.72	–
Hypolagus balearicus	1	–	60.12	–
Pronolagus rupestris (A. Smith, 1834)	5-4	66.12-59.90	63.27	3.06
Bunolagus monticularis (Thomas, 1903)	2	65.40-61.77	63.58	2.57
Pentalagus furnessi (Stone, 1900)	3	65.11-62.77	64.26	1.30
Pronolagus randensis Jameson, 1907	2	69.52-67.38	68.45	1.50
Pronolagus crassicaudatus (I. Geoffroy, 1832)	3	73.76-65.88	70.34	4.04
Lepus capensis Linnaeus, 1758	4	82.93-71.92	76.07	5.05
Lepus californicus Gray, 1837	6	78.70-74.47	76.41	1.49
Lepus granatensis Rosenhauer, 1856	3	78.96-75.10	77.03	2.72
Lepus saxatilis F. Cuvier, 1823	6	83.79-69.86	78.02	5.58
Lepus crawshayi De Winton, 1899	3	82.71-77.71	80.36	2.51
Lepus castroviejoi Palacios, 1976	2	88.81-83.06	85.93	4.06
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	2-20	102.53-93.34	97.93	6.49

	Shaft width		
Taxon	**Max.-min.**	**Mean**	**SD**
Sylvilagus audubonii	3.57-2.43	3.14	0.35
Sylvilagus brasiliensis	3.33-3.26	3.29	0.04
Sylvilagus nuttallii	3.63-2.99	3.31	0.44
Sylvilagus floridanus	4.06-3.38	3.80	0.26
Oryctolagus cuniculus	4.43-3.44	3.90	0.30
Nesolagus netcheri	–	4.21	–
Bunolagus monticularis	4.64-4.08	4.36	0.39
Lepus californicus	4.91-4.23	4.56	0.27
Hypolagus balearicus	–	4.61	–
Poelagus marjorita	–	4.70	–
Lepus granatensis	5.95-4.28	4.88	0.93
Pentalagus furnessi	5.06-4.89	4.95	0.09
Caprolagus hispidus	–	5.00	–
Pronolagus rupestris	6.49-4.24	5.01	1.01
Lepus capensis	5.77-4.28	5.06	0.64
Lepus castroviejoi	5.16-5.00	5.08	0.10
Pronolagus randensis	5.58-4.93	5.25	0.45
Lepus crawshayi	5.50-4.84	5.25	0.35
Lepus saxatilis	6.42-4.46	5.30	0.78
Pronolagus crassicaudatus	6.18-4.87	5.48	0.65
Nuralagus rex	9.45-6.22	8.35	0.77

similar to *O. cuniculus* and clearly smaller than that in *L. granatensis*. The transversal diameter of *H. balearicus* tibia is slightly larger than that of *O. cuniculus* but smaller than that of *Bunolagus monticularis* (Thomas, 1903) (Table 10).

Navicular (IPS-61660, right incomplete bone, see Fig. 9D)

The astragalus pit shows a subquadrangular outline and a little marked concavity. On the plantar process, the ventral surface is slightly convex without any groove.

