



General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

First evidence of faunal succession in terrestrial vertebrates of the Plio-Pleistocene of the Balearic Islands, western Mediterranean



Première évidence d'une succession faunique chez les vertébrés terrestres du Plio-Pléistocène des îles Baléares, Méditerranée occidentale

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ABSTRACT

Terrestrial vertebrates from the karst filling in Cap d'Artrutx, situated in the extreme Southwest of Menorca (Balearic Islands, western Mediterranean) have yielded interesting information on the migration and extinction dynamics in the terrestrial island vertebrate faunas in Mallorca and Menorca between the late Pliocene and early Pleistocene. In this site, remains of the Minorcan giant tortoise (*Testudo* *gymnesica* Bate, 1914) and two mammals (*Nesiotites* sp. and *Hypnomys* sp.) have been found. The remains of the Minorcan giant tortoise represent the youngest record of this species and of the so-called second faunistic group of the island. The morphology and size of *Nesiotites* sp. are comparable to those of *Nesiotites* aff. *ponsi* Reumer, 1979 from the Plio-Pleistocene of Pedrera de S'Ònix (Mallorca) and *Nesiotites* *meloussae* Pons and Moyà, 1980 (= *Nesiotites* aff. *ponsi* sensu Pons-Monjo et al., 2012) from the lower Pleistocene of Binigaus (Menorca). *Hypnomys* sp. can belong to an archaic species not yet described. They represent the first evidence of the entrance of the third faunistic group, which originally evolved on the neighbouring island of Mallorca. This association is interpreted, therefore, as the first evidence of a faunal succession in the Plio-Pleistocene in the Balearic Islands.

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R É S U M É

L'étude d'ossements de vertébrés terrestres du gisement d'origine karstique du cap d'Artrutx, situé dans l'extrême Sud-Ouest de Minorque (îles Baléares, en Méditerranée occidentale), ont fourni des données très intéressantes relatives à la dynamique de migration et d'extinction des faunes de vertébrés terrestres insulaires de Majorque et Minorque pendant le Pliocène supérieur et le Pléistocène inférieur. Dans le gisement ont été découverts des restes de la tortue géante de Minorque (*T. » gymnesica*) et de deux mammifères

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(*Nesiotites* sp. et *Hypnomys* sp.). Dans ce contexte, les restes de tortue géante de Minorque représentent l'enregistrement le plus récent de cette espèce et du soi-disant deuxième groupe faunique de l'île, alors que les deux espèces de mammifères correspondent à la première évidence de l'arrivée d'un troisième groupe faunique originaire de Majorque, île voisine où il a évolué. Cette association est donc interprétée comme une première évidence de succession faunique dans le Plio-Pléistocène des îles Baléares.

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1. Introduction

Of the three islands that form the Balearic archipelago, Menorca is the second largest in size (702 km²) and the island which is located furthest from the European and African continents, as it is situated in the centre of the western Mediterranean. Its reduced size and isolation have had a notable influence during the periods of colonization of the different groups of terrestrial vertebrates between the middle Miocene and the Pleistocene (Quintana and Agustí, 2007; Quintana and Moncunill-Solé, 2014).

In the case of the Balearic Islands, the reciprocal influences among the faunas of each island is evident from, principally, the palaeontological record preserved in the red limestones deposited in the interior part of caves. The influence between islands is not surprising, given their proximity (Mallorca, which is located in the centre of the archipelago is separated from Eivissa and Menorca by 81.5 and 36.5 km, respectively). Because of this, Mallorca presents some common faunistic elements with the so-called early faunas of Eivissa (Bover et al., 2014; Quintana and Moncunill-Solé, 2014). Until now, Mallorca was considered to be the origin of the Pleistocene fauna in Menorca (Moyà-Solà and Pons-Moyà, 1980), which, seemingly abruptly, appears in the fossil record of the island.

