



General palaeontology, systematics and evolution (Vertebrate palaeontology)

New data on the origin of *Nesiotites* (Soricidae, Mammalia) in Menorca (Balearic Islands, Spain)

Nouvelles données sur l'origine de Nesiotites (Soricidae, Mammalia) à Minorque (Îles Baléares, Espagne)

Guillem Pons-Monjo^a, Salvador Moyà-Solà^b, Marc Furió^{a,*}

^a Institut Català de Paleontologia M. Crusafont, Edifici ICP, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, 08193 Barcelona, Spain

^b ICREA at Institut Català de Paleontologia M. Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

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ABSTRACT

The presence of the shrew *Nesiotites* in Menorca is not yet adequately explained. Some authors consider that its ancestor arrived during the Messinian Salinity Crisis, as happened in Mallorca. Other authors consider that fossil populations in Menorca are the result of a later migration from Mallorca. In this work, several biometrical and morphological characters of abundant fossil populations from both islands have been studied. The results indicate that Early Pleistocene populations in Mallorca and Menorca are rather indistinguishable. Therefore, an early post-Messinian (Pliocene) isolation of *Nesiotites* in both islands is quite unlikely.

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RÉSUMÉ

Mots clés :

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La présence de la musaraigne *Nesiotites* à Minorque n'est pas encore bien expliquée. Certains auteurs considèrent que son ancêtre est arrivé pendant la Crise de Salinité du Messinien au même moment que la colonisation de Majorque. D'autres auteurs considèrent que les populations fossiles de Minorque ont immigré ultérieurement depuis Majorque. Dans ce travail, divers caractères biométriques et morphologiques, d'abondantes populations fossiles provenant des deux îles, ont été étudiés. Les résultats indiquent que les populations du Pléistocène inférieur de Majorque et Minorque sont difficiles à distinguer. Par conséquent, un isolement précoce post-Messinien (Pliocène) de *Nesiotites* dans les deux îles semble peu probable.

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1. Introduction

Nesiotites Bate, 1944 is an extinct genus of shrews that inhabited the Mediterranean islands of Mallorca, Corsica and Sardinia. It was originally described by Dorothea

* Corresponding author.

E-mail address: marc.furio@icp.cat (M. Furió).

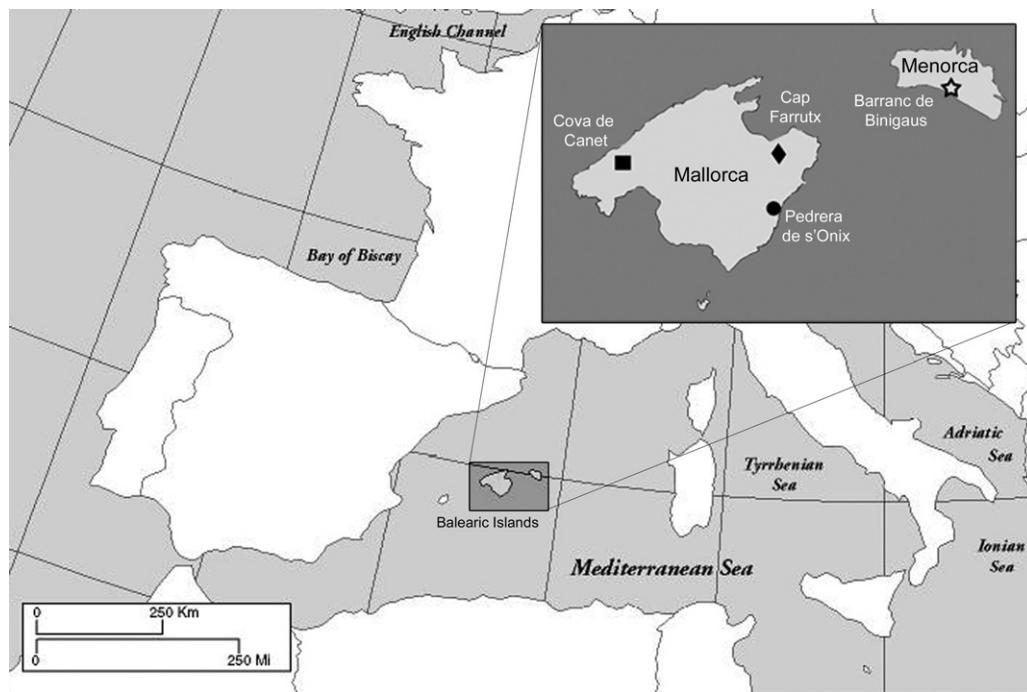


Fig. 1. Map of the Mediterranean area and the Balearic Islands, showing the placement of the three different sites under study and Cap Farrutx.
Fig. 1. Carte de la zone méditerranéenne et des îles Baléares, montrant l'emplacement des trois sites compris dans l'étude et Cap Farrutx.

M.A. Bate to combine several species found in these islands. Hitherto, five different species of this genus have been described: *Nesiotites hidalgo* Bate, 1944 from Mallorca, *Nesiotites corsicanus* Bate, 1944 from Corsica, and *Nesiotites similis* (Hensel, 1855) from Sardinia (originally described as *Sorex similis*). Later, two new species were described in the Balearic Islands: *Nesiotites ponsi* Reumer, 1979, the smallest and oldest species from Mallorca, and *N. meloussae* Pons-Moyà and Moyà-Solà, 1980 from Menorca. Reumer (1981) noted the presence of an intermediate form between the two species from Mallorca, making reference to it as *Nesiotites ex. interc. ponsi-hidalgo*.

