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Dental variation in *Hypnomys mahonensis* Bate, 1918 (Gliridae, Rodentia, Mammalia) from the newly rediscovered type-locality of Punta Esquitxador 17 (Menorca, Balearic Islands, Western Mediterranean).

Running head: Dental variation in *Hypnomys mahonensis*

Josep Quintana Cardona (a)(b)*

Jordi Agusti (c)

(a) Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

* Corresponding autor, e-mail adress: picoguevo@gmail.com

(b) Carrer Gustau Mas, 79-1er, 07760 Ciutadella de Menorca, Illes Balears, Spain

(c) ICREA, Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Universitat Rovira i Virgili, Carrer Marcel·lí Domingo s/n (Edifici W3), Campus Sescelades, 43007 Tarragona, Spain

Introduction

The original description of genus *Hypnomys* and the type species, *Hypnomys mahonensis* Bate, 1918, were based on only a few specimens from some karstic fillings (the sites termed 2 and 3), located on the Miocene limestones near Cap de Bajoli, on the farnorth-western coast of Menorca, in the grounds of the SesTruqueries estate (Bate 1914). Although it is true that both sites appear on the geological map of Menorca published by Bate (1914: 342), there is no figure, section, or sketch of them, so that the origin of the type series of *H. mahonensis* (preserved at the Natural History Museum, London) remains somewhat ambiguous.

In the same work, the English researcher also describes *Hypnomys morpheus* Bate, 1918, a smaller species originally described from remains from Mallorca. In addition to the two taxa mentioned above, the genus *Hypnomys* includes several chronospecies described in Mallorca (*Hypnomys* sp: Lower Pliocene [Bover *et al* 2014]; *Hypnomys waldreni* Reumer, 1979: Upper Pliocene; *Hypnomys onicensis* Reumer, 1994 [=*Hypnomys intermedius* Reumer, 1981]: Upper Pliocene-Lower Pleistocene) and Menorca (*Hypnomys* sp. Upper Pliocene– Lower Pleistocene [Quintana and Agustí 2019]; *Hypnomys eliomyoides* Agustí, 1980: Upper Pliocene –Lower Pleistocene), while in the Pleistocene of Eivissa the presence of the genus *Hypnomys* cannot be confirmed (Agustí *et al*. 2020).

H. mahonensis and *H. morpheus* appear to be present in the Pleistocene of Mallorca and Menorca, although Bauzá (1962) citation of *H. mahonensis* in the Early Pliocene of Cala Morlanda (Mallorca) is considered doubtful by Alcover *et al*. (1981). In Menorca, *H. mahonensis* has also been reported from the island of Lazareto (Port of Mahón) by Obrador and Mercadal (1969) on the basis of a sole incisor. Pons (1975) identifies, although with certain reservations, this same species in Cala Blanca (Ciutadella de Menorca).

Reumer (1982) reports the presence of *H. mahonensis* in Son Bou 1 (Alayor, Menorca) and *H. morpheus* in Cala en Blanes (Ciutadella de Menorca) and Son Bou 2. According to his description of *H. mahonensis*, the dental pattern of the upper molars is composed of 5 main ridges: anteroloph, protoloph, precentroloph, postcentroloph and posteroloph. As a rule, the precentroloph is isolated but in one case it reaches the endoloph. Moreover, according to the material figured by Reumer (1982), the postcentroloph can be small or absent. In the lower molars a posterotropid is present in m1 and m2, while it is small or absent in m3. According to the teeth figured by Reumer (1982), there is a centrolophid whose lingual end is connected to the metalophid, while the anterolophid is fused to the protoconid. Also its size is larger than *H. morpheus* from the nearby site of Son Bou 2, particularly the M3, and presents a simpler dental pattern.

Quintana and Moncunill-Solé (2014) conduct a study on the locomotion of *Hypnomys* based on the allometric changes recorded in the long bones of the limbs (humerus, ulna, tibia and femur), using samples from five locations, among which the site of Punta Esquitxador 17 (Ciutadella de Menorca), described, albeit very briefly, by Quintana (1998), stands out due to the larger size of the postcranial elements. In neither of these two works is a specific range attributed to the population of Punta Esquitxador 17, as there is no detailed study of dental morphology.

Given the ambiguity regarding the origin of the type material and the few specimens originally described, it is considered that *H. mahonensis* has been, until now, a poorly known species and incompletely described (Alcover *et al.* 1981). For these reasons, it is necessary to study the type series in detail and to complement the original description by studying new specimens from the locality from which Bate (1914, 1918) described the species.

Location

In July 1991, one of the authors (JQ) carried out a prospecting campaign on the coastal stretch between Cap de Bajolí and Punta Perpinyà de Dins (Fig. 1), where seven sites of karstic origin (Quintana 1998) were discovered on Late Miocene (Messinian) calcarenites (Rosell *et al.* 1989), including the sites 15, 16 and 17, all located near Punta Esquitxador (Quintana, *op. cit.*).

Sites 15 and 16 are located on the northern and southern flanks of a small gorge and cover a fracture that reaches a maximum of approximately two metres at its lower part. They are made up of very hard, rosy-coloured silt, which include a rather high proportion of coarse bioclastic sand of marine origin and abundant angular and very heterometric rocks of calcarenite, stalagmite calcite and red silt, which sometimes include poorly preserved remains of the Menorcan giant tortoise *("Testudo" gymnesica* [Bate, 1914]). During the prospecting campaign, a series of loose blocks formed by pink silt were found in the upper part of site 15, in which abundant remains of *Myotragus* sp. were preserved.

Site 17 at Punta Esquitxador is located about 130 m north of these two sites. Despite its small size (Fig. 2), a large amount of bird remains is preserved (Seguí 1998), as well as *Hypnomys* sp. and *Podarcis* sp. (Quintana 1998: Fig. 9).

In general terms, Quintana (1998) description of sites 15, 16 and 17 at Punta Esquitxador concur with Bate (1914) description of sites 2 and 3 at "Sestrucaries, Bajolí" (=SesTruqueries, Bajolí). Specifically, the (non-coeval) association of the Menorcan giant tortoise and *Myotragus* sp. from sites 15 and 16 would correspond to site 3, while site 17 (the richest in bone remains in the area) would correspond to site 2, which is described by Bate (1914: 343) as "a small crevice [with a] red matrix containing a mass of small remains".

Most probably, site 17 of Punta Esquitxador (from now on referred to as Punta Esquitxador 17) is the type site from which the original remains of *H. mahonensis* described and figured by Bate (1918) came from. Given the undeniable interest of this site, both its geological characteristics and those of its fauna are described. Likewise, the different dental morphotypes of *H. mahonensis* recovered during the 1991 prospecting campaign are also described and numbered.

Geological description of Punta Esquitxador 17

The site is located on Late Miocene (Messinian) calcarenites which form part of the reef slopes in the area (Rosell *et al.* 1990). Other authors (Fornós 1987; Obrador & Pomar 2004) include these sediments in the so-called “Lower Bar Unit”, without specifying the type of facies from which they come (internal ramp, intermediate, external or ramp slope).

The site with abundant *Hypnomys* remains is located at the top of the southern slope of a small promontory (Fig. 2). It is formed by small concentration of very reddish silt, and its northeastern margin is flanked by Messinian calcarenites. On the edge, these silts give way (on the northwestern and southern margins) to breccia formed by angular calcarenite rocks of centimetric and decimetric dimensions.