In contrast to what occurred in Mallorca and Eivissa, up to now, no sites have been found in Menorca preserving evidence of the arrival of the early faunas of the Messinian or early Pliocene, which should include, hypothetically, remains from the ancestor of the Menorcan giant rabbit (*Nuralagus rex*, Quintana, Köhler and Moyà-Solà, 2011). Until now, there was no “early evidence” of the first arrival in Menorca of the Pleistocene fauna from Mallorca, that is, the concurrence, at the same site, of remains belonging to the two faunistic groups.

In this way, the fauna described at Binigaus (Es Migjorn Gran, Menorca) (Agustí, 1980; Moyà-Solà and Pons-Moyà, 1980; Pons-Moyà and Moyà-Solà, 1980) cannot be considered as an early evidence, given that, only remains from one faunistic group have been found. The fauna present in the promontory of Bajolí described by Bate (1914) (equivalent to sites 15 and 16 in the Punta Esquixador area, located in the Northeast of Bajolí) (Quintana, 1998) cannot be considered an early evidence site either, given that the remains of the Menorca giant tortoise and *Myotragus* sp. were found in two clearly different outcrops, both from a geological and temporal point of view. A confirmation of the latter is that, on occasions, the clear coloured limestones with

Myotragus sp. include re-sedimented red limestones stones with remains of “*Testudo*” *gymnesica* (Quintana, 1998).

This paper arises from the study of two known Menorcan sites (Cala en Bastó and Bol de Ses Sirvies; Quintana, 1995, 1998) and an unpublished one (Cap d'Artrutx). At first, the main purpose of this study was to find deposits with remains of the ancestor of the Menorcan giant rabbit. In Cala en Bastó and Bol de Ses Sirvies, no remains of mammals have been found. However, the study of the Cap d'Artrutx deposit has provided very few but very interesting remains, the study of which is presented now.

2. Methods

The remains studied were recovered by chemical means, treating the matrix with acetic acid diluted to 10%. Once separated from the matrix, the remains were submerged in water to neutralize the residual acid and calcium acetate. Subsequently the fossils were dried and consolidated by applying Paraloid B-72. The acid treatment affected, unexpectedly, the most fragile parts of one of the examples (the mandibular branch of *Nesiotites* sp.), in such a way that the chemical treatment was stopped, in order to avoid breakage of the mandibular body. Once consolidated, the mandible was separated using manual methods, reducing the matrix with a rounded file of a small caliber (1 mm in diameter).

The measurements of the specimens were done based on photographs, using a digital camera incorporated in a stereoscopic microscope with a micrometric eyepiece. The measurements made on the photographs were taken with a digital calibrator with a ± 0.01 mm margin of error. The specimens are stored in the Museu Municipal des Bastio de sa Font (acronym: MMBF) (Ciutadella de Menorca, Balearic Islands, Spain).

2.1. Geographical and geological context

The studied site is located on the eastern margin of Punta des Bregarol, to the east of Cap d'Artrutx (Ciutadella de Menorca) (Fig. 1). The red limestones with the remains of the vertebrates are found inside a small cave (Fig. 2) very close to the sea. The red limestones cover the base of the cave and the west wall, where they are better exposed. On the floor, the thickness is less, as it has suffered more wear due to erosion, as can be deduced from the irregular morphology in the area.