Within the Balearic species of *Nesiotites*, the main character to differentiate them was the general size (Alcover et al., 1981; Reumer, 1979). *Nesiotites ponsi* is the smallest species, *N. hidalgo* is the largest one, and *N. meloussae* is intermediate between both. Almost all the dentognathic elements follow this relationship proportionally. Reumer (1982) noticed that the size of the upper molars of *N. meloussae* was similar to that of *N. ponsi*, and that the lower ones matched within the range of *N. ex. interc. ponsi-hidalgo*. According to this author, both species were equivalent and thus *N. meloussae* did not deserve the status of a separate species. Apart from the immediate nomenclatural problem created, such discrepancy acquired paleogeographic significance (Pons-Monjo et al., 2010). If *N. meloussae* represents a real case of endemism in Menorca, it evidences an independent evolutionary history in both islands. If, on the contrary, *N. meloussae* and *N. ex. interc. ponsi-hidalgo* were synonyms, it means that both islands were somehow connected, thus permitting

the genetic flow, or that the two fossil populations of *Nesiotites* are close in age to the moment of split, and they had no time enough to develop autapomorphic traits.

Other than the criterion of size, the definition of *N. meloussae* was based on some other morphological traits found in the fourth upper antemolar, the mandibular condyle, the secondary cuspules in m1 and m2, and the length of the rostrum (Pons-Moyà and Moyà-Solà, 1980). In this work, we review the validity of these traits in order to elucidate the phyletic relationships between the Balearic forms of *Nesiotites*.

2. Location and age of the sites

The *Nesiotites* remains studied in the present work belong to the Joan Pons Collection stored at the Institut Català de Paleontologia (ICP). This material comes from three different karstic deposits (Fig. 1): Cova de Canet and Pedrera de s'Onix (Mallorca), and Binigaus (Menorca). Canet yielded remains of *N. hidalgo* and it has been dated as Holocene (Alcover et al., 1981; Reumer, 1980b). The fossils studied herein come from the Level B, dated at 7200 BC (Pons-Moyà and Coll Conesa, 1986) and they are associated to remains of *Myotragus balearicus* (Bover et al., 2010; Moyà-Solà et al., 2007). Pedrera de s'Onix is a Plio-Pleistocene site, and it has provided fossils attributed to *Nesiotites ex. interc. ponsi-hidalgo* by Reumer (1981, 1982) (*Nesiotites aff. ponsi* in Alcover et al., 1981). The karstic site of Binigaus is the type locality of *N. meloussae*, with an estimated age older than Middle Pleistocene, probably Early Pleistocene (Moyà-Solà

and Pons-Moyà, 1980; Pons-Moyà and Moyà-Solà, 1980; Reumer, 1982). In this locality, *Nesiotites* is associated to *Myotragus batei/binigausensis* (Bover et al., 2010 contra Moyà-Solà et al., 2007).

3. Material and methods

We have inspected 3484 specimens of *Nesiotites* from Pedrera de s'Ónix, 496 from Canet and 341 from Barranc de Binigaus. For morphological comparison, we have considered the total of specimens available from each locality. For comparisons of size, however, we considered that such a high number of measures would not provide anything new. Thus, we have measured only 25 specimens from each locality randomly selected within those in good state of preservation. When the number of specimens was less than 25, we have measured all the specimens available. The measurements were taken with a Nikon Measurescope 10, connected to a Nikon SC-112 counter following the methods of Reumer (1984). For some measures of the skull, we have followed Carraway and Verte (2005). Additional parameters to compare partial cranial remains are given in Fig. 2. The results of the measurements taken are given in Table 1. *Nesiotites ponsi* from Cap Farrutx, its type locality, is also included in Fig. 3. However, it is only represented by its M1 because the rest of elements or measurements detailed in Reumer (1979) were not comparable.

4. Results

4.1. Size

In general terms, all the measurements get higher values in the sample of Canet, and the material from Pedrera de s'Ónix and Binigaus are similar, but the elements from the latter locality are slightly larger (Table 1; Fig. 3). In the following lines we will limit ourselves to highlighting the exceptions to this general rule.

Contrary to the trend, the sample from Canet shows the smallest I1 of the three localities. At the same time, however, it shows the highest standard deviation. In the other two populations, the LT (Length of the Talon) is on average the same, but in Pedrera de s'Ónix the I1 are slightly shorter and higher than in Binigaus. The W (Width) of the P4 gets similar values in the three localities, but in Binigaus it reaches its maximum. In this locality, however, the PE (Posterior Emargination) and the LL (Lingual Length) are smaller. The M1 and M2 are wider in both AW (Anterior Width) and PW (Posterior Width) in the sample of Binigaus than in the localities from Mallorca.

With respect to the i1, it must be emphasized that the shortest ones are found in Binigaus. In m1, the lowest values of the TRW (Trigonid Width) do not correspond to Pedrera de s'Ónix, but to Binigaus. The m3 from the Menorcan locality are also the narrowest.

The mandibular characters also follow this trend with the exception of the LLF (Length of the Lower Facet) of the condyle, which is somewhat shorter in Binigaus than in Pedrera de s'Ónix.