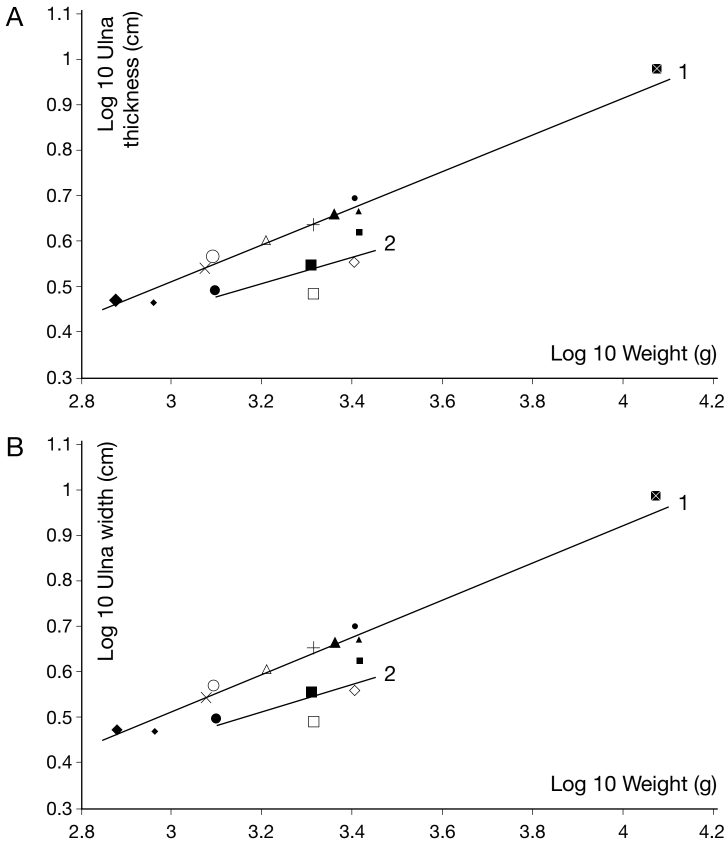

Fig. 8. — Allometric representation of the anteroposterior (**A**) and transversal diameter (**B**) of the ulna diaphysis of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 in relation to other extant and fossil leporids. The allometric relationships are defined by the equations: **A**, *log body mass* = 0.4062 *log anteroposterior diameter of the ulna diaphysis* – 0.7057 (r^2 = 0.9628) (1: all the leporids except for the species included in the *Lepus* genus) and *log body mass* = 0.2987 *log anteroposterior diameter of the ulna diaphysis* – 0.4448 (r^2 = 0.4925) (2: for the species included in the *Lepus* genus); **B**, *log body mass* = 0.4064 *log transversal diameter of ulna diaphysis* – 0.7062 (r^2 = 0.9633) (1: for all the leporids except the species included in the *Lepus* genus) and *log body mass* = 0.2987 *log transversal diameter of ulna diaphysis* – 0.4445 (r^2 = 0.4911) (2: for the species included in the *Lepus* genus). Symbols: +, *Hypolagus balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010; •, *Pentalagus furnessi* (Stone, 1900); ⊠, *Nuralagus rex* Quintana, Köhler & Moyà-Solà, 2011; ▲, *Pronolagus randensis* Jameson, 1907; ▴, *Pronolagus crassicaudatus* (I. Geoffroy, 1832); △, *Pronolagus rupestris* (A. Smith, 1834); ×, *Sylvilagus floridanus* (J. A. Allen, 1890); ◆, *Sylvilagus nuttallii* (Bachman, 1837); ⬩, *Sylvilagus audubonii* (Baird, 1858); ○, *Oryctolagus cuniculus* (Linnaeus, 1758); ●, *Bunolagus monticularis* (Thomas, 1903); ■, *Lepus capensis* Linnaeus, 1758; □, *Lepus granatensis* Rosenhauer, 1856; ◇, *Lepus californicus* Gray, 1837; ▪, *Lepus saxatilis* F. Cuvier, 1823.

Remarks. Due to its special traits, the recovered navicular of *H. balearicus* is interpreted as belonging to a juvenil individual. The astragalus fossa is notably more opened than in *H. petenyii* (Fostowicz-Frelik 2007: fig. 13), *O. cuniculus* and *L. granatensis*. The size of the navicular of *H. balearicus* is smaller in comparison to *P. furnessi*, *Sylvilagus floridanus* (J. A. Allen, 1890) or *Lepus europaeus* Pallas, 1778 (Fostowicz-Frelik 2007: pl. 3, p. 474).

Calcaneus (IPS-41732, right incomplete bone, see Fig. 10)

The proximal facet of the astragalus shows a very acute anterior extreme and a concave surface, while the distal facet presents an elliptic outline (with the major axis slightly oblique in relation to the calcaneus length) and a slightly convex surface. The boundary between both facets shows a gentle outline. From medial view, the posterior half of

Table 6. — Anteroposterior diameter (in mm) of the proximal radius epiphysis of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 compared with other leporids. Data sources of *H. petenyii* Čermák & Fladerer *in* Čermák, 2009 and *H. brachygnathus* (Petényi, 1864): Fostowicz-Frelik (2007a, b).

Taxon	n	Max.-min.	Mean	SD
Sylvilagus nuttallii (Bachman, 1837)	2	2.82-2.77	2.79	0.03
Sylvilagus audubonii (Baird, 1858)	19	3.27-2.56	2.84	0.19
Sylvilagus brasiliensis (Linnaeus, 1758)	2	3.24-2.99	3.12	0.17
***Hypolagus balearicus* (Mallorca)**	1	–	3.39	–
Sylvilagus floridanus (J. A. Allen, 1890)	6	3.73-3.15	3.43	0.24
Nesolagus netscheri (Schlegel, 1880)	1	–	3.49	–
Pronolagus rupestris (A. Smith, 1834)	2	3.54-3.48	3.51	0.03
Oryctolagus cuniculus (Linnaeus, 1758)	15	4.01-3.31	3.63	0.21
***Hypolagus balearicus* (Eivissa)**	1	–	3.70	–
Bunolagus monticularis (Thomas, 1903)	2	3.88-3.69	3.79	0.13
Hypolagus petenyii	1	–	3.80	–
Hypolagus petenyii	11	–	3.80	0.30
Hypolagus petenyii	41	–	3.90	0.30
Hypolagus petenyii	3	–	3.90	–
Hypolagus petenyii	32	–	3.90	0.20
Poelagus marjorita (St. Leger, 1932)	1	–	4.07	–
Hypolagus petenyii	10	–	4.20	0.20
Pronolagus randensis Jameson, 1907	1	–	4.30	–
Pronolagus crassicaudatus (I. Geoffroy, 1832)	3	4.68-4.34	4.51	0.16
Caprolagus hispidus (Pearson, 1839)	1	–	4.60	–
Hypolagus brachygnathus	24	–	4.70	0.40
Lepus californicus Gray, 1837	7	5.17-4.67	4.80	0.17
Lepus capensis Linnaeus, 1758	4	5.39-4.53	4.89	0.36
Lepus saxatilis F. Cuvier, 1823	6	5.56-4.40	5.01	0.39
Lepus granatensis Rosenhauer, 1856	3	5.17-4.83	5.02	0.17
Pentalagus furnessi (Stone, 1900)	3	5.23-4.90	5.10	0.17
Lepus castroviejoi Palacios, 1976	2	5.38-4.98	5.18	0.28
Lepus crawshayi De Winton, 1899	3	5.29-5.21	5.26	0.04
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	26	8.88-7.30	8.27	0.48

the facet for the tibia shows a circular outline. The cuboid facet shows a piriform outline with a rather enlarged and slightly concave surface.

Remarks. The caudal half of calcaneus is proportionally robuster in *H. balearicus* than in *O. cuniculus* and *L. granatensis* because the caudal side of the cuboid facet is less pronounced. The lateroproximal astragalus facet is concave in *H. balearicus*, while it shows a marked convexity in *O. cuniculus* and *L. granatensis*. The form of the lateral outline of the tibial facet of *H. balearicus* shows an intermediate curvature, different from those in *L. granatensis* (clearly circular) and *O. cuniculus* (eliptico-oval).The mediolateral diameter of calcaneus of *H. balearicus* is larger than in *O. cuniculus* but smaller than in *B. monticularis* (Table 11).