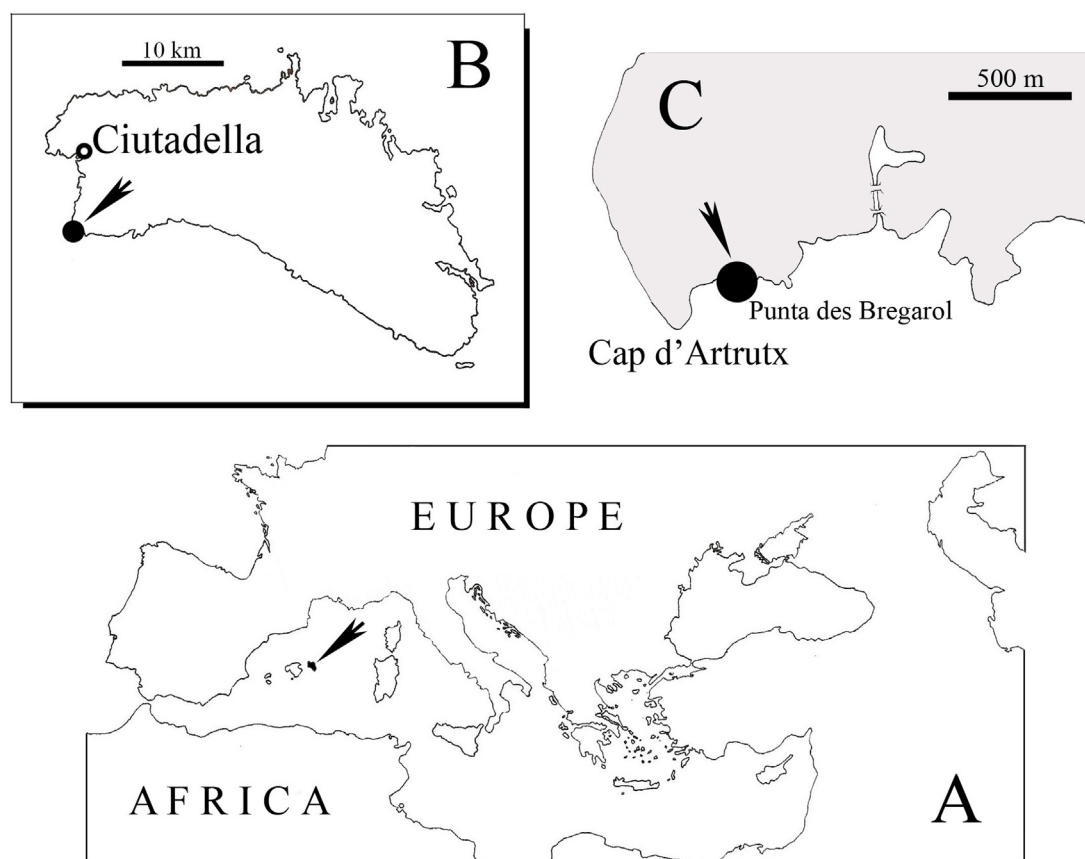


Fig. 1. Geographical situation of the Punta des Bregarol cave (Menorca, Balearic Islands).

Fig. 1. Situation géographique de la grotte de Punta des Bregarol (Minorque, îles Baléares).

The Miocene calcarenites in which the cave is excavated are interpreted as belonging to a reef formation of Messinian age by Rosell et al. (1989). Moreover, Obrador and Pomar (2004: fig. 4.1) consider that the margin of the southwestern end of Menorca (where the studied site is located) is included in the Reef Unit, which Pomar (2001 and Pomar et al., 1996) situate in the upper Tortonian-lower Messinian. Taking into consideration the geological evidence and the chronology that this provides, it is only possible to say that the reddish silts and the fauna that they contain are, at least, after the lithification, emersion and carstification of the limestones of the Reef Unit, which is to say, after the early Messinian. However, the chronological context of the site is established more precisely from its faunal peculiarities and the relation with the different groups of terrestrial vertebrates present in the Neogene in the Balearic Islands, as will be discussed in more detail in the section on biogeographical implications.

2.2. Systematic Palaeontology

“Testudo” gymnesica Bate, 1914

The giant tortoise from the Pliocene in Menorca is undergoing taxonomic revision. Therefore, in this paper the original name is preserved. Luján et al. (2017)

tentatively assigned the type specimens stored at the National History Museum (London, United Kingdom) to aff. *Titanochelon gymnesica* (Bate, 1914). The genus *Cheirogaster* Bergounioux, 1935, which was used by various authors (Jiménez Fuentes and Martín de Jesús, 1991; Luján et al., 2014; Quintana, 1995, 1998), is only valid for one species from the Eocene in France (Pérez-García et al., 2016).