The cranial parameters (Fig. 4, Table 1) follow the general rule, but, the parameters 1a, 2, 5, 6 and 8 get

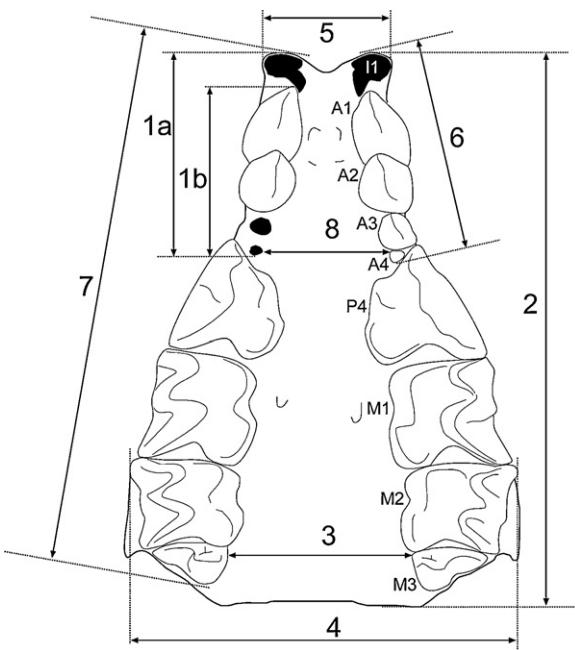


Fig. 2. Methods employed to measure cranial parameters: 1. Length of upper antemolar tooth row parallel to the sagittal plane, from alveolus of A3 to: a: alveolus of I1; b: anterior tip of A1. 2. Palatilar length. 3. Width of palate. 4. Width across M2-M2. 5. Width across I1-I1. 6. Maximum length of upper antemolar tooth row. 7. Maximum tooth row length, from alveolus of I1 to posterior tip of M3. 8. Palatilar width between alveoli of A3 (measurements 1b, 2, 3, 4 and 5 adapted from Carraway and Verte, 2005; fig. 2).

Fig. 2. Méthodes employées pour mesurer les paramètres crâniens : 1. Longueur de la rangée des ante-molaires supérieures parallèle au plan sagittal, depuis l'alvéole de A3 jusqu'à : a : l'alvéole du I1 ; b : l'extrémité mésiale de A1. 2. Longueur palatine. 3. Largeur palatine. 4. Largeur entre les M2. 5. Largeur entre les I1. 6. Longueur maximale de la rangée des ante-molaires supérieures. 7. Longueur maximale de la rangée dentaire, depuis l'alvéole de I1 jusqu'à l'extrémité distale de M3. 8. Largeur palatine entre les alvéoles des A3 (mesures 1b, 2, 3, 4 et 5 adaptées de Carraway and Verte, 2005; fig. 2).

mildly lower values in Binigaus than in Pedrera de s'Ónix. However, all these values from Binigaus fall within the range of Pedrera de s'Ónix. Fig. 4 represents the relationship between parameters 6 and 7 to evaluate a potential shortening of the snout in the only sufficiently complete specimen from Binigaus. As evidenced by this ratio, the snout of this specimen also falls within the range of the sample from Pedrera de s'Ónix.

4.2. Morphologic characters

4.2.1. Fourth Upper Antemolar

The antemolars of the soricids are the teeth located between the incisor and the fourth premolar, either upper or lower. In recent shrews, the row of upper antemolars varies from two (e.g., *Diplomesodon*) to five (e.g., *Sorex*) elements (Dannelid, 1998; Hutterer, 2005; Repenning, 1967; Reumer, 1984). Its number in *Nesiotites* fluctuates between three and four (Table 2). In the original diagnosis of *N. hidalgo*, it was specified that there were only three upper antemolars (Bate, 1944). Nevertheless,

Table 1

Measurements of the dental, mandibular and cranial elements from Pedrera de s'Ónix, Binigaus and Canet.

Tableau 1

Mesures des éléments dentaux, mandibulaires et crâniens de Pedrera de s'Ónix, Binigaus et Canet.