The breccia extends to the coastline. It is formed by very heterometric angular calcarenite blocks, some of which are very large (metric dimensions), cemented by reddish silts with a variable concentration of biogenic sands of marine origin, which, exceptionally, include some badly preserved vertebrate remains (possibly of the genus *Myotragus*) and some species of terrestrial molluscs endemic to Menorca and Mallorca (*Chondrula [Mastus] gymnesica* Quintana, 1996), Menorca, Ibiza and Formentera (*Allognathus [Iberellus] hispanicus minoricensis* [Mittre, 1842]) (Chueca *et al.* 2013) (Fig. 2.3) and Menorca (*Xerocrassa nyeli* [Mittre, 1842]). A. (I.) *hispanicus minoricensis* is the most abundant species and occasionally forms coquina.

The origin of the red silt with abundant remains of the genus *Hypnomys* is related to the silting of a small cavity at the top of the promontory, now almost completely eroded, with elements of angular rocks from the adjacent calcarenite walls. The sediments and breccia below the site can be considered as slope debris, caused by the fall of large boulders from the calcarenite wall, with terrigenous contributions from the upper part of the cliff and biogenic sands from the sea.

Faunal content of Punta Esquitxador 17

Birds. Punta Esquitxador 17 is marked by a rich ornithic fauna, made up of twelve species and an undetermined number of passerine (Seguí 1998) (Table 1). From a palaeoecological point of view, this fauna is indicative of a steppe-like herbaceous and marshy environment (Seguí, *op. cit.*).

Reptiles. In describing *H. mahonensis*, Bate (1918) indicates that this species is found together with incomplete mandibles of lacertidae belonging to the *Lacerta viridis-ocelata* group and a species of *Chalcides*. This genus (cf. *Chalcides*) is also mentioned in the Upper Miocene/Lower Pliocene of Mallorca from a small fragmentary dentary (Bover *et al.* 2014: Fig. 2g). Although the presence of the genus *Chalcides* in the Pleistocene of Menorca cannot be ruled out, it seems quite likely that the citation by Bate (1918) is due to a misidentification due to the lack of preparation of the specimen preserved at the Natural History Museum in London (see comments by Alcover *et al.* 1981: 49). In this sense, the only abundant Lacertidae present at Punta Esquitxador 17 is *Podarcis lilfordi* (Günther, 1874). This population is characterised by the presence of relatively large specimens (Fig. 3). On the other hand, Alcover *et al.* (1981) hypothesize that the remains of *Chalcides* sp. originally appeared together with the giant tortoise of Pliocene Menorca, which cannotbe ruled out, given the presence of this taxon at Punta Esquitxador 15 and 16.

Mammals. The Pliocene-Holocene endemic fauna of the Balearic Islands consists of three mammals included in the genera *Myotragus* Bate, 1909 (Bovidae), *Nesiotites* Bate, 1944 (Soricidae) and *Hypnomys* Bate, 1918 (Gliridae), being the only one present at Punta Esquitxador 17. The remains of *Hypnomys* recovered at this site are characterised by their relatively large size (Quintana and Moncunill-Solé 2014: Table 2), a characteristic that concur with the data provided by Bate (1918). The recovery of new dental remains of *H. mahonensis* from Punta Esquitxador 17 now allows us to complement the original description and describe in detail the characteristics of the different morphotypes present at this locality.

Methods

The recovery of the vertebrate remains from Punta Esquitxador 17 was carried out using chemical methods, immersing the red silt in an aqueous solution of acetic acid at a concentration of 10%, generally following the methodology of López Martínez (1989) and Rutzky *et al.* (1994). Once removed from the rock matrix, the bone remains were sieved and immersed in water for several days in order to eliminate any remaining acid or calcium acetate. After the aqueous bath, they were dried and consolidated with Acryloid B67.

Each tooth was then glued (using water-soluble white glue) to the end of an entomological pin. Once mounted, they were fixed and are kept inside 50x50 mm transparent plastic boxes with a high-density cross-linked polyethylene base, duly separated (according to the type of tooth) and numbered. The mandibles and maxillae have been grouped and preserved separately, in smaller boxes.

In order to facilitate the study of the teeth and to make the contrast between valleys and ridges more evident, an emulsion of graphite powder in Acryloid B67 has been applied to each tooth.

The dental terminology follows Freudenthal (2004: Fig. 2). Upper molars are designated as M1 and M2. Lower molars are designated as m1 and m2.

The specimens described and presented in this work are currently kept in the Natural History collection of one of the authors (JQ, Ciutadella de Menorca).

Systematics

Order Rodentia Bowdich, 1821

Family Gliridae Thomas, 1897

Genus *Hypnomys* Bate, 1918

***Hypnomys mahonensis* Bate, 1918**

***Type-locality*:** Punta Esquitxador-17 (Ciutadella de Menorca, Illes Balears, Spain).

Material. *Isolated teeth*: 5 left P4 (CBQ 2023-2027); 2 right P4 (CBQ 2028-2029; 12 left M1-2 (CBQ 2030-2041); 9 right M1-2 (CBQ 2042-2050); 7 left M3 (CBQ 2051-2057); 3 right M3 (CBQ 2058-2060); 5 left p4 (CBQ 2061-2065); 5 right p4 (CBQ 2066-2070); 9 left m1-2 (CBQ 2071-2079); 10 right m1-2 (CBQ 2080-2089); 3 left m3 (CBQ 2090-2092); 3 right m3 (CBQ 2093-2095). *Left mandibles*: 1 with p4-m3 (CBQ 369a), 2 with p4-m1 (CBQ 369b), 2 with m1-m3 (CBQ 369c-d); 2 with m1-m2 (CBQ 369e-f) and 2 with m2 (CBQ 369g-h); *Right mandibles*: 1 with p4-m3 (CBQ 369i), 1 with p4-m1 (CBQ369j), 2 with m1-m3 (CBQ 369k-l), 4 with m1-m2 (CBQ 369m-o), 2 with m2-m3 (CBQ 369p-q) and 2 with m1 (CBQ 369r-s). *Left maxillas*: 1 with P4-M2 (CBQ 369A) and 1 with M1 (CBQ 369B); *Right maxillas*: 2 with P4-M3 (CBQ 369C-D) and 1 with P4-M2 (CBQ 369E).

Description

Lower teeth (Fig. 4 y 5, Table 2)

p4. The anterolophid and the mesolophid are labially and lingually fused, forming a kind of ring. In 2 cases, however, they can be hardly recognized, formed of a number of cuspules which results in a crenulated shape. In four cases, a very reduced, cuspule-like centrolophid can be recognized. There is a long, well-developed mesolophid. Protoconid, mesoconid and hypoconid are isolated among them. Well developed, isolated posterotropid.

m1. This tooth presents 6 main ridges: anterolophid, metalophid, centrolophid, mesolophid, posterotropid and posterolophid. The anterolophid and the metalophid are lingually connected in all the cases. These two ridges are labially connected in 15 cases, while they are labially disconnected in one case. In 2 cases a number of cuspules forms a kind of pseudo-anterotropid. In 6 cases there is discontinuous, crenulated metalophid. In 2 cases a transverse connection is established between metalophid and anterolophid, while a transverse connection to centrolophid is observed in 6 cases. A discontinuous, crenulated centrolophid is observed in 3 cases. In 5 cases a connection is established between metalophid and centrolophid. A well-developed posterotropid is always present, which can be isolated (14 cases) or connected to the entoconid (6 cases).