Despite their fragmentary state, the attribution of the remains to the giant turtle of Menorca is safe, because of their relatively large size and their characteristic bone structure.

Nesiotites sp. (Fig. 3)

Material. A right mandible (MMBF/CA-1), which is missing the anterior end of the incisor and the condylar process.

Description. The premolars and molars show no significant morphological differences when compared with *Nesiotites* aff. *ponsi* Reumer, 1979, *Nesiotites meloussae* Pons and Moyà, 1980 (= *Nesiotites* aff. *ponsi* sensu Pons-Monjo et al., 2012) and *Nesiotites hidalgo* Bate, 1944. Notably, there are cusps on the oblique ridge of the m1 and the m2 of *Nesiotites* sp., although it is true that this characteristic has also been observed in the aforementioned species (Pons-Monjo et al., 2012). The size of the molars of *Nesiotites* sp. coincide with the range of variation of *Nesiotites*

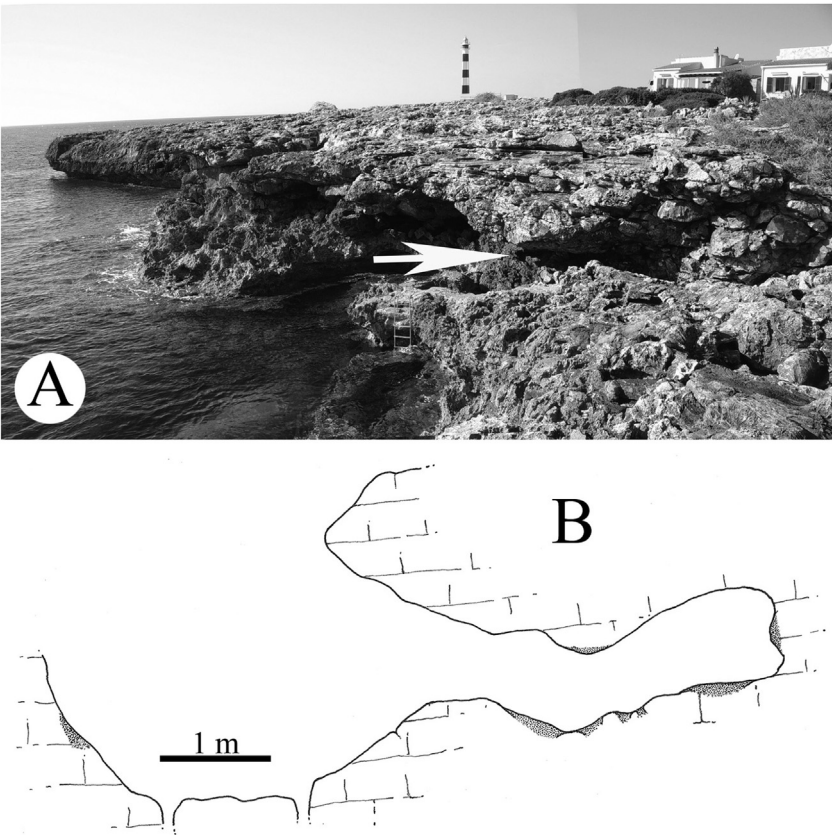


Fig. 2. (A) Panoramic view of the coastal area in which the cave is located with the remains of vertebrates, marked with a white arrow. In the background, towards the west, the lighthouse of Cap d'Artrutx. (B) Cross section of the cave (east–west direction), excavated in the Miocene calcarenites. The grey areas inside the cave represent the red silts in which the remains of vertebrates are conserved.