El.	Par.	P. Ónix					Binigaus					Canet				
		Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N
I1	LT	0.63	0.76	0.95	0.09	25	0.62	0.76	1.00	0.08	25	0.45	0.72	0.94	0.10	25
	L	2.02	2.14	2.30	0.08	25	2.01	2.18	2.44	0.11	25	1.81	2.07	2.26	0.13	25
	H	1.68	1.81	1.94	0.07	25	1.60	1.78	1.94	0.08	25	1.56	1.76	1.88	0.09	25
P4	PE	1.12	1.32	1.53	0.10	25	1.11	1.26	1.44	0.10	25	1.29	1.47	1.50	0.10	25
	LL	1.17	1.45	1.60	0.11	25	1.28	1.42	1.67	0.10	25	1.34	1.62	1.82	0.12	25
	BL	2.00	2.20	2.37	0.10	25	2.17	2.31	2.48	0.07	25	2.21	2.42	2.66	0.09	25
	W	1.77	1.89	1.95	0.06	25	1.731	1.90	2.06	0.09	25	1.63	1.90	2.03	0.08	25
M1	PE	1.33	1.48	1.62	0.07	25	1.44	1.53	1.66	0.06	25	1.37	1.61	1.82	0.08	25
	LL	1.71	1.88	2.07	0.08	25	1.85	1.97	2.05	0.06	25	1.81	2.07	2.36	0.12	25
	BL	1.82	1.92	2.02	0.06	25	1.86	2.00	2.11	0.07	25	1.77	2.06	2.30	0.11	25
	AW	1.95	2.06	2.17	0.07	25	2.02	2.17	2.37	0.09	25	1.87	2.15	2.26	0.08	25
M2	PW	2.19	2.34	2.49	0.08	25	2.34	2.50	2.68	0.10	25	2.27	2.48	2.66	0.11	25
	PE	1.22	1.30	1.43	0.05	25	1.22	1.33	1.47	0.06	25	1.28	1.45	1.56	0.07	25
	LL	1.52	1.62	1.74	0.06	25	1.49	1.63	1.87	0.07	25	1.47	1.75	1.95	0.11	25
	BL	1.56	1.65	1.77	0.06	25	1.57	1.68	1.79	0.05	25	1.57	1.79	1.98	0.09	25
M3	AW	2.02	2.16	2.33	0.09	25	2.10	2.26	2.47	0.09	25	1.99	2.25	2.37	0.09	25
	PW	1.74	1.95	2.11	0.08	25	1.81	2.04	2.21	0.10	25	1.66	1.98	2.15	0.11	25
	L	0.80	0.86	0.94	0.03	22	0.80	0.88	0.96	0.05	16	0.75	0.92	1.07	0.07	25
	W	1.34	1.49	1.63	0.07	22	1.53	1.60	1.69	0.05	16	1.47	1.66	1.81	0.09	25
i1	L	4.40	4.84	5.16	0.20	25	4.40	4.78	5.14	0.21	20	4.30	4.98	5.31	0.20	25
m1	L	1.85	2.00	2.20	0.08	25	1.93	2.04	2.19	0.07	25	2.09	2.17	2.31	0.06	25
	TAW	1.04	1.27	1.40	0.08	25	1.16	1.30	1.38	0.05	25	1.37	1.43	1.55	0.04	25
	TRW	1.02	1.15	1.29	0.08	25	1.03	1.14	1.22	0.06	25	1.13	1.23	1.35	0.05	25
m2	L	1.72	1.84	1.96	0.07	25	1.75	1.87	1.95	0.06	25	1.88	1.99	2.10	0.07	25
	TAW	1.03	1.12	1.18	0.04	25	1.02	1.12	1.25	0.06	25	1.09	1.21	1.26	0.04	25
	TRW	1.01	1.09	1.15	0.05	25	1.00	1.09	1.23	0.06	25	1.12	1.21	1.29	0.04	25
m3	L	1.28	1.36	1.45	0.06	25	1.35	1.44	1.55	0.05	21	1.38	1.50	1.73	0.08	25
	W	0.73	0.83	0.94	0.05	25	0.72	0.81	0.90	0.05	21	0.77	0.86	0.98	0.05	25
MN	H	5.46	5.72	6.09	0.16	25	5.30	5.78	6.05	0.22	14	6.01	6.24	6.50	0.14	25
	L	5.73	6.06	6.69	0.22	25	5.30	6.23	6.75	0.46	10	6.53	6.79	7.08	0.15	25
	Lm13	4.76	4.96	5.09	0.08	25	4.95	5.11	5.36	0.15	7	5.20	5.43	5.64	0.12	25
MC	HC	3.06	3.40	3.78	0.16	25	2.87	3.47	3.76	0.23	15	3.38	3.62	3.91	0.12	25
	LLF	1.72	2.09	2.33	0.15	25	1.77	2.08	2.21	0.11	17	2.25	2.43	2.58	0.09	25
	LUF	1.14	1.38	1.62	0.12	25	1.08	1.44	1.60	0.12	17	1.44	1.56	1.74	0.08	25
SK	1a	3.48	3.75	4.09	0.18	12	3.48	3.71	3.95	0.23	3	3.87	4.05	4.12	0.10	5
	1b	2.87	3.12	3.52	0.16	14	3.04	3.16	3.28	0.17	2	2.97	3.19	3.31	0.14	5
	2	9.32	9.90	10.45	0.36	7		9.65			1	10.25	10.70	11.06	0.37	5
	3	2.87	2.97	3.07	0.14	2						3.09	3.20	3.32	0.16	2
	4	6.72	6.85	6.99	0.19	2						7.06	7.48	7.68	0.28	4
	5	2.51	2.59	2.68	0.07	5	2.42	2.54	2.66	0.18	2	2.55	2.66	2.81	0.10	5
	6	3.68	3.86	4.16	0.16	10	3.65	3.85	4.02	0.19	3	4.01	4.12	4.30	0.13	5
	7	9.17	9.44	9.68	0.26	4		9.58			1	9.95	10.45	10.84	0.42	4
	8	2.14	2.34	2.48	0.11	6		2.26			1	2.38	2.51	2.64	0.10	6

Dental nomenclature and abbreviations according to Reumer (1984). Skull parameters measured according to Fig. 2. MC: mandibular condyle; MN: mandible; SK: skull.

Nomenclature et abréviations suivant Reumer (1984). Paramètres du crâne mesurés suivant Fig. 2. MC : condyle mandibulaire ; MN : mandibule ; SK : crâne.

Reumer (1980a) emended the diagnosis, stating that sometimes a fourth antemolar could be retained. The A4 was also found in *N. meloussae* from Binigaus (Pons-Moyà and Moyà-Solà, 1980) and in 76 out of 80 specimens in the sample of *N. ex. interc. ponsi-hidalgo* from Pedrera de s'Ónix (Reumer, 1981). The A4, if present, is the smallest of the upper antemolar series, and it occupies the most distal position of the row, close to the parastyle of the P4. Usually, even when this tooth has been

disarticulated after deposition, its corresponding alveolus is discernible.

In our sample from Canet, with 81 maxillary fragments of *N. hidalgo* available, 61 did not have the A4, or any trace of it. Within the rest, six fragments preserved an alveolus for this tooth. The other 14 maxillaries were divided into eight specimens with the A4 or its corresponding alveolus, and six asymmetric specimens with the alveolus of the A4 present only at one side.