m2. As in the case of the m1, this tooth presents 6 main ridges: anterolophid, metalophid, centrolophid, mesolophid, posterotropid and posterolophid. The anterolophid and the metalophid are lingually connected in all the cases. These two ridges are labially connected in 18 cases, while they are labially disconnected in 2 cases. In 2 cases a number of cuspules forms a kind of pseudo-anterotropid. In 3 cases there is discontinuous, crenulated metalophid. In one case a transverse connection is established between metalophid and anterolophid, while a transverse connection to centrolophid is observed in 14 cases. A discontinuous, crenulated centrolophid is observed in 8 cases. In one case a connection is established between metalophid and centrolophid. A discontinuous mesolophid is observed in one case. A well-developed posterotropid is always present, which can be isolated (18 cases) or connected to the entoconid (2 cases).

m3. As for other lower molars, this tooth presents 6 main ridges: anterolophid, metalophid, centrolophid, mesolophid, posterotropid and posterolophid. Anterolophid and metalophid are labially connected in 4 cases, while they are disconnected in 5 cases. A connection between metalophid and metaconid is always present. A distinct anterotropid can be recognized in 4 cases. A very small centrolophid, sometimes reduced to a cuspule, is present in 6 cases, while it is absent in 3 cases. The mesolophid is always long, segmented in 2 cases. A well-developed posterotropid is present in 2 cases, in one of them connected to the entoconid. The posterotropid is very small in 6 cases, while it is absent in one case.

Upper teeth (Fig. 6 y 7, Table 3)

P4. There are 5 main ridges: anteroloph, protoloph, centroloph, metaloph and posteroloph. There is a continuous endoloph connecting protoloph, metaloph and posteroloph in 6 cases. The anteroloph is always small. It is isolated in 5 cases, labially connected to the protoloph in one case, lingually connected in another case, while labially and lingually connected to the protoloph in a third case. The centroloph is isolated in 4 cases and lingually connected to the protoloph in other 4 cases. The posteroloph is always labially isolated, while it is lingually isolated in 2 cases.

M1-2. There are 6 main ridges: anteroloph, protoloph, precentroloph, postcentroloph, metaloph and posteroloph. A continuous endoloph connecting anteroloph, protoloph, metaloph and posteroloph is always present. When present, the prototrope is labially fused to the protoloph in 11 cases. A transverse connection between anteroloph and protoloph is observed in 6 cases, forming a lingual ring. A very small prototrope can be distinguished in 6 cases, while it is absent in another 6. The precentroloph is isolated in 15, while in the others a labial connection with the protoloph is established. The precentroloph reaches the posteroloph in 2 cases. A well developed postcentroloph is present in 5 cases, while it is very small in 9 cases and absent in another 9 cases. In 8 cases it reaches the precentroloph.

M3. There are 6 main ridges: anteroloph, protoloph, precentroloph, postecentroloph, metaloph and posteroloph. An endoloph connects lingually the anteroloph, protoloph, metaloph and posteroloph. The precentroloph is labially connected to the metaloph in 5 cases and remains isolated in 4. Besides the precentroloph, a postcentroloph is present in only one case. In this case they are lingually connected, while they are labially connected to the protoloph and the metaloph, respectively. In another case the precentroloph or postcentroloph are absent.

Remarks. The teeth of *H. mahonensis* coming from Punta Esquitxador 17 have been compared with casts of the original material of this species described by Bate (Agustí *et al*., 2020: Fig. 9). The sample from Punta Esquitxador 17 displays larger size than any previously described species of *Hypnomys*, with the exception of *H. mahonensis*. The holotype of *H. mahonensis* is composed of a maxilla which preserves left P4, M1, M2, M3 and right M1. The P4 presents 5 main ridges: anteroloph, protoloph, centroloph, metaloph and posteroloph. The protoloph and the posteroloph are connected by a endoloph, while anteroloph, centroloph and metaloph are isolated. Both the anteroloph and the centroloph are small. The two M1 presents 5 ridges: anteroloph, protoloph, centroloph, metaloph and posteroloph. A continuous endoloph connects anteroloph, metaloph and posteroloph. The protoloph is isolated, as it is also the case of the centroloph. The M2 presents 6 ridges: anteroloph, protoloph, precentroloph, postcentroloph, metaloph and posteroloph. As in the case of the M1, it presents a continuous endoloph. The precentroloph is labially connected to the protoloph. A very small, isolated postcentroloph can be recognized. The M3 presents 5 ridges: anteroloph, protoloph, centroloph, metaloph and posteroloph. An endoloph connects lingually the anteroloph, protoloph, metaloph and posteroloph, while the centroloph remains isolated. The holotype of *H. mahonensis* presents a more simplified dental pattern than most of the sample from Punta Esquitxador 17, especially in the case of the M1, with isolated ridges being a common feature of this specimen. However, its fits easily within the variability of the sample from Punta Esquitxador 17, as in the case of the maxilla (Fig. 6C).

The presence of a small transverse ridge connecting the anteroloph and the protoloph is a derived feature which is present in a number of specimens from Punta Esquitxador 17 while it is absent in the populations of *H. morpheus*. This transverse connection is also absent at the holotype of *H. mahonensis*. However, although absent, in the M1 from the holotype a small spur departing from the protoloph and directed towards the anteroloph can be observed, which is an indication that this feature could have been present in the original population of *H. mahonensis*. If the sample from Punta Esquitxador 17 really corresponds to the original *H. mahonensis*, this latter species could be distinguished from *H. morpheus* not only because of its larger size but also because of the presence of this derived character.

The sample from Punta Esquitxador 17 has been also compared with the material assigned to *H. mahonensis* by Reumer (1982). The upper molars from Punta Esquitxador 17 differ from those of Son Bou 1 because of the presence of a very small prototrope. Moreover, the precentroloph never reaches the metaloph and form a continuous, diagonal ridge, as in the case of Fig. 5c from Son Bou 1. Both in the holotype of *H. mahonensis* and in *Hypnomys* from Punta Esquitxador 17 the protolophe is isolated in the M1, while the precentroloph is isolated or connected labially the paracone, a condition which seems to be absent in *Hypnomys* from Son Bou 1. At Punta Esquitxador 17 the postcentroloph can be absent or very small, as it is the case of Son Bou 1, but in a few specimens can be large.

In terms of size, *Hypnomys* from Son Bou 1 is considerably smaller than *Hypnomys mahonensis* from the type-locality and Punta Esquitxador 17 being only slightly larger than *Hypnomys morpheus* from the nearby site of Son Bou 2. In this way, the teeth of Son Bou 1 also fit within the range of size variability of *Hypnomys morpheus* from Son Bauzà (Agustí *et al*. 2020). The morphology of the upper molars can be observed as well in specimens of *Hypnomys morpheus* from Sa Bassa Blanca, while the morphology of the lower molars fits also that of *Hypnomys* from Pedrera de s´Onix, Son Bauzà and Sa Bassa Blanca (Agustí *et al.* 2020). Therefore, we can conclude that the assignment of *Hypnomys* from Son Bou 1 to *H. mahonensis* is questionable, differing in a number of respects of the sample from the type-localitiy of this species as well as that of Punta Esquitxador 17. However, it cannot be excluded that the sample from Son Bou 1 corresponds to a transitional population between *H. eliomyoides* and *H. mahonensis*, in particular, the M3 figured by Reumer (1982: Fig. 5d), presents a shape which resembles that of the M3 of *H. eliomyoides*, the labial width being narrower that the lingual width, which fits as a possible transitional population between the two species.