BODY SIZE

The postcranial of *H. balearicus* (Tables 5, 7-10) provides overall smaller values than the European species included in the *Hypolagus* genus. This is also the case of the toothrow length, whereas in some North American species values are inferior (*Hypolagus furlongi* Gazin, 1934 and *Hypolagus edensis* Frick, 1921) or similar (*Hypolagus gidleyi* White, 1988) to the maximum value of *H. balearicus* (Table 2). In contrast, the maximum value of the mandibular body height in *H. balearicus* lies within the range of *Hypolagus peregrinus* Fladerer & Fiore, 2003 and is slightly larger than single specimen of *Hypolagus brachygnatus* Petényi, 1864 (Fostowicz-Frelik 2007a: table 12).

The estimated body mass ranges between 1.3 and 2.7 kg. However, it is likely that the maxi-

FIG. 9. — **A**, Distal epiphysis of the right tibia of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 (IPS-61659) in ventral (**left**), caudal (**middle**) and lateral (**right**) views; **B**, Proximal epiphysis of the second metacarpal of *H. balearicus* (IPS-61607) in dorsal (**left**), medial (**middle-left**), lateral (**middle-right**) and caudal (**right**) views; **C**, Proximal epiphysis of the left femur of *H. balearicus* (IPS-26589) in dorsal (**left**) and ventral (**right**) views; **D**, Right navicular of *H. balearicus* (IPS-61660) in caudal (**left**), cranial (**middle**), cranial (**right**) and lateral (**below**) views. Abbreviations: **1**, calcaneus facet; **2**, separation zone between the calcaneus facet and the astragalus facet; **3**, lateral astragalus facet; **4**, medial astragalus facet; **5**, trapezoid pit; **6**, capitatum facet; **7**, first metacarpal facet; **8**, third metacarpal facet; **9**, astragalus pit; **10**, plantar process; **11**, cuboid facet; **a**, separation line between the lateral portion and the medial of the lateral astragalus facet. Scale bars: A, D, 3 mm; B, 2 mm; C, 10 mm.

TABLE 7. — Anteroposterior and transvesal diameter (in mm) of the ulnar diaphysis of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 in relation to other leporids.

		Thickness		
Species	**n**	**Max.-min.**	**Mean**	**SD**
Lepus capensis Linnaeus, 1758	4	1.66-0.96	1.32	0.32
Sylvilagus audubonii (Baird, 1858)	13	1.87-1.15	1.43	0.22
Lepus californicus Gray, 1837	5	1.61-1.05	1.43	0.22
Bunolagus monticularis (Thomas, 1903)	2	1.57-1.47	1.52	0.06
Lepus granatensis Rosenhauer, 1856	3	1.98-1.16	1.56	0.40
Sylvilagus brasiliensis (Linnaeus, 1758)	2	1.66-1.58	1.62	0.05
Lepus callotis Wagler, 1830	1	–	1.62	–
Lepus saxatilis F. Cuvier, 1823	6	2.30-0.73	1.64	0.55
Sylvilagus nuttallii (Bachman, 1837)	2	1.87-1.45	1.66	0.29
Lepus crawshayi De Winton, 1899	3	1.99-1.47	1.68	0.27
Sylvilagus floridanus (J. A. Allen, 1890)	5	1.98-1.63	1.76	0.15
Lepus castroviejoi Palacios, 1976	2	1.87-1.82	1.84	0.03
Nesolagus netcheri (Schlegel, 1880)	1	–	2.00	–
Oryctolagus cuniculus (Linnaeus, 1758)	15	2.50-1.61	2.07	0.22
Pronolagus rupestris (A. Smith, 1834)	3	2.69-1.82	2.33	0.45
Poelagus marjorita (St. Leger, 1932)	1	–	2.41	–
Caprolagus hispidus (Pearson, 1839)	1	–	2.64	–
Hypolagus balearicus	1	–	2.64	–
Pentalagus furnessi (Stone, 1900)	3	2.90-2.60	2.78	0.15
Pronolagus randensis Jameson, 1907	2	3.19-2.74	2.97	0.31
Pronolagus crassicaudatus (I. Geoffroy, 1832)	3	3.32-2.74	3.08	0.30
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	7-6	5.92-4.91	5.23	0.42

	Width		
Species	**Max.-min.**	**Mean**	**SD**
Sylvilagus audubonii	3.42-2.48	2.94	0.29
Sylvilagus nuttallii	3.05-2.88	2.97	0.12
Sylvilagus brasiliensis	3.26-2.77	3.02	0.34
Bunolagus monticularis	3.15-3.12	3.13	0.02
Lepus granatensis	3.69-2.97	3.24	0.39
Sylvilagus floridanus	3.91-3.33	3.49	0.22
Lepus capensis	3.88-3.40	3.55	0.22
Lepus californicus	3.88-3.30	3.60	0.26
Nesolagus netcheri	–	3.71	–
Oryctolagus cuniculus	4.31-3.34	3.72	0.30
Lepus crawshayi	4.27-3.00	3.75	0.66
Pronolagus rupestris	4.49-3.71	4.03	0.41
Lepus callotis	–	4.17	–
Lepus saxatilis	4.96-3.26	4.20	0.65
Caprolagus hispidus	–	4.26	–
Lepus castroviejoi	4.47-4.06	4.26	0.28
Hypolagus balearicus	–	4.37	–
Pronolagus randensis	4.66-4.56	4.61	0.06
Pronolagus crassicaudatus	4.96-4.23	4.67	0.38
Poelagus marjorita	–	4.86	–
Pentalagus furnessi	5.31-4.74	5.00	0.28
Nuralagus rex	10.22-7.95	9.65	0.84

mum value was slightly larger, due to the larger size of one of the mandibles from Ses Fontanelles (IPS-26591).