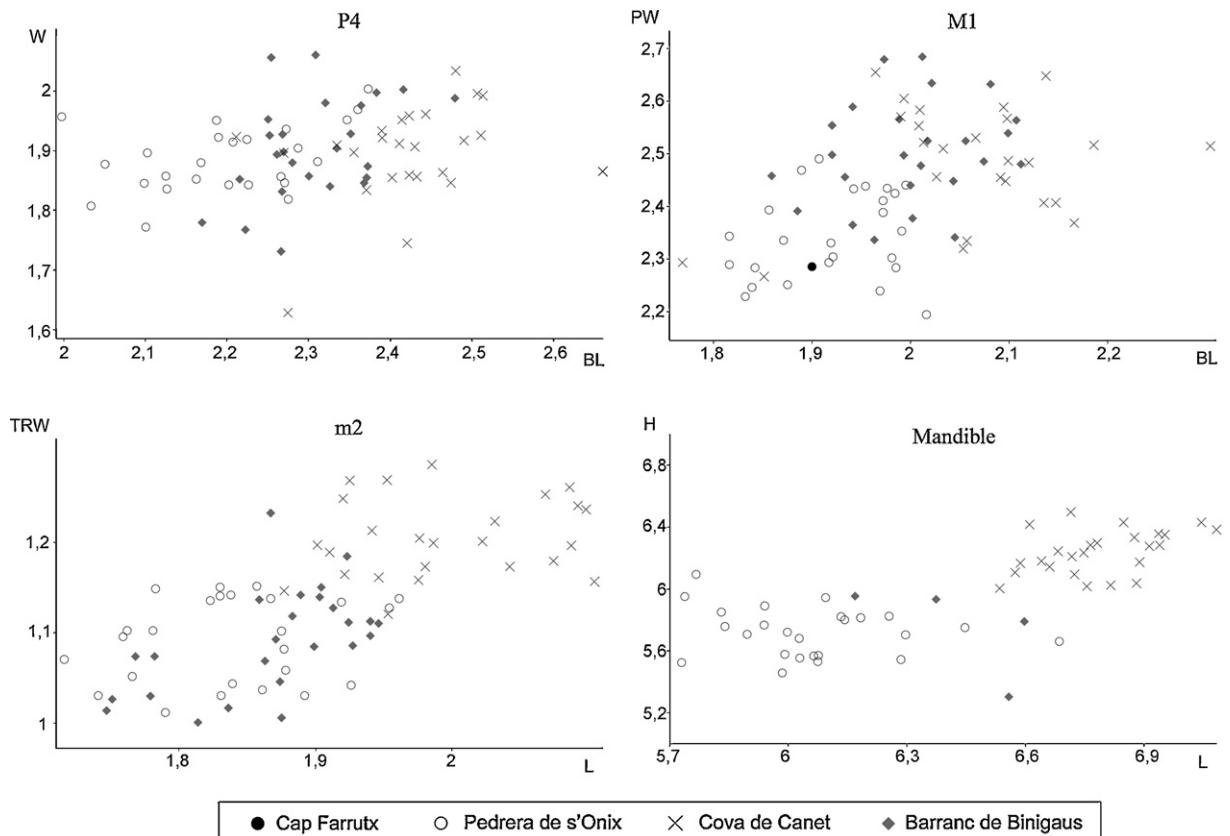


Fig. 3. Scatter diagram for measures of P4, M1, m2 and Mandible (from top to bottom) of the three studied populations: Pedrera de s'Onix (open circles), Cova de Canet (crosses) and Barranc de Binigaus (diamonds). Average value of the M1 in *N. ponsi* from Cap Farrutx (Reumer, 1979) represented with a black circle. Measures and abbreviations follow Reumer (1984). The remains from Binigaus are smaller than those from Canet, but they get similar values as the ones from Pedrera de s'Onix. Notice that the only comparable element of *N. ponsi* is included in the range of *Nesiotites* from Pedrera de s'Onix.

Fig. 3. Diagramme de dispersion des mesures de P4, M1, m2 et mandibule des trois populations étudiées : Pedrera de s'Onix (cercles ouverts), Cova de Canet (croix) et Barranc de Binigaus (losange). La valeur moyenne de la M1 dans *N. ponsi* de Cap Farrutx (Reumer, 1979) est représentée par un cercle noir. Mesures et abréviations selon Reumer (1984). À noter : les éléments de Binigaus sont plus petits que ceux de Canet, mais les valeurs obtenues sont similaires à celles de Pedrera de s'Onix. De plus, le seul élément comparable de *N. ponsi* est inclus dans la gamme de *Nesiotites* de Pedrera de s'Onix.

In Pedrera de s'Onix, the A4 is present more frequently. Within a total of 311 specimens, 27 maxillary fragments show this tooth (Fig. 5a) and in 264 its corresponding alveoli is present. In nine specimens there are no A4 or trace of it (Fig. 5b). In eleven maxillaries, ten showed the trace of A4 (the tooth or its alveoli) at both sides, and only one maxillary was asymmetric, with one alveolus at one side, but missing at the other.

Table 2

Number of specimens and percentages of maxillary and hemimaxillary bones with evidence of presence or absence of A4 in each locality.

Tableau 2

Nombre de spécimens et pourcentage des os maxillaires et hémimaxillaires montrant des preuves de la présence ou de l'absence d'A4 pour chaque localité.

	P. Ónix		Binigaus		Canet	
	n (311)	%	n (23)	%	n (81)	%
Presence	301	96.78	23	100.00	14	17.28
Absence	9	2.89	0	0.00	61	75.31
Asymmetry	1	0.32	0	0.00	6	7.41

In Binigaus there are only 23 specimens of *N. meloussae* available. Of this sample, 22 specimens correspond to hemimaxillary fragments and one is an almost complete maxillary. All of them show evidence of an A4 present (Fig. 5c), mostly in form of an alveolus, but one still preserves this tooth.