Discussion

Three faunal episodes have been described in the Neogene of the Balearic Islands, all characterized by the absence of predators and an impoverished vertebrate fauna which evolved under insular conditions. The Middle Miocene (Serravalian) regression prompted the arrival, both in Mallorca and Menorca, of the representatives of the first faunal stage, with common taxa (genera *Gymnesicolagus* and *Margaritamys* [Mein and Adrover, 1982]) between the two islands and extending to the Late Miocene (Tortonian) (Mein and Adrover 1982; Adrover *et al.* 1985; Quintana and Agustí 2007).

The second faunal episode, although caused by a similar geological event (the Messinian regression, in the Late Miocene), is characterised by marked taxonomic differences between Mallorca and Menorca (Quintana and Moncunill-Solé 2014), but with certain common elements between Mallorca and Eivissa (Quintana *et al.* 2010; Quintana and Moncunill-Solé, *op. cit.*). In Mallorca, some of the taxa present in the Early Pliocene (*Myotragus, Nesiotites* and *Hypnomys* genera) will survive until the arrival of the first humans on the island (Alcover *et al.* 1981; Bover *et al.* 2010, 2014). In contrast, in Menorca, the second faunal episode (formed by the giant dormouse *Muscardinus cyclopeus* Agustí, Moyà-Solà& Pons-Moyà, 1982, the giant rabbit *Nuralagus rex* Quintana, Köhler &Moyà-Sola, 2011 and the giant tortoise *"T." gymnesica*, among others) will be significantly shortened by the first Pliocene glaciations and the consequent entry of endemic mammals from Mallorca, which, in Menorca, will make up the third faunal episode.

The first record of the genus *Hypnomys* in Menorca comes from the site of Cap d'Artrutx (Ciutadella de Menorca), tentatively dated between the Late Pliocene and Early Pleistocene. The few remains of *Hypnomys* sp. (Fig. 8: *Hypnomys* sp. 2) recovered from this site correspond to an ancestral species not yet identified (Quintana and Agustí 2019). From a biogeographical point of view, these remains reflect the first entry into Menorca of the elements of the "classic" Plio-Pleistocene vertebrate fauna of Mallorca (Quintana and Agustí, 2019). In this way, *Hypnomys* sp. could represent the beginning of an independent phyletic lineage, of which *H. eliomyoides* would also form part (Agustí *et al*. 2020) (Fig. 8).

Thus, when explaining the origin of *H. mahonensis*, two possible scenarios are to be considered: 1) *H. mahonensis* would be part of the phyletic lineage originating in Menorca. This hypothesis is based on the sample of *H. mahonensis* as described by Reumer (1982) in Son Bou 1 (Alaior, Menorca), and whose morphology share traits between those of *H. eliomyoides* and *H. mahonensis* and 2) *H. mahonensis* is a species endemic to Menorca, with a short phylogenetic trajectory, whose origin can be related to *H. morpheus* from the Middle Pleistocene of Mallorca (Agustí *et al*. 2020) (Fig. 8).

Given the geographical proximity of Mallorca and Menorca and the climatic cycles typical of the Middle and Late Pleistocene, with alternating cold and warm periods, it seems quite likely that the relationships between the mammal populations of the two islands was affected by complex dynamics, with periods of reproductive isolation alternating with times that enabled geographical connection and gene flow (Moyà-Solà and Pons-Moyà 1980; Pons-Monjo *et al*. 2012). In this way, the presence of *H. morpheus* in Menorca (Reumer 1982) (Fig. 8) would be a result of this same dynamic.

Conclusions

From a geological point of view, Punta Esquitxador 17 can be described as a site of small dimensions, located on calcarenites from the Late Miocene, formed by very hard, reddish silt, with abundant remains of *H. mahonensis*, *P. lilfordi* and birds. Some of the mandibles of *P. lilfordi* are remarkably large compared to the current populations of this species (distributed among the different islets around Menorca and Mallorca), which is why it is suggested that the remains originally attributed to the genus *Chalcides* by Bate (1918) in fact orrespond to a large specimen of *P. lilfordi* from Punta Esquitxador 17.

The rediscovery of the type-locality of *H. mahonensis* (equivalent to site 2 of Bate [1914]) has allowed us to describe the different dental morphotypes of this species, its degree of variability, its comparison with other species of the genus and the possible relationships with the phylogenetic lineages of Mallorca and Menorca. Certainly, doubts still remain as to which of these two lineages *H. mahonensis* is more closely related. In general, *H. mahonensis* tends to have simpler teeth patterns than *H. morpheus*, with isolated ridges in upper M1. However, the presence of derived specific features in *H. mahonensis* wich are absent in *H. morpheus*, such as the presence of a small transverse ridge connecting the anterolophe and the protolophe, enables one to differentiate both species.

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Figures and tables captions

Figure 1. Location of Punta Esquitxador 17, indicated with a black arrow in B and C. The grey areas correspond, in both cases, to the Upper Miocene calcarenites on which the site is located.

Fig. 2. 1: Geomorphological context of the *H. mahonensis* type site, with exact indication of the location of the site (white arrow), the Upper Miocene calcarenites (A) and the slope debris at the lower area (B); 2: detailed view of the site and the associated calcarenitic rocks (B'); 3: detailed view of the slope debris. The calcarenitic blocks are cemented by reddish silt with a more or less high proportion of bioclastic sand of marine origin associated with some terrestrial molluscs (the black arrows indicate the presence of several specimens of *A. [I.] hispanicus minoricensis*); 4: geological section of the site (NW-SE direction).

Figure 3. Right mandibles of *P. lilfordi* from the Pleistocene of Punta Esquitxador 17 (A-B) and the Holocene of Es Pas den Revull (Barranc d'Algendar, Ferreries, Menorca)(C).

Figure 4. p4-m3 of *H. mahonensis* (in anatomical position) left (A-H) and right (I-R). E: left m2; P-Q: right m1; R: right m2.

Figure 5. Lower teeth of *H. mahonensis*. A1-A4: right p4; A5-A9: left p4. B1-B10: right m1-2; B11-B19: left m1-2; C1-C3: right m3; C4-C6: left m3.

Figure 6. P4-M3 of *H. mahonensis* (in anatomical position) left (A-B) and right (C-D). B: M1.

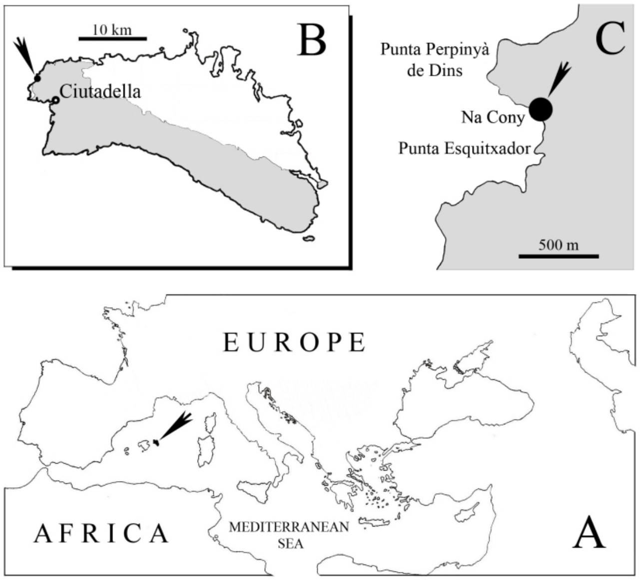
Figure 7. Upper teeth of *H. mahonensis*. A1-A2: right P4; A3-A7: left P4; B1-B8: right M1-2; B9-B18: left M1-2; C1-C3: right M3; C4-C9: left M3.