Broadly speaking, *H. balearicus* could be considered a small species in comparison to other Eurasian species included in the same genus

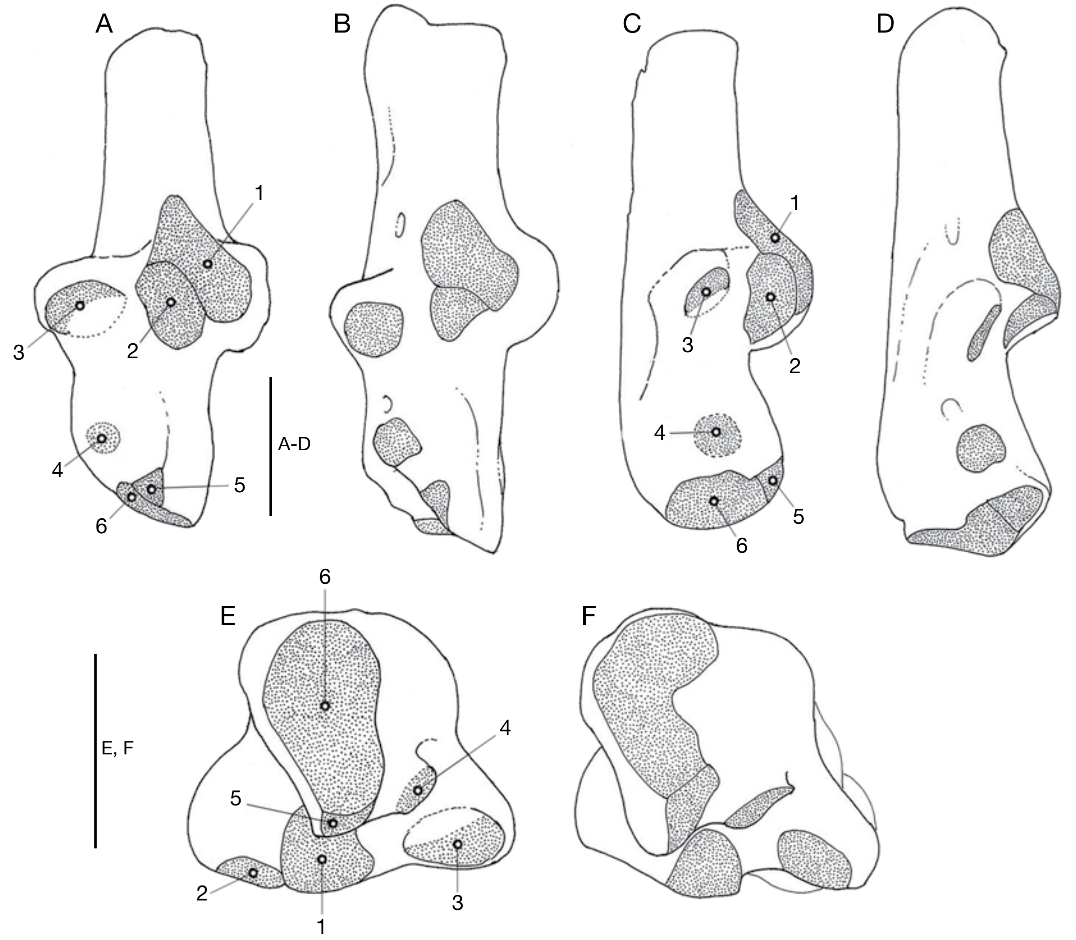

Fig. 10. — Right calcaneus of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 (IPS-41732) in cranial (**A**), medial (**C**) and ventral (**E**) views and of *O.cuniculus* (Linnaeus, 1758) in cranial (**B**), medial (**D**) and ventral (**F**) views. Abbreviations: **1**-**5**, astragalus facets; **6**, cuboid facet. Scale bars: 5 mm.

(*H. petenyii*, *H. schreuderae* Teilhard de Chardin, 1940 and *H. gromovi* Gureev, 1964).

DISCUSSION

Our allometric analysis, which relates length of humerus and transversal diameter of the distal humerus with the body mass, offers very interesting preliminary results. Here, *H. balearicus* shows similar proportions to *P. furnessi* (Fig. 6). The robustness of the humerus (relation between length and transversal diameter of the diaphysis) is 13.04, similar to that observed in both the Jameson's Red Rock Hare (*Pronolagus randensis* Jameson, 1907) (13.03) and *P. furnessi* (12.98).

On the other hand, the relation between the transversal and the anteroposterior diameter of the diaphysis of the ulna and body mass (Fig. 8) indicates that the proportions of *H. balearicus* are similar to that of the rest of leporids, except for those species included in the genus *Lepus* Linnaeus, 1758. Regarding the shape of the diaphysis (relation between the transversal diameter and the

Table 8. — Proximal anteroposterior and transversal diameter (in mm) of the second metacarpal of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 in relation to other leporids. Data sources of *H. petenyii* Čermák & Fladerer *in* Čermák, 2009 and *H. brachygnathus* (Petényi, 1864): Fostowicz-Frelik (2007a, b).