Our observations indicate that A4 is more frequently preserved in the older populations (Binigaus and Pedrera de s'Onix) than in the younger one (Canet). Frequencies vary from the constant occurrence of this trait in Binigaus (100% of the specimens of *N. meloussae*) to the 17.28% in Canet. The sample from Pedrera de s'Onix is closer in terms of frequency to Binigaus than to Canet with a 96.78% of the specimens showing this tooth or its alveolus. It is noteworthy that the populations from Mallorca show a small percentage of anomalous asymmetric individuals in which either the A4 or its alveolus is present at one side of the maxillary but missing at the other (Pedrera de s'Onix: one specimen out of 311 = 0.32%; Canet: six out of 81 = 7.41%). All these data are summarized in Table 2.

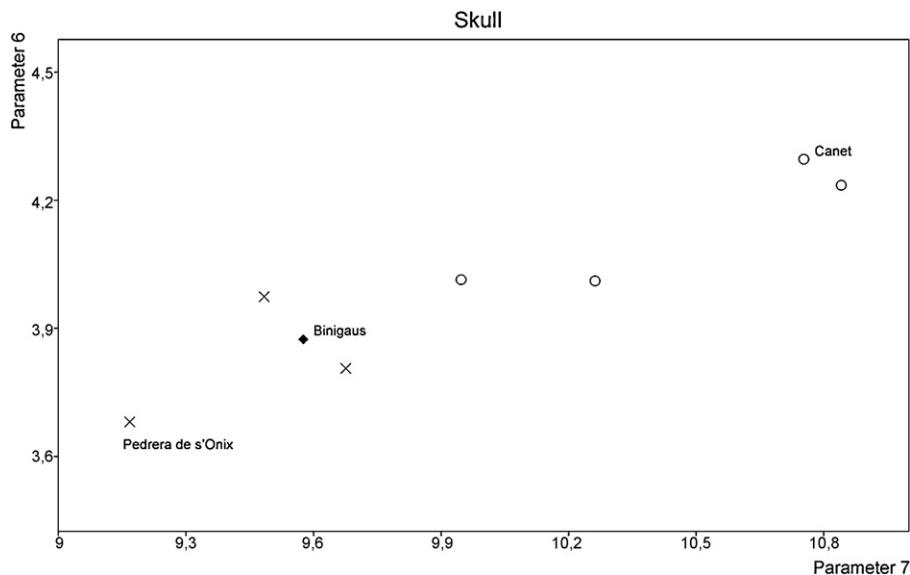


Fig. 4. Scatter diagram for measures of cranial parameters 6 and 7, according to Fig. 2.

Fig. 4. Diagramme de dispersion des paramètres crâniens 6 et 7, selon Fig. 2.

4.2.2. Double Mental Foramen

Unlike other insectivores such as moles, shrews have usually only one mental foramen. Nonetheless, a double mental foramen has been detected in several specimens of *Nesiotes* during this study (Fig. 5d–f). As far as we know, there is no evidence of this feature in any other soricid.

A double mental foramen has been found in *N. hidalgo* from Canet in six specimens of 238 individuals (2.52% of the cases). In the Pedrera de s'Onix sample, seven hemimandibles from a total of 990 specimens presented this condition (0.71% of the cases). In Binigaus, nine of 29 hemimandibles showed these two foramina (31.03% of the cases).

The first mental foramen is always placed under the talonid of the m1. The second mental foramen, however, does not follow a strict uniform pattern, although in Canet a rather similar disposal of this foramen can be discerned in five out of six specimens. In these cases, one foramen is placed beneath the protoconid of the m1 and the other one under the talonid basin. This pattern does not dominate in the sample from Binigaus, where half of the doubled-mental foramen specimens display a different trend. The sample from Pedrera de s'Onix shows an apparent random disposal of the second mental foramina. This trait shows a certain potential to be discriminative within the Balearic species of *Nesiotes*, but it deserves a more detailed revision before being considered as a diagnostic character.

4.2.3. Cuspules on the Oblique Cristid of m1 and m2

The secondary cuspules are small elevations on the oblique cristid of the first and second lower molars. Reumer (1979) stated that *Nesiotes ponsi* from Cap Farrutx often displayed this character. Pons-Moyà and Moyà-Solà (1980) observed that this trait was also present in *N. meloussae* from Binigaus. Reumer (1981) noticed that a 'mesoconid-like' cusp was sometimes present in the sample from

Pedrera de s'Onix, but not as developed as in *N. ponsi* from Cap Farrutx. There is no reference to the frequency of this character in *N. hidalgo*. In the original description of Bate (1944), the teeth of the holotype were apparently too worn to be described.

In all the sites of the present study the cuspules are present more frequently in the m1 than in the m2. In Canet, 102 m1 display this character within a total of 179 elements available (i.e., in 56.98% of the cases). The m2 from this site show well-differentiated cuspules in 83 cases of 156 (i.e., in 53.21% of the cases). In Binigaus, 30 of the 36 specimens of m1 available show this character (83.33% of the cases). In 16 of the 30 m2 found the cuspule is discerned (53.33% of the cases). Pedrera de s'Onix has provided a total of 453 m1, 361 of which had cuspules on its oblique cristid (79.69%). Within the m2 from this locality, 202 of a total of 331 specimens showed this trait (61.03%). Examples of specimens with and without cuspules from this latter locality are provided in Fig. 5g–h.