Fig. 2. (A) Vue panoramique de la zone côtière où est située la grotte avec les restes de vertébrés, marquée par une flèche blanche. À l'arrière-plan, vers l'ouest, le phare du cap d'Artrutx. (B) Coupe est–ouest de la grotte creusée dans les calcarénites miocènes. La zone grise dans la grotte représente les silts rouges dans lesquels les restes de vertébrés sont conservés.

Table 1
Dental measurements of *Nesiotites* sp. (MMBF/CA-1) from Cap d'Artrutx compared with *Nesiotites* aff. *ponsi* (Pedrera de s'Onix, Mallorca), *Nesiotites hidalgo* (Cova de Canet, Mallorca) and *Nesiotites meloussae* (= *Nesiotites* aff. *ponsi* sensu Pons-Monjo et al., 2012) (Barranc de Binigaus, Menorca). Data source: Pons-Monjo et al., 2012. L: length; taw: talonid width; triw: trigonid width; W: width.

Tableau 1
Mesures dentaires de *Nesiotites* sp. (MMBF/CA-1) du cap d'Artrutx, comparées à celles de *Nesiotites* aff. *ponsi* (Pedrera de s'Onix, Majorque), *Nesiotites hidalgo* (cova de Canet, Majorque) et *Nesiotites meloussae* (= *Nesiotites* aff. *ponsi* sensu Pons-Monjo et al., 2012) (Barranc de Binigaus, Minorque). Source des données : Pons-Monjo et al., 2012. L : longueur ; taw : largeur du talonide ; triw : largeur du trigonide ; W : largeur.

		Artrutx		Ònix				Binigaus				Canet			
		<i>n</i>		<i>n</i>	max–min	mean	SD	<i>n</i>	max–min	mean	SD	<i>n</i>	max–min	Mean	SD
m1	<i>L</i>	1	2	25	2.20–1.85	2	0.08	25	2.19–1.93	2.04	0.07	25	2.31–2.09	2.17	0.06
	taw	1	1.36	25	1.40–1.04	1.27	0.08	25	1.38–1.16	1.3	0.05	25	1.55–1.37	1.43	0.04
	triw	1	1.19	25	1.29–1.02	1.15	0.08	25	1.22–1.03	1.14	0.06	25	1.35–1.13	1.23	0.05
m2	<i>L</i>	1	1.71	25	1.96–1.72	1.84	0.07	25	1.95–1.75	1.87	0.06	25	2.10–1.88	1.99	0.07
	taw	1	1.12	25	1.18–1.03	1.12	0.04	25	1.25–1.02	1.12	0.06	25	1.26–1.09	1.21	0.04
	triw	1	1.04	25	1.15–1.01	1.09	0.05	25	1.23–1.00	1.09	0.06	25	1.29–1.12	1.21	0.04
m3	<i>L</i>	1	1.35	25	1.45–1.28	1.36	0.06	21	1.55–1.35	1.44	0.05	25	1.73–1.38	1.5	0.078
	<i>W</i>	1	0.87	25	0.94–0.73	0.83	0.05	21	0.90–0.72	0.81	0.05	25	0.98–0.77	0.86	0.05

aff. *ponsi* (Pedrera de s'Onix, Mallorca) and *Nesiotites meloussae* (Barranc de Binigaus, Menorca) In their smaller size, they are clearly different from those of *Nesiotites hidalgo* (Table 1).

Hypnomys sp. (Fig. 4; Table 2)
Material. An incomplete left mandible with p4-m3 (MMBF/CA-2) and a right mandible, also incomplete, with m1-m3 (MMBF/CA-3).