Fig. 8. Timeline and biogeographical scheme representing the two hypotheses on the phylogenetic origin of *H. mahonensis*.

Table 1. List of birds present at Punta Esquitxador 17 (according to Seguí, 1998).

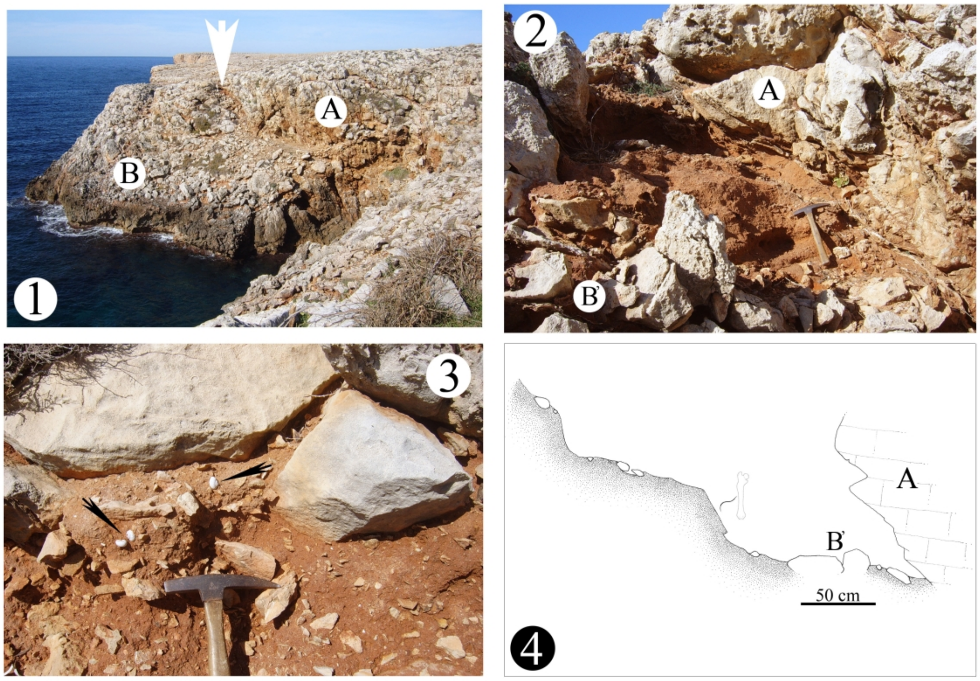
Table 2. Measurements of the lower teeth (in mm). ∗: Punta Esquitxador 17; 1: Reumer (1982); 2: Agustí (1980); 3: Reumer (1979); 4: Reumer (1980). n: number of individuals; SD: standard deviation.

Table 3. Measurements of upper teeth (in mm).∗:Punta Esquitxador 17; 1: Reumer (1982); 2: Agustí (1980); 3: Reumer (1979); 4: Reumer (1980). n: number of individuals; SD: standard deviation.



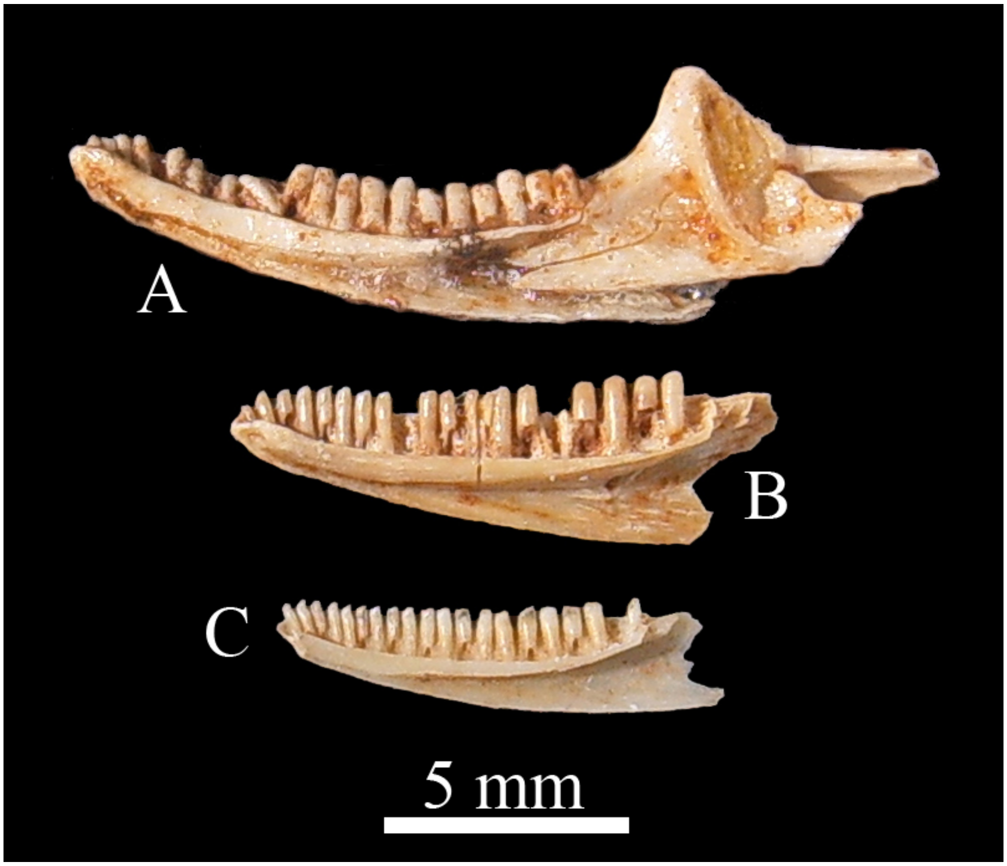
Location of Punta Esquitxador 17, indicated with a black arrow in B and C. The grey areas correspond, in both cases, to the Upper Miocene calcarenites on which the site is located.

249x165mm (300 x 300 DPI)