Our observations indicate that this character is indeed very frequent in all the species and sites, always present in more than the 50% of the specimens, either m1 or m2. In fact, only a slight trend to the reduction of these cuspules in the youngest locality could possibly be discerned. However, it must be highlighted that these cuspules rapidly disappear in worn teeth. This fact could lead to underestimation of the real cases (in form of 'false negatives') due to an overrepresentation of worn specimens. Consequently, this feature does not seem advisable as a diagnostic specific character within the Balearic *Nesiotes* from now on.

5. Discussion and biogeographic implications

The morphological characters of *Nesiotes* indicate that its most likely ancestor is a species of *Asoriculus* (Brady pers. comm. in Alcover et al., 1981; Kotsakis, 1980; Reumer,

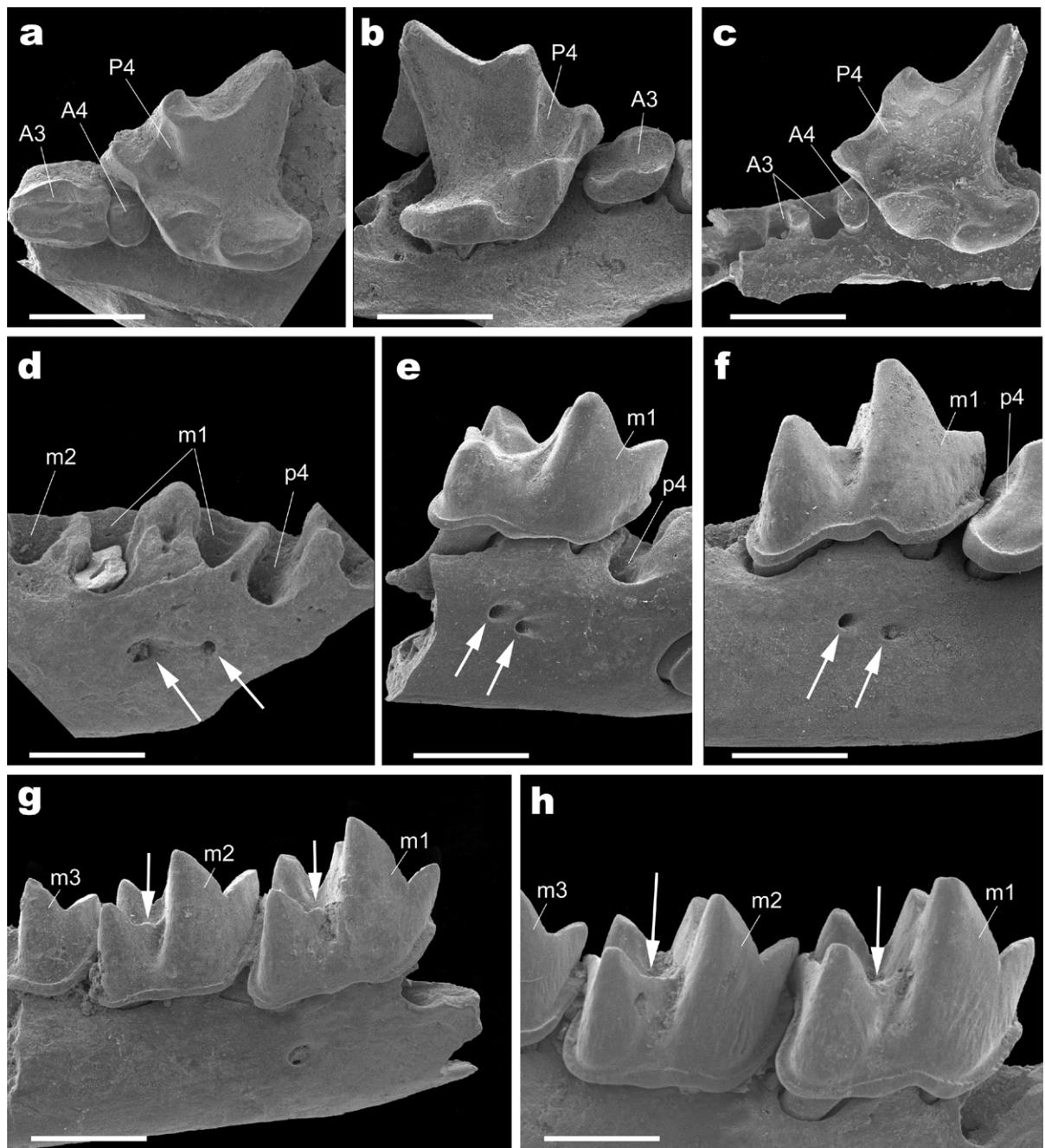


Fig. 5. a–c: examples of the presence/absence of the A4 in the maxillary. a: IPS-52186, left hemimaxillary from Pedrera de s'Ónix with P4, A4 and A3; b: IPS-52359, right hemimaxillary from Pedrera de s'Ónix with P4 and A3; notice that the A4 is absent and there is no trace of alveolus in the place that it should occupy; c: IPS-51073, left hemimaxillary from Binigaus with P4, A4 and the alveoli of the A3; d–f: examples of hemimandible showing a double mental foramen; d: IPS-51914, right toothless hemimandible from Pedrera de s'Ónix; e: IPS-51174, left hemimandible (reversed) with m1 from Binigaus; f: IPS-50392, right hemimandible with p4 and m1 from Canet; g–h: examples of lower molars rows from Pedrera de s'Ónix; g: IPS-52934, right hemimandible with m1-m3 in which the oblique cristids of m1 and m2 bear small cuspsules (indicated by arrows); h: IPS-52497, right hemimandible with m1-m3 in which the oblique cristids of m1 and m2 do not show cuspsules. Scale bar equals 1 mm.