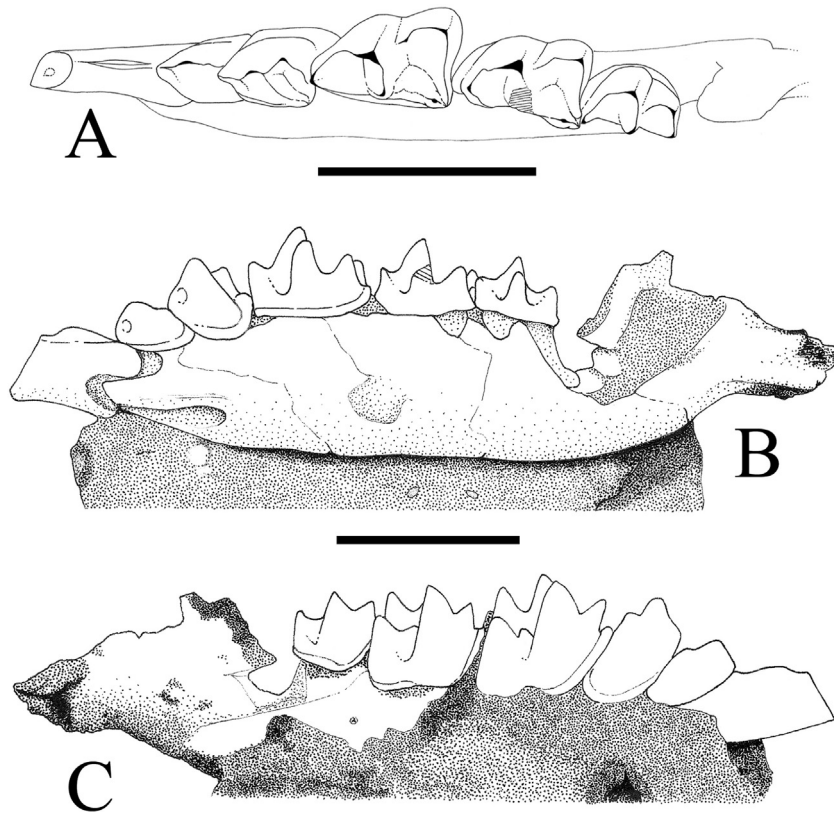


Fig. 3. Right mandible (MMBF/CA-1) of *Nesiotites* sp. in occlusal (A), lingual (B), and lateral (C) views. Scale bar: 3 mm.
Fig. 3. Mandibule droite (MMBF/CA-1) de *Nesiotites* sp. En vues occlusale (A), linguale (B) et latérale (C). Barre d'échelle : 3 mm.



Fig. 4. Left (MMBF/CA-2, A) and a right mandible (MMBF/CA-3, B) of *Hypnomys* sp. Scale bar: 3 mm.
Fig. 4. Mandibules gauche (MMBF/CA-2, A) et droite (MMBF/CA-3, B) d'*Hypnomys* sp. Barre d'échelle : 3 mm.

Table 2Dental measurements of *Hypnomys* sp. from Cap d'Artrutx. L: length; W: width.**Tableau 2**Mesures dentaires d'*Hypnomys* sp. du cap d'Artrutx. L : longueur ; W : largeur.

	p4		m1		m2		m3	
	L	W	L	W	L	W	L	W
MMBF/CA-2	1.43	1.52	2.25	2.21	–	2.58	2.17	2.1
MMBF/CA-3	–	–	2.37	2.1	2.36	2.33	2	1.8

Description. p4: The only available p4 is lingually damaged. Even so, four transverse ridges can be distinguished: anterolophid, metalophid, mesolophid, and posterolophid. The anterolophid and metalophid are almost fused and can hardly be distinguished. The mesolophid and posterolophid, which are labially connected, are well developed.

The m1 has six transverse ridges: anterolophid, metalophid, centrolophid, mesolophid, posterotripid, and posterolophid. The anterolophid is medially interrupted. The metalophid is short, its lingual end connecting the lingual segment of the anterolophid. The centrolophid is long, its labial end connecting with the mesolophid and forming a “Y”-like pattern. The long mesolophid reaches the labial wall of the tooth. The isolated posterotripid is short in one case and long in the other. The hypoconid is anteriorly directed, although it does not connect to the mesoconid, even at a high level of wear.