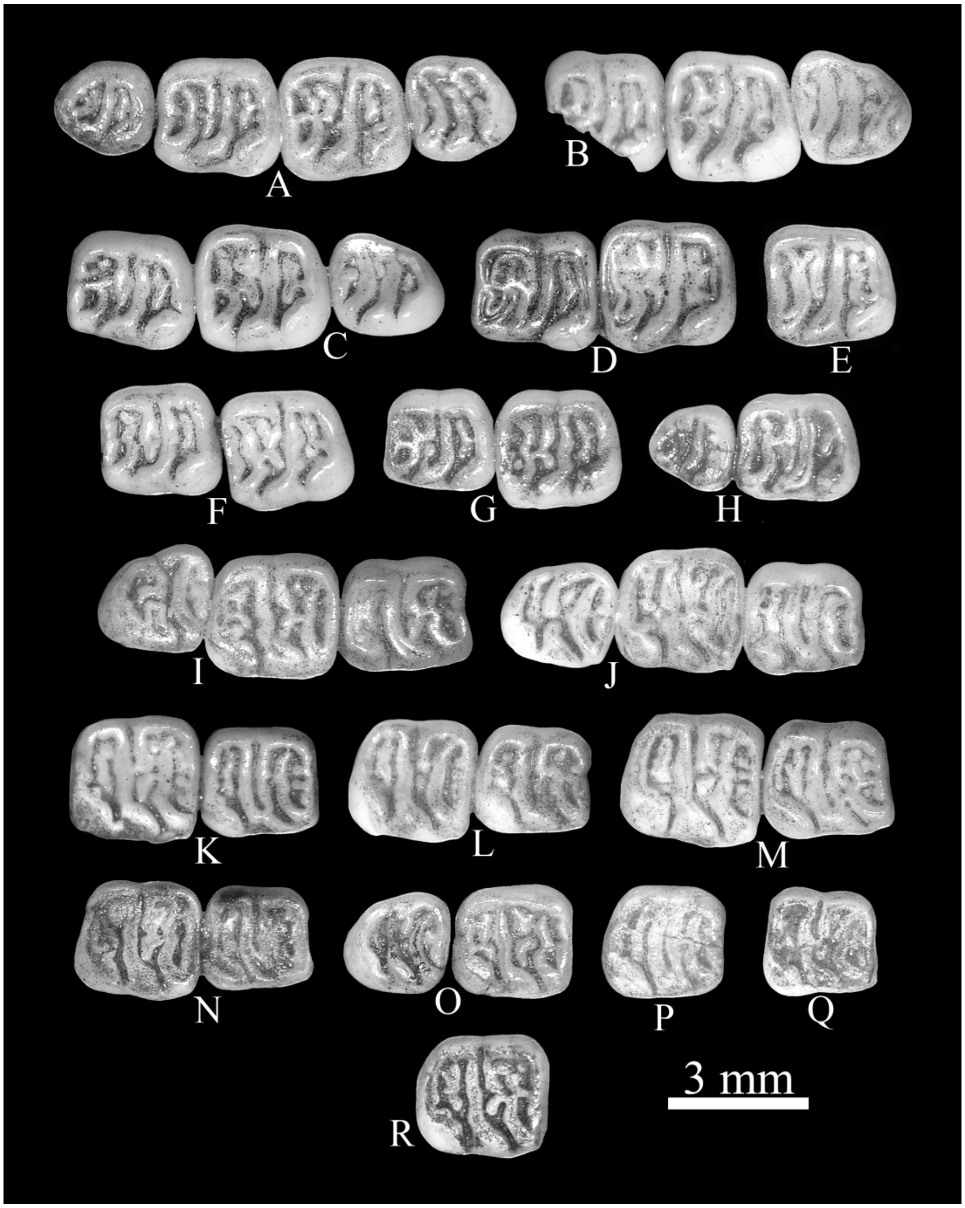
Geomorphological context of the H. mahonensis type site, with exact indication of the location of the site (white arrow), the Upper Miocene calcarenites (A) and the slope debris at the lower area (B); 2: detailed view of the site and the associated calcarenitic rocks (B'); 3: detailed view of the slope debris. The calcarenitic blocks are cemented by reddish silt with a more or less high proportion of bioclastic sand of marine origin associated with some terrestrial molluscs (the black arrows indicate the presence of several specimens of A. [I.] hispanicus minoricensis); 4: geological section of the site (NW-SE direction).

292x206mm (300 x 300 DPI)



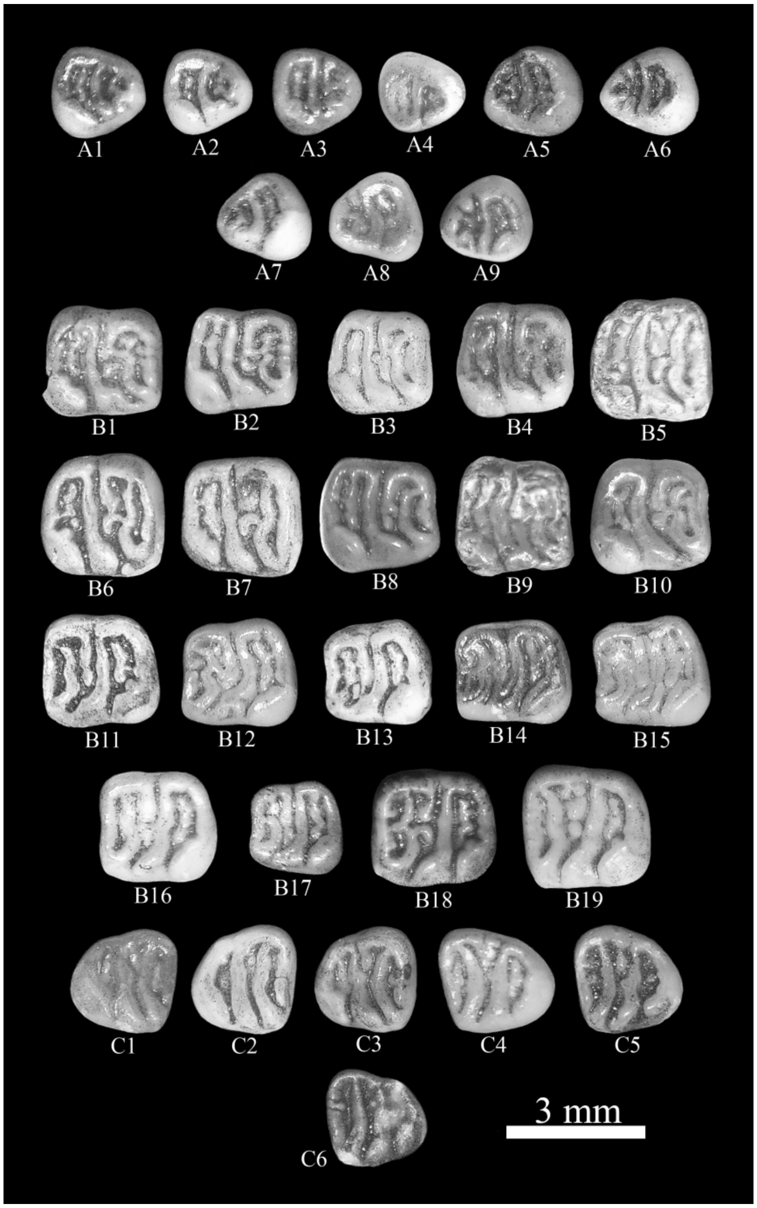
Right mandibles of P. lilfordi from the Pleistocene of Punta Esquitxador 17 (A-B) and the Holocene of Es Pas den Revull (Barranc d'Algendar, Ferreries, Menorca)(C).