		Proximal width		
	n	**Max.-min.**	**Mean**	**SD**
Sylvilagus audubonii (Baird, 1858)	4	2.73-2.28	2.50	0.18
Sylvilagus nuttallii (Bachman, 1837)	2	2.58-2.52	2.55	0.04
Sylvilagus brasiliensis (Linnaeus, 1758)	2	2.80-2.69	2.74	0.07
Sylvilagus floridanus (J. A. Allen, 1890)	3	2.98-2.66	2.76	0.18
Oryctolagus cuniculus (Linnaeus, 1758)	15	3.36-2.64	3.03	0.21
Bunolagus monticularis (Thomas, 1903)	2	3.27-3.10	3.18	0.11
Hypolagus balearicus	2	3.71-3.02	3.36	0.48
Lepus granatensis Rosenhauer, 1856	1	–	3.44	–
Hypolagus petenyii	4	–	3.50	–
Lepus californicus Gray, 1837	5	4.03-3.36	3.63	0.24
Pronolagus rupestris (A. Smith, 1834)	2	3.77-3.53	3.65	0.17
Hypolagus petenyii	14	–	3.70	0.30
Poelagus marjorita (St. Leger, 1932)	1	–	3.79	–
Hypolagus petenyii	5	–	3.80	0.30
Pentalagus furnessi (Stone, 1900)	2	3.89-3.87	3.88	0.01
Lepus capensis Linnaeus, 1758	2	3.98-3.90	3.94	0.05
Lepus saxatilis F. Cuvier, 1823	6	4.68-3.04	3.94	0.53
Hypolagus petenyii	21	–	4.00	0.30
Lepus castroviejoi Palacios, 1976	1	–	4.11	–
Hypolagus brachygnathus	5	–	4.50	0.20
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	13	8.45-6.26	7.46	0.57

		Proximal thickness		
	n	**Max.-min.**	**Mean**	**SD**
Sylvilagus audubonii	4	3.60-2.89	3.20	0.32
Sylvilagus nuttallii	2	3.41-3.22	3.31	0.13
Sylvilagus brasiliensis	2	3.55-3.39	3.47	0.11
Sylvilagus floridanus	3	4.01-3.09	3.58	0.46
Hypolagus balearicus	2	4.01-3.23	3.62	0.55
Oryctolagus cuniculus	15	4.16-3.34	3.69	0.24
Bunolagus monticularis	2	3.85-3.66	3.76	0.13
Lepus granatensis	1	–	4.17	–
Hypolagus petenyii	5	–	4.40	0.20
Lepus californicus	5	4.78-4.12	4.42	0.23
Hypolagus petenyii	4	–	4.60	–
Poelagus marjorita	1	–	4.65	–
Hypolagus petenyii	14	–	4.70	0.30
Pronolagus rupestris	2	5.09-4.47	4.78	0.44
Lepus saxatilis	6	5.65-3.78	4.82	0.62
Lepus capensis	2	5.00-4.71	4.85	0.20
Hypolagus petenyii	21	–	4.90	0.40
Lepus castroviejoi	1	–	5.09	–
Hypolagus brachygnathus	4	–	5.10	–
Pentalagus furnessi	2	5.48-5.22	5.35	0.18
Nuralagus rex	12	8.84-7.00	7.80	0.57

anteroposterior diameter), *H. balearicus* is situated (with a value of 1.65) between *Caprolagus hispidus* (Pearson, 1839) (1.61) and *Pronolagus rupestris* (1.72).

The robust diaphysis distinguishes clearly *H. balearicus* from the *Lepus* genus, the leporid group better adapted to races. The similitudes between the proportions of *H. balearicus*, *P. furnessi*

Table 9. — Transversal diameter (in mm) of the femoral head of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 compared to other leporids. Data sources of *H. petenyii* Čermák & Fladerer *in* Čermák, 2009: Fostowicz-Frelik (2007b).

		Width of the head		
	n	**Max.-min.**	**Mean**	**SD**
Sylvilagus audubonii (Baird, 1858)	18	5.71-4.72	5.15	0.29
Sylvilagus nuttallii (Bachman, 1837)	2	5.36-5.30	5.33	0.04
Sylvilagus brasiliensis (Linnaeus, 1758)	2	6.08-5.49	5.79	0.41
Sylvilagus floridanus (J. A. Allen, 1890)	6	6.93-5.84	6.16	0.43
Oryctolagus cuniculus (Linnaeus, 1758)	17	6.99-5.40	6.18	0.43
Nesolagus netscheri (Schlegel, 1880)	1	–	6.24	–
Bunolagus monticularis (Thomas, 1903)	2	7.02-6.69	6.85	0.23
Pronolagus rupestris (A. Smith, 1834)	4	8.29-6.03	6.98	0.95
Hypolagus balearicus	1	–	7.29	–
Hypolagus petenyii	33	–	7.60	0.40
Lepus capensis Linnaeus, 1758	4	8.42-7.58	7.86	0.37
Lepus californicus Gray, 1837	6	8.19-7.83	8.01	0.13
Poelagus marjorita (St. Leger, 1932)	1	–	8.11	–
Pronolagus randensis Jameson, 1907	2	8.40-7.93	8.16	0.33
Lepus granatensis Rosenhauer, 1856	3	8.44-8.11	8.23	0.18
Lepus saxatilis F. Cuvier, 1823	6	9.86-7.00	8.34	0.96
Pronolagus crassicaudatus (I. Geoffroy, 1832)	3	8.88-7.97	8.47	0.46
Caprolagus hispidus (Pearson, 1839)	1	–	8.54	–
Pentalagus furnessi (Stone, 1900)	4	8.99-7.83	8.59	0.53
Lepus crawshayi De Winton, 1899	3	9.22-8.27	8.85	0.51
Lepus castroviejoi Palacios, 1976	2	9.19-8.72	8.95	0.32
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	26	15.84-13.74	14.57	0.54

and the genera *Pronolagus* Lyon, 1904 and *Caprolagus* Blyth, 1845 are likely indicative of a locomotion not based on the velocity, contrary of what happens in *Lepus* and most of the extant leporids. Thus, the species included on the *Pronolagus* and *Caprolagus* genera are adapted to life in rock or high grass "islands" developed on mainland territories (Oliver 1980; Smithers 1983). The existence of secure refuges makes unnecessary the strategy of fast escape, during long time, as defense in front of predators. *Pentalagus furnessi* is a typical insular leporid, evolved in absence of predators and, thus, not a runner. As regard *H. balearicus*, it can be said that, as whether it is an insular leporid or an adapted species to a particular mainland environment, its seems evident that it is not a species adapted specially to race, on the contrary of what happens on *H. petenyii* and *H. brachygnathus* (Petényi, 1864). In these two species, the bones of the limbs are elongated and show locomotor adaptations between *O. cuniculus* and the *Lepus* genera (Fostowicz-Frelik 2007a).