As in the m1, the m2 has six transverse ridges: anterolophid, metalophid, centrolophid, mesolophid, posterotripid and posterolophid. Other than in the m1, there is in the two cases a continuous anterolophid along the anterior wall of the tooth. Long metalophid, that in one case reaches the metaconid.

The m3 has four transverse ridges: anterolophid, metalophid, mesolophid and posterolophid. A short posterotripid can be distinguished in one of the specimens. Anterolophid and metalophid are both fused labially and lingually, as it is also the case of the mesolophid and posterolophid. In one case, the mesoconid is anteriorly projected, not reaching the protoconid. Metaconid and entoconid are connected, forming a continuous endolophid along the lingual wall of the tooth.

Remarks. Although provisionally included in the genus *Hypnomys*, the two mandibles from Cap d'Artrutx display some features which are different from those observed in that taxon, particularly the medially fused centrolophid and mesolophid, which is present in all of the molars of both mandibles. This characteristic is present in the lower molars of *Margaritamyx llulli* Mein and Adrover, 1982, an endemic glirid from the middle Miocene of Mallorca, described from the sites of Santa Margarita (Mein and Adrover, 1982) and San Lorenzo (Adrover et al., 1985). However, as a difference with the species from Cap d'Artrutx, the lower molars of *Margaritamyx* never present a posterotripid, a characteristic which is always present in *Hypnomys*. Therefore, we assume that the specimens from Cap d'Artrutx can belong to an archaic, not yet described, species of *Hypnomys*. More material will be needed in order to clarify the relationships of the Cap d'Artrutx species with respect other species included in that genus.

3. Biogeographical implications

The finding of three species belonging to two faunal episodes in the same site (Cap d'Artrutx) establishes the first evidence of faunal succession in the terrestrial vertebrates in the Plio-Pleistocene in Menorca. In this site, an endemic vertebrate from the island can be found, belonging to the so-called “second faunal episode of Menorca” (the giant tortoise “*Testudo*” *gymnesica*) together with some species belonging to the “second faunal episode of Mallorca” (*Nesiotites* sp. and *Hypnomys* sp.). These two mammals form, along with the genus *Myotragus* Bate, 1909 (not present in Cap d'Artrutx), the so-called “classic” fauna of the Plio-Pleistocene in Mallorca and the Pleistocene in Menorca. The presence of *Nesiotites* sp. and *Hypnomys* sp. together with the Menorcan giant tortoise is very relevant from a biogeographical point of view, given that it is early evidence of this faunal succession.

Cap d'Artrutx is comparable, to a certain extent, with the Holocene site located at Pas den Revull (Barranc d'Algendar, Ferreries, Menorca) where remains of *Myotragus balearicus* Bate, 1909 occur together with *Oryctolagus cuniculus* (Linnaeus, 1758), clearly of anthropogenic origin (Quintana et al., 2003, 2016). This represent, therefore, early evidence of the entrance into the island of the first domestic faunas. Radiocarbon dating indicates a difference in age of 1170 years in comparing two samples of *Myotragus balearicus*, and between 3655 and 2485 years in comparing the samples of *Myotragus balearicus* with *Oryctolagus cuniculus*. Thus, the presence of different species in the same site does not imply, necessarily, the temporal coexistence of the species. Radiocarbon datings reflect, clearly, a short interval of time during which the endemic species became extinct, supposedly, and domestic species were introduced.

In the specific case of Cap d'Artrutx, it is unknown whether *Nesiotites* sp., *Hypnomys* sp. and “*Testudo*” *gymnesica* are contemporaries and to what extent the age differences are significant. In spite of the lack of absolute dating, several hypotheses have been presented which try to explain the reasons why most of the representatives of the second faunal episode of Menorca became extinct.