212x182mm (96 x 96 DPI)



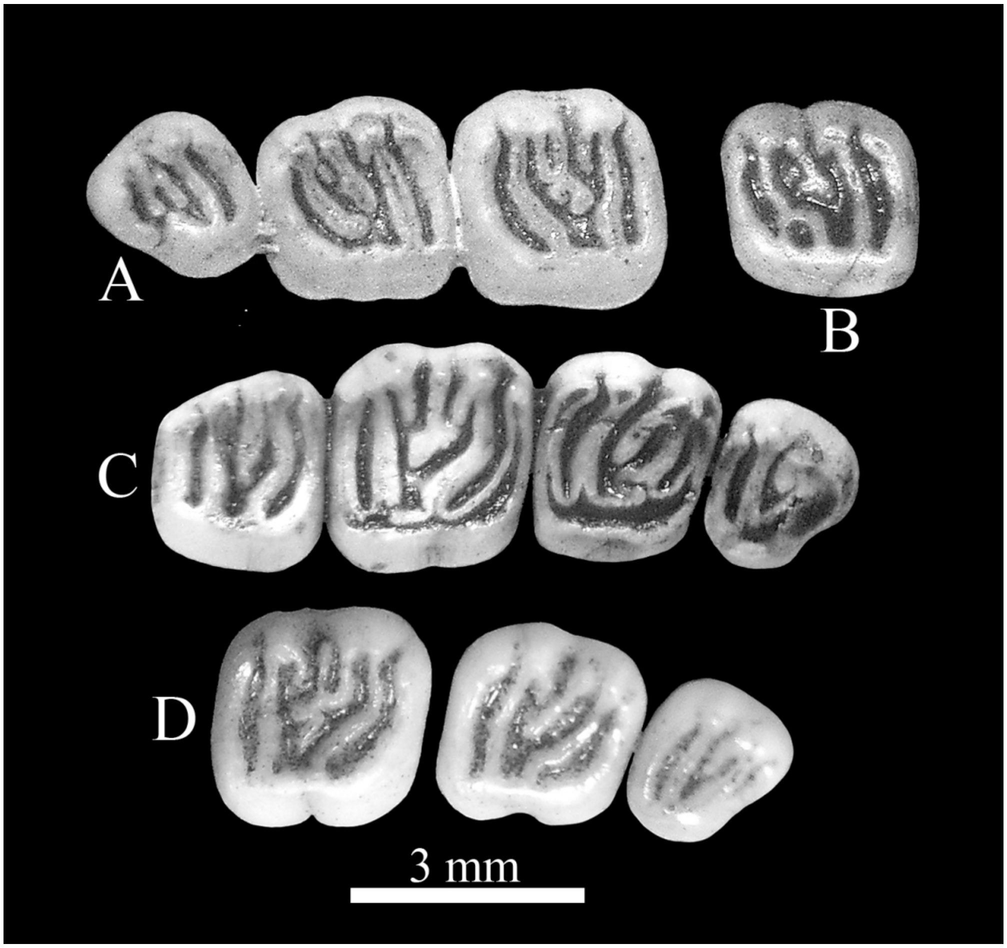
p4-m3 of H. mahonensis (in anatomical position) left (A-H) and right (I-R). E: left m2; P-Q: right m1; R: right m2.

197x246mm (300 x 300 DPI)



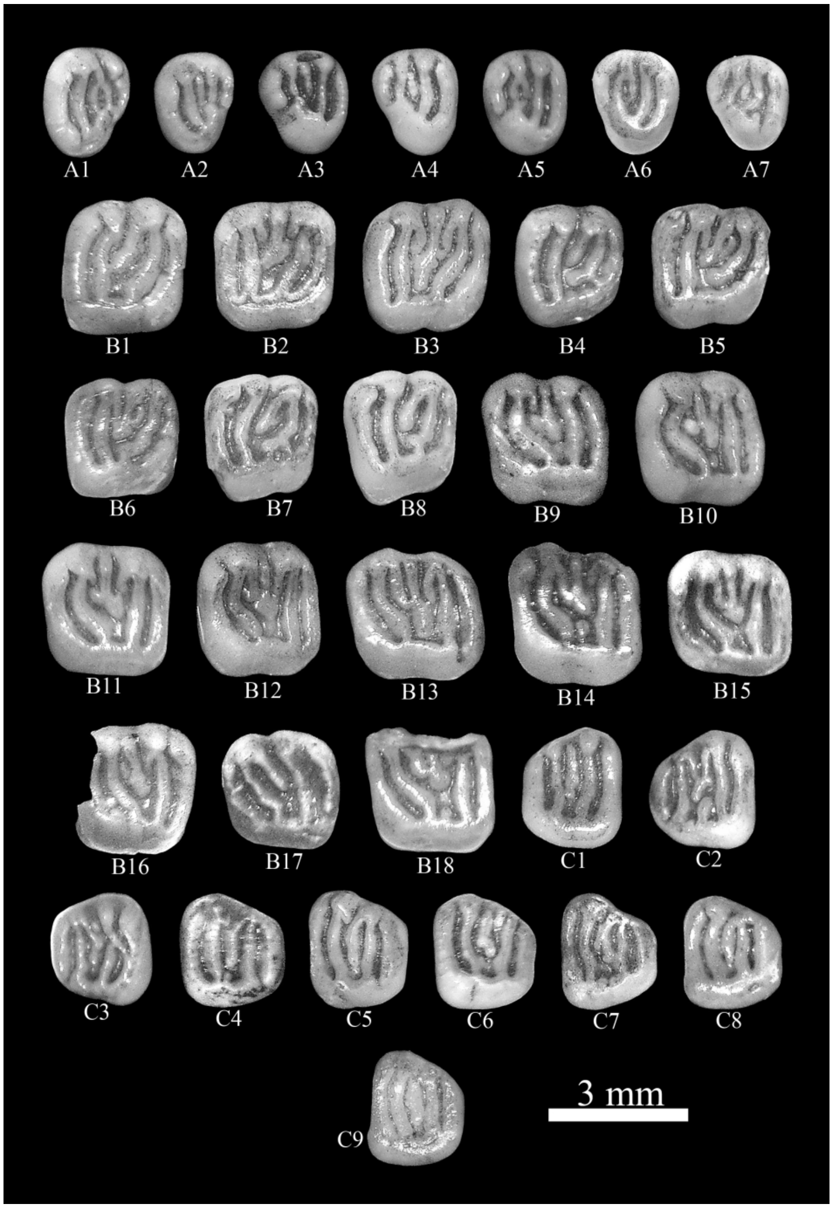
Lower teeth of H. mahonensis. A1-A4: right p4; A5-A9: left p4. B1-B10: right m1-2; B11-B19: left m1-2; C1-C3: right m3; C4-C6: left m3.

197x315mm (300 x 300 DPI)



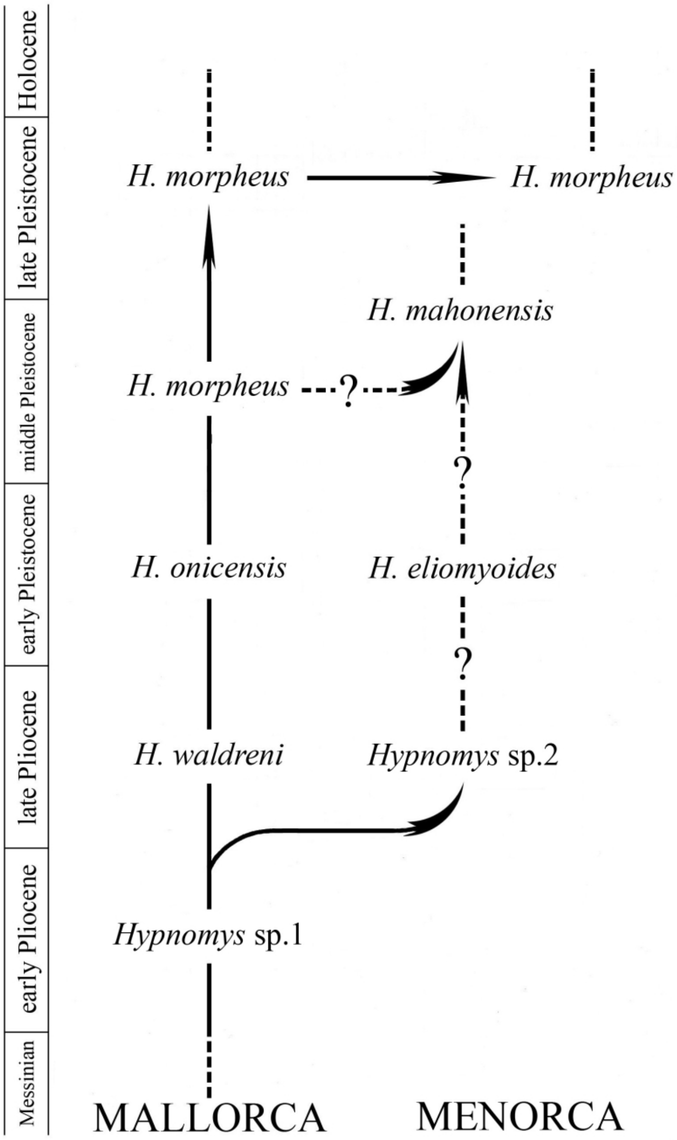
P4-M3 of H. mahonensis (in anatomical position) left (A-B) and right (C-D). B: M1.