Nevertheless, it seems clear that *H. balearicus* presents certain particular skeletal characteristics that separate it from the other species included in this genus. The fact that the p3 morphology of this taxon corresponds to *Hypolagus* but the postcranial skeleton is quite different in morphology and proportions calls for a reconsideration of the taxonomical position of *H. balearicus*. To a certain extent, some parallelisms can be established between *H. balearicus* and *N. rex*. The Minorcan giant rabbit is an extreme case of insular evolution with a highly modified skeleton (Quintana *et al.* 2011), as the case of *P. furnessi* (Hayashida *et al.* 1976; Otsuka *et al.* 1980, 1981; Yamada & Cervantes 2005). Although this deep skeletal modifications, *N. rex* kept a basic scheme which characterized the p3 of *Alilepus* genus (faced hypoflexus and metaflexus). *H. balearicus* would be a derived species of *Hypolagus* genus (as p3 morphology shows) but adapted to a particular environmental conditions, as some proportions of the postcranial skeleton indicate.

TABLE 10. — Transversal diameter (in mm) of the tibia distal epiphysis of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 compared with other leporids. Data sources of *H. petenyii* Čermák & Fladerer *in* Čermák, 2009 and *H. brachygnathus* (Petényi, 1864): Fostowicz-Frelik (2007a, b).

	n	Max.-min.	Mean	SD
Sylvilagus nuttallii (Bachman, 1837)	1	–	9.03	–
Sylvilagus audubonii (Baird, 1858)	5	10.03-8.41	9.20	0.71
Sylvilagus brasiliensis (Linnaeus, 1758)	2	9.92-9.35	9.63	0.39
Nesolagus netcheri (Schlegel, 1880)	1	–	10.28	–
Sylvilagus floridanus (J. A. Allen, 1890)	5	11.20-9.84	10.48	0.53
Oryctolagus cuniculus (Linnaeus, 1758)	15	12.38-10.16	11.24	0.55
Hypolagus balearicus	1	–	11.35	–
Bunolagus monticularis (Thomas, 1903)	2	12.28-11.55	11.91	0.51
Hypolagus petenyii	1	–	12.00	–
Pronolagus rupestris (A. Smith, 1834)	4	13.28-11.37	12.09	0.89
Hypolagus petenyii	45	–	13.00	0.60
Poelagus marjorita (St. Leger, 1932)	1	–	13.08	–
Hypolagus petenyii	12	–	13.10	0.60
Lepus californicus Gray, 1837	6	14.03-11.99	13.10	0.65
Lepus granatensis Rosenhauer, 1856	3	13.42-13.00	13.24	0.21
Caprolagus hispidus (Pearson, 1839)	1	–	13.26	–
Lepus capensis Linnaeus, 1758	4	14.64-12.13	13.36	1.04
Lepus saxatilis F. Cuvier, 1823	6	15.64-11.45	13.54	1.39
Hypolagus petenyii	6	–	13.70	0.40
Lepus crawshayi De Winton, 1899	3	14.31-12.84	13.81	0.84
Pronolagus crassicaudatus (I. Geoffroy, 1832)	3	14.49-13.51	13.94	0.50
Pronolagus randensis Jameson, 1907	2	14.05-14.00	14.02	0.03
Lepus castroviejoi Palacios, 1976	2	15.17-13.86	14.51	0.92
Hypolagus brachygnathus	19	–	14.90	0.70
Pentalagus furnessi (Stone, 1900)	3	15.72-15.48	15.58	0.12
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	8	25.06-22.28	23.98	0.99

PALAEOBIOGEOGRAPHIC CONSIDERATIONS

Several authors, especially in the early eighties of the last century, have proposed different biogeographic scenarios and theories to explain the colonization and evolution of the post-Messinian vertebrate faunas of the Balearic Islands (Moyà-Solà & Pons-Moyà 1980; Alcover *et al.* 1981; Pons-Moyà *et al.* 1981; Moyà-Solà *et al.* 1984b, 1999; Alcover & Agustí 1985; Quintana 1998, 2005; Quintana & Agustí 2007; Bover *et al.* 2008; Pons-Monjo *et al.* 2010).

The discovery of the so-called post Messinian "Early Faunas" from Eivissa and Mallorca (Moyà-Solà *et al.* 1984b; Quintana *et al.* 2010) and the (chronologically proximate) equivalent from Menorca (Quintana *et al.* 2011) has provided relevant data of the colonization process and the post-Messinian evolution. In order to understand properly the significance of the fauna found in Ses Fontanelles and the special anatomical traits of *H. balearicus*, it is necessary to locate and relate this fauna with the different faunistic events which define the evolution of the insular vertebrate faunas during Balearic Neogene (Fig. 11). In this paleobiogeographic context, the following aspects should be taken into account:

– 1) an important biodiversity decline occurred during the Early Pliocene after the isolation of the faunal assemblages probably arrived during Messinian;

– 2) between the Late Pliocene and the Early Pleistocene, a new faunal impoverishment took place, likely triggered by climatic factors affecting the herpetological faunas of the three islands and the mammals from Eivissa and Menorca. In fact, some authors (Bailon 1991; García-Porta *et al.*