Fig. 5. a–c: exemples de présence/absence de l'A4 sur le maxillaire ; a : IPS-52186, hémimaxillaire gauche de Pedrera de s'Ónix avec P4, A4 et A3 ; b : IPS-52359, hémimaxillaire droit de Pedrera de s'Ónix avec P4 et A3 ; à noter que l'A4 est absent et qu'il n'y a aucune trace d'alvéole à la place qu'il doit occuper ; c : IPS-51073, hémimaxillaire gauche de Binigaus avec P4, A4 et les alvéoles de l'A3 ; d–f: exemples d'hémimandibule montrant un double trou mentonnier ; d : IPS-51914, hémimandibule droite édentée de Pedrera de s'Ónix ; e : IPS-51174, hémimandibule gauche (inversée) avec m1 de Binigaus ; f : 50392-IPS, hémimandibule droite avec p4 et m1 de Canet ; g–h : exemples de rangées de molaires inférieures de Pedrera de s'Ónix ; g : IPS-52934, hémimandibule droite avec m1-m3 dans lesquelles les cristides obliques de m1 et m2 ont de petits cuspules (indiquées par des flèches) ; h : IPS-52497, hémimandibule droite avec m1-m3 dans lesquelles les cristides obliques de m1 et m2 n'ont pas de cuspules. Échelle : 1 mm.

1980a). This genus includes fossil European nectogalin shrews formerly ascribed to the recent genus *Episoriculus*. The only opinion against this relationship comes from Hutterer (1994), who suggested that *Nesiotites* could be probably more closely related with the genus *Neomys*. However, this hypothesis is not supported at all by the fossil record, which rather suggests a rapid peri-Mediterranean dispersion of *Asoriculus* during the Messinian Salinity Crisis (MSC), followed by isolation of some populations in several islands. Fossils of *Nesiotites* and/or *Asoriculus* have been found in Mallorca (Bate, 1944; Reumer, 1979, 1980a, 1981; Rofes et al., 2011), Menorca (Pons-Moyà and Moyà-Solà, 1980; Reumer, 1982), Corsica (Bate, 1944), Sardinia (Abbazzi et al., 2008; Esu and Kotsakis, 1979; Furió and Angelone, 2010), Sicily (Masini and Sarà, 1998), Rhodes (De Bruijn et al., 1970). *Asoriculus* probably reached also the North of Africa during the MSC, as evidenced by the fossils of this genus found in some Pliocene and Pleistocene sites from Morocco (Geraads, 1995; Rzebik-Kowalska, 1988).

Reumer (1980a, 1984) assumed a progressive colonization of *Asoriculus* through Central Europe, the Italian mainland, Corsica and Sardinia, finally reaching the Balearic Islands. However, Kotsakis (1980) did not concur with the two final steps, and found more likely independent arrivals of *Asoriculus* to Corsica and Sardinia and to the Balearic Islands. In that case, *Nesiotites* as originally described by Bate (1944) would be polyphyletic.

Bover et al. (2008) stated that after the Messinian Salinity Crisis, Mallorca and Menorca developed a different faunal content. The Pliocene assemblages in Menorca included a dormouse (*Muscardinus*), a bat (*Rhinolophus*) and the giant rabbit *Nuralagus* (Quintana et al., 2011). During the same period, *Nesiotites* already inhabited Mallorca together with the bovid *Myotragus*, and the dormouse *Hypnomys*. According to Bover et al. (2008), the endemic mammalian fauna from Menorca was apparently replaced by these latter genera from Mallorca during a glacial period close to the Plio-Pleistocene transition, when a connection between both islands permitted them to take over the minor island. After that, these faunas remained unaltered until their rapid extinction after the first human occupations dated at about 3000 BC (Bover and Alcover, 2008).

After our study, we could not assess the validity of any of the supposed diagnostic characters of *N. meloussae* as a real autoapomorphy. The criterion of size, including the mandibular condyle, clearly separates the material from Menorca from that of Canet, but it mostly overlaps with the values from Pedrera de s'Óníx. The length of the rostrum, as defined by Pons-Moyà and Moyà-Solà (1980), is too subjective to recognize the species. The new measurements carried out herein (Fig. 4) do not provide further evidence of the validity of this character. With respect to the fourth upper antemolar and the secondary cuspules in m1 and m2, we assessed that both characters are present in all the species, only changing their relative abundance in each locality. Unfortunately, these frequencies are not sufficient to discriminate at the species level. The new peculiarity found in some specimens (double mental foramen) is also not an autoapomorphy of the Menorcan forms, as it has been found in some mandibles from Canet and Pedrera de s'Óníx.

So, the populations from Binigaus and Pedrera de s'Óníx are, overall, morphologically undistinguishable and their dental and mandibular measurements overlap considerably. Moreover, island mammals usually present a large intraspecific variation (Van der Geer et al., 2010, and references therein) and slight differences are not enough to separate different species. Considering that morphological evolution is faster in these faunas than in their mainland relatives (Millien, 2006), we do not find evidence of an independent evolution of *Nesiotites* in the two islands, or the populations from Binigaus and Pedrera de s'Óníx were not separated the sufficient time to develop own specific characters. Given the estimated age for these two localities, our results rather argue in favor of the dispersal of *Nesiotites* to Menorca from Mallorca at an unknown moment close to the Pliocene-Pleistocene boundary, as suggested by Bover et al. (2008).

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