123x116mm (300 x 300 DPI)



Upper teeth of H. mahonensis. A1-A2: right P4; A3-A7: left P4; B1-B8: right M1-2; B9-B18: left M1-2; C1-C3: right M3; C4-C9: left M3.

216x313mm (300 x 300 DPI)



Timeline and biogeographical scheme representing the two hypotheses on the phylogenetic origin of H. mahonensis.

142x228mm (300 x 300 DPI)

AVES
Puffinus sp. 1
Puffinus sp. 2
Hydrobates pelagicus (Linnaeus, 1758)
Coturnix cf. *coturnix* (Linnaeus, 1758)
Rallus cf. *aquaticus* Linnaeus, 1758
Rallus sp. 2
Gallinula chloropus (Linnaeus, 1758)
Scolopax rusticola Linnaeus, 1758
Tyto balearica Mourer-Chauviré, Alcover, Moyà et Pons, 1980
Athene noctua (Scopoli, 1769)
Erithacus sp.
Sylvia sp.
Passeriformes indet.

p4

		Length				Width			
Taxon		**n**	**Max.-min.**	**Mean**	**SD**	**n**	**Max.-min.**	**Mean**	**SD**
H. mahonensis	*	12	2.25-1.83	2.01	0.1140	12	2.01-1.69	1.87	0.0835
H. mahonensis	1	3	-	1.94	-	3	-	1.78	-
H. eliomyoides	2	-	1.56-1.37	1.45	-	-	1.94-1.75	1.85	-
H. waldreni	3	13	1.58-1.39	1,50	-	13	1.45-1.29	1.36	-
H. onicensis	4	8	1.76-1.41	1.56	-	8	1.60-1.32	1.46	-
H. morpheus	1	2	-	1.87	-	2	-	1,67	-

m1

		Length				Width			
Taxon		**n**	**Max.-min.**	**Mean**	**SD**	**n**	**Max.-min.**	**Mean**	**SD**
H. mahonensis	*	14	2.78-2.29	2.55	0.1603	14	2.57-2.13	2.37	0.1133
H. mahonensis	1	2	-	2.31	-	2	-	2.29	-
H. waldreni	3	13	2.00-1,71	1.86	-	13	1.93-1.67	1.79	-
H. onicensis	4	44	2.31-1.93	2.13	-	44	2.21-1.82	1.97	-
H. morpheus	1	1	-	2.31	-	1	-	2.29	-

m2

		Length				Width			
Taxon		**n**	**Max.-min.**	**Mean**	**SD**	**n**	**Max.-min.**	**Mean**	**SD**
H. mahonensis	*	15	3.16-2.60	2.78	0.1424	15	2.99-2.51	2.66	0.1334
H. mahonensis	1	1	-	2.39	-	1	-	2.47	-
H. waldreni	3	5	1.99-1.81	1.93	-	6	1.91-1.77	1.87	-
H. onicensis	4	26	2.31-1.98	2.17	-	25	2.29-1.99	2.11	-
H. morpheus	1	1	-	2.29	-	1	-	2.51	-

m3

		Length				Width			
Taxon		**n**	**Max.-min.**	**Mean**	**SD**	**n**	**Max.-min.**	**Mean**	**SD**
H. mahonensis	*	12	2.76-2.17	2.36	0.1616	12	2.62-2.14	2.30	0.1301
H. mahonensis	1	5	-	1.98	-	5	-	2.23	-
H. eliomyoides	2	18	1.74-1.45	1.64	-	18	2.11-1.80	1.98	-
H. waldreni	3	8	1.70-1.48	1.63	-	8	1.68-1.49	1.60	-
H. onicensis	4	9	1.82-1.62	1.71	-	9	1.85-1.69	1.77	-
H. morpheus	1	2	-	1.92	-	2	-	2.03	-

P4

Taxon		Length				Width			
		n	Max.-min.	Mean	SD	n	Max.-min.	Mean	SD
H. mahonensis	*	10	1.95-1.67	1.84	0.0817	10	2.37-2.03	2.25	0.0878
H. mahonensis	1	3	-	1.58	-	3	-	2.07	-
H. eliomyoides	2	8	1.56-1.37	1.45	-	8	1.94-1.75	1.85	-
H. waldreni	3	9	1.42-1.18	1.33	-	9	1.84-1.28	1.65	-
H. onicensis	4	8	1.55-1.34	1.47	-	8	1.91-1.76	1.86	-

M1

Taxon		Length				Width			
		n	Max.-min.	Mean	SD	n	Max.min.	Mean	SD
H. mahonensis	*	4	2.51-2.23	2.41	0.1297	4	2.83-2.62	2.72	0.1053
H. mahonensis	1	2	-	2.21	-	2	-	2.47	-

M2

Taxon		Length				Width			
		n	Max.-min.	Mean	SD	n	Max.min.	Mean	SD
H. mahonensis	*	3	2.69-2.63	2.65	0.0305	3	3.06-2.86	2.97	0.1040
H. mahonensis	1	5	-	2.34	-	5	-	2.64	-

M1-2

Taxon		Length				Width			
		n	Max.-min.	Mean	SD	n	Max.min.	Mean	SD
H. mahonensis	*	39	2.39-2.00	2.58	0.1745	39	3.06-2.01	2.62	0.2325
H. eliomyoides	2	15	2.31-1.89	2.05	-	13	2.51-2.22	2.34	-
H. waldreni	3	19	2.10-1.60	1.86	-	19	2.27-1.87	2.06	-
H. onicensis	4	73	2.45-2.09	2.27	-	74	2.26-1.89	2.07	-
H. morpheus	1	4	-	2.21	-	4	-	2.48	

M3

Taxon		Length				Width			
		n	Max.-min.	Mean	SD	n	Max.-min.	Mean	SD
H. mahonensis	*	12	2.34-2.06	2.20	0.0716	12	2.68-2.45	2.57	0.0624
H. mahonensis	1	7	-	1.92	-	7	-	2.30	-
H. eliomyoides	2	18	1.74-1.45	1.64	-	18	2.11-1.80	1.98	-
H. waldreni	3	12	1.62-1.40	1.53	-	12	1.91-1.66	1.81	-
H. onicensis	4	9	1.84-1.58	1.67	-	10	2.07-1.85	1.97	-
H. morpheus	1	1	-	1.84	-	1	-	2.16	-