TABLE 11. — Calcaneous transversal diameter (in mm) of *H. balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 compared to other leporids. Data sources of *H. petenyii* Čermák & Fladerer *in* Čermák, 2009: Fostowicz-Frelik (2007b).

	n	Max.-min.	Mean	SD
Sylvilagus nuttallii (Bachman, 1837)	1	–	6.93	–
Sylvilagus audubonii (Baird, 1858)	4	7.65-6.95	7.28	0.36
Sylvilagus brasiliensis (Linnaeus, 1758)	2	8.01-7.70	7.86	0.21
Oryctolagus cuniculus (Linnaeus, 1758)	15	9.16-7.96	8.49	0.37
Sylvilagus floridanus (J. A. Allen, 1890)	3	9.04-8.69	8.83	0.18
Hypolagus balearicus	1	–	9.05	–
Bunolagus monticularis (Thomas, 1903)	2	9.27-9.20	9.23	0.05
Hypolagus petenyii	63	–	9.50	0.60
Pronolagus rupestris (A. Smith, 1834)	2	11.33-9.10	10.21	1.58
Lepus californicus Gray, 1837	6	10.90-9.71	10.29	0.41
Lepus granatensis Rosenhauer, 1856	3	10.74-10.33	10.49	0.22
Poelagus marjorita (St. Leger, 1932)	1	–	10.53	–
Lepus capensis Linnaeus, 1758	2	11.55-10.22	10.88	0.94
Lepus saxatilis F. Cuvier, 1823	6	12.65-9.22	11.02	1.21
Caprolagus hispidus (Pearson, 1839)	1	–	11.26	–
Pronolagus randensis Jameson, 1907	2	11.50-11.23	11.36	0.19
Lepus castroviejoi Palacios, 1976	1	–	11.61	–
Pentalagus furnessi (Stone, 1900)	3	13.35-11.66	12.59	0.86
Nuralagus rex Quintana, Köhler & Moyà-Solà, 2011	16	20.09-16.29	18.43	1.01

2002) appeal to climatic causes to explain the biodiversity declines of the herpetological faunas from Western Europe during the Late Pliocene;
– 3) associated to this climatic event was the disappearance of large terrestrial turtles on Mallorca and Menorca. Nevertheless, some authors (Alcover *et al.* 1981; Bour 1985; Alcover & Bover 2002; Bover *et al.* 2008) situate the Eivissa turtle in the Early or Middle Pleistocene, without any type of geological argument supporting this affirmation. The findings of large terrestrial turtles at certain sites of the Balearic Islands could be interpreted as a reliable criterion for dating these sites as pre-Pleistocene in Mallorca and Menorca but not in Ibiza, where a more precision dating of the terrestrial turtles sites is need;
– 4) on Mallorca, the taxa that survived the Early Pliocene event are present during the whole Pleistocene on the island until the arrival of the first humans;
– 5) the climatic changes in the Late Pliocene-Early Pleistocene were especially important for the faunas of Mallorca and Menorca. On the one hand, it may have caused the extinction of the faunas associated to *N. rex* on Menorca. On the other hand, due to the geographic proximity of the two islands and the little bathymetric differences, it facilitated the Mallorcan faunal complex associated to the genus *Myotragus* Bate, 1909 to colonize Menorca during the Early Pleistocene (Alcover *et al.* 1981).

From this event onwards, the Pleistocene faunas of Mallorca and Menorca remain very similar, because periods of isolation and genetic differentiation between populations of the two islands (warm climatic periods) alternate with homogenization periods during colder intervals (Pons-Monjo *et al.* 2010).
– and 6) the arrival of the first humans at Balearic Islands led to the extinction of almost all endemic vertebrates of the archipelago (Ramis & Alcover 2001a, b; Ramis & Bover 2001; Alcover *et al.* 2001; Ramis *et al.* 2002).

CONCLUSIONS

The recovery of new remains of *H. balearicus* from the Pliocene site of Ses Fontanelles (Eivissa) provides a more precise understanding of the adaptations of a