In this sense, Alcover et al. (1999) considers that *Myotragus* and the accompanying fauna (*Nesiotites* and *Hypnomys*) would have colonized Menorca during the first Pliocene glaciations, being responsible for the extinction of *Nuralagus rex* and the majority of the vertebrates from the second faunal episode in Menorca (among which “*Testudo*” *gymnesica*), due to a displacement of competitive nature. In contrast to this opinion, Quintana and Moncunill-Solé (2014) consider that it was not a displacement of competitive nature: the extinction of “*Testudo*” *gymnesica* was

motivated by a climate change and was prior to the arrival of *Myotragus*, *Nesiotites* and *Hypnomys* from Mallorca.

The scarcity of remains of micromammals in Cap d'Artrutx also is not only interesting from a taphonomic point of view, but also because of its biogeographical implications. The rarity of these might reflect the existence of populations with few individuals at the moment of formation of the site or it may be due to the lack of vectors responsible for the concentration of these remains, despite the existence of high densities of individuals (e.g., absence, in the vicinity of the site of nocturnal birds of prey).

Notably, the site considered to have the oldest representatives of the genus *Nesiotites*, *Hypnomys* and *Myotragus* in Menorca up to now, Barranc de Binigaus (Es Migjorn Gran; Agustí, 1980; Moyà-Solà and Pons-Moyà, 1980; Pons-Moyà and Moyà-Solà, 1980) is characterized for being extraordinarily rich in remains of small vertebrates and by the absence of “*Testudo*” *gymnesica*. Moyà-Solà and Pons-Moyà (1980) place it, tentatively, in the Early Pleistocene. The characteristics of the site at Binigaus seem to indicate that, once the Menorcan giant tortoise became extinct, there was a significant increase in the density of micromammals originating from Mallorca, whose populations were already established, definitively, in the early Pleistocene.

4. Conclusions

The fauna from the site at Cap d'Artrutx, located in the extreme Southeast of the island of Menorca, consists of two mammals (*Nesiotites* sp. and *Hypnomys* sp.) and the Menorcan giant tortoise (“*Testudo*” *gymnesica*). The Menorcan giant tortoise is, along with *Nuralagus rex*, one of the most representative taxa of the Pliocene and the so-called second faunal episode in Menorca, while *Nesiotites* sp. and *Hypnomys* sp. belong to the third faunal episode. This association is interpreted as the first evidence of a faunal succession in the Plio-Pleistocene in Menorca. It establishes, therefore, early evidence of the presence of the genus *Nesiotites* and *Hypnomys* in Menorca and, apparently, the last record of “*Testudo*” *gymnesica* on the island. The two mammals form part of the faunal “stock” which evolved in Mallorca from the Messinian until the Holocene. Their arrival in Menorca from Mallorca would have occurred in the interval of time situated between the late Pliocene and the early Pleistocene.

The presence of “*Testudo*” *gymnesica* at Cap d'Artrutx indicates that this site is older than the site at Binigaus, which was until now considered to be the site with the oldest representatives of the third faunal episode in Menorca (*Nesiotites meloussae*, *Hypnomys eliomyoides* Agustí, 1980 and *Myotragus binigausensis* Moyà and Pons, 1980) and in which, moreover, remains of the Menorcan giant tortoise had not been found. Cap d'Artrutx is also different from Binigaus in the shortage of remains recovered from *Nesiotites* sp. and *Hypnomys* sp. and by the absence of *Myotragus*. Such characteristics could indicate that Cap d'Artrutx would represent a moment in which the populations of *Nesiotites* and *Hypnomys* sp. were composed of a low number of individuals, at a time in which it is not possible to know precisely whether the Menorcan giant tortoise was extinct and whether *Myotragus* was present on the island. From a

chronological point of view, the site at Cap d'Artrutx is situated, therefore, among the Pliocene sites of Menorca (Punta Nati, Binibèquer, among others), where the remains of “*Testudo*” *gymnesica* are abundant and Binigaus, where the Menorcan giant tortoise appears to be definitively extinct.

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