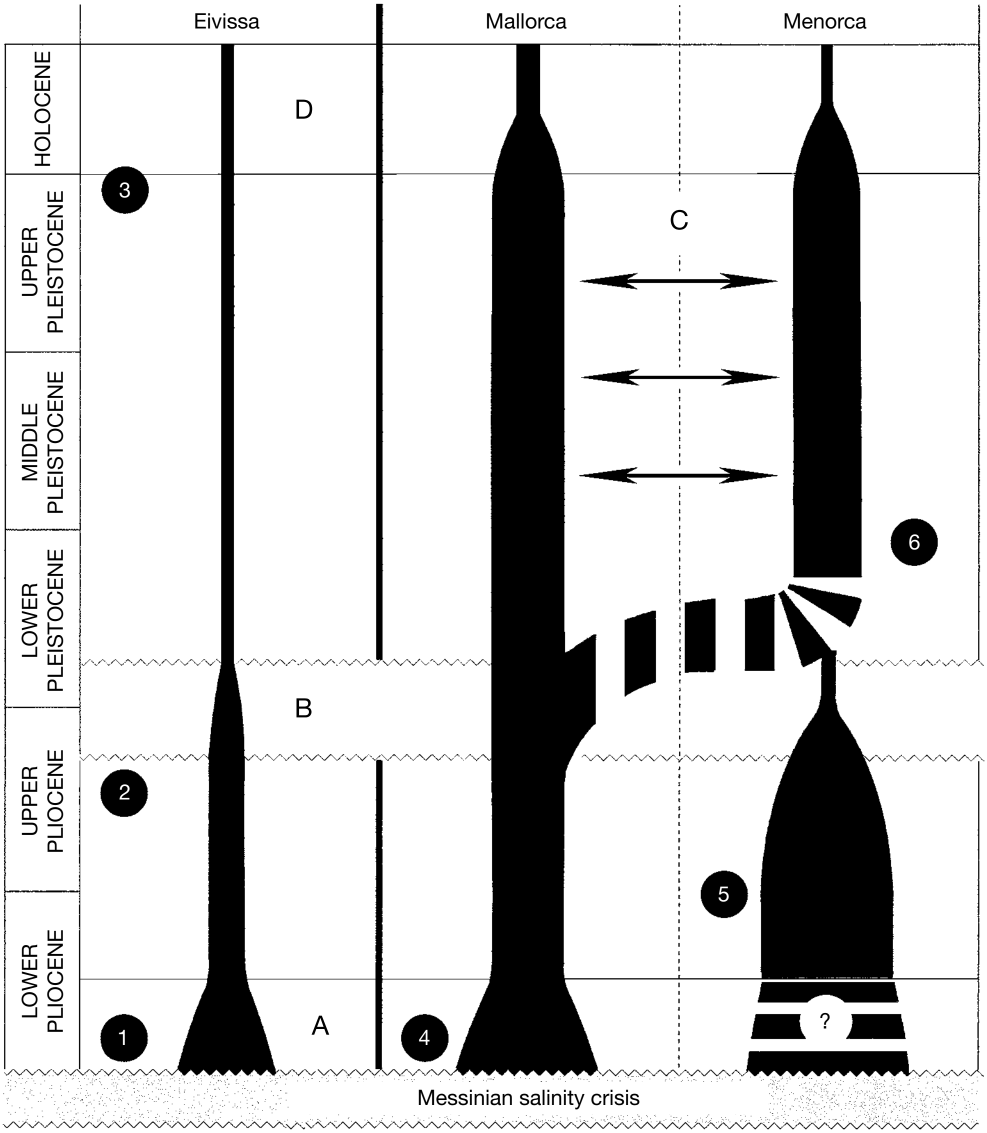

Fig. 11. — Biogeographic scheme of the Balearic Islands, from the Messinian regression to the arrival of the first humans to the archipelago. The diameter of the vertical columns is proportional to the number of flightless terrestrial vertebrates present in each island. Chronological interval corresponding to the "Early Faunas" (**A**), the climatic cooling of the Plio-Pleistocene limit (**B**), faunistic exchanges between Mallorca and Menorca (**C**) and the arrival of the first humans to the Balearic archipelago (**D**). The sites represented here are: Ses Fontanelles (❶), Caló d'en Rafelino (❹), Punta Nati (❺), Cova de Ca na Reia and inferior (❷) and superior levels of Es Pouàs (❸) and Binigaus deposit (❻).

leporid originally described from some scarce remains from Mallorca (Quintana *et al.* 2010). The differences found between both populations are rather negligible and most likely attributable to intraspecific variation amongst individuals of the two geographically (and temporally) proximate populations of this species.

Hypolagus balearicus, together with the associated faunal elements of Ses Fontanelles, forms part of the so-called "Early Faunas" that colonized the Balearic Islands during the Messinian regression. The Mallorcan equivalent corresponds to the faunal complex described from the Caló d'en Rafelino site (Quintana *et al.* 2010). The chronological equivalent of these "Early Faunas" has not yet been discovered in Menorca. However, a slightly younger faunistic group described from that island shows a similar composition characterized by a giant rabbit (*N. rex*) that is, however, unrelated (according the p3 morphology) to the genus *Hypolagus*, but instead it is related to the genus *Alilepus* Dice, 1931.

Compared with other European representatives of the same genus, *H. balearicus* must be considered a species of relatively small size, comparable to a medium sized *H. peregrinus* or a small sized *H. brachygnatus*. From the obtained data is not possible to know if the size of *H. balearicus* was similar of its mainland ancestors ones, or, if contrary, it changed as a consequence of the evolution on an island. A reduction of the size seems little probable, due to that the evolutive patterns of the lagomorphs from Balearic Neogene (*N. rex* and *Gymnesicolagus gelaberti* Mein & Adrover, 1982) are characterized by an important increase of the size, which supposes an exception of the "island rule" (van der Geer *et al.* 2010). In this regard, the corporal size of *H. balearicus* (1.3-2.7 kg) is further from the optimal body mass (0.1-1 kg) proposed by "island rule".

The elbow articulation shows a particular morphology in that some pits and crests show an unusually smooth outline. In relation to body mass, length and transversal diameter of the distal epiphysis of the humerus are similar to those of *P. furnessi*. In contrast, the proportions of the transversal and anteroposterior diameter of the ulnar diaphysis are similar to those of the rest of leporids except for the genus *Lepus*.

These differences in morphology of the humerus between *H. balearicus* and other species of *Hypolagus*, and the similarities between the proportions of the humerus of *H. balearicus* and *P. furnessi*, are intriguing, the same as the similitarities in robustness of humerus and ulna of *H. balearicus*, *P. randensis*, *P. rupestris* and *C. hispidus*.

We propose two different hypotheses to explain these observations: a) The morphology and proportion of the humerus and ulna of *H. balearicus* are derived traits as a consequence of the evolution on an island; b) They reflect an adaptation to particular ecological conditions, not necessary connected to an "island" in the classical sense.

Some mainland leporids, such as the African Red Rock Hares (genus *Pronolagus*) or the Assam rabbit (*C. hispidus*), live in rock "islands" or zones with high grass (Ghose 1978; Oliver 1980; Smithers 1983). These rock shelters, or the thick vegetation (especially in *C. hispidus*), do not permit fast race over large distances to escape from predators, as typical in *Lepus*, which could explain the similarities with these taxa. The question of whether *H. balearicus* evolved or not under isolation, however, cannot be resolved on the basis of this limited sample.

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