UNIVERSITAT DE BARCELONA

Vertebrats post-messinians de Mallorca i Eivissa (Illes Balears, Mediterrània occidental): descripció, origen i extinció d'espècies

Enric Torres Roig

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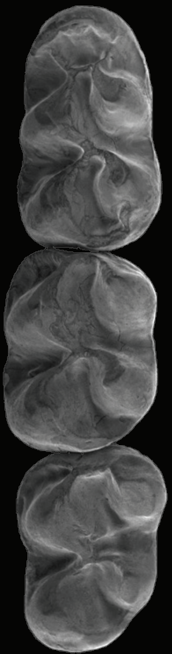
TESI DOCTORAL

ENRIC TORRES ROIG

Directors. Pere Bover i Josep Antoni Alcover



2020

UNIVERSITAT DE BARCELONA

Facultat de Ciències de la Terra.
Departament de Dinàmica de la Terra i de l'Oceà

TESI DOCTORAL

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Vertebrats post-messinians de Mallorca i Eivissa (Illes Balears, Mediterrània occidental): descripció, origen i extinció d'espècies

Programa de Doctorat en Ciències de la Terra

Enric Torres Roig

Memòria presentada per optar al títol de Doctor per la Universitat de Barcelona

Co-Directors:

Dr Josep Antoni Alcover Tomàs i Dr Pere Bover Arbós

Tutor:

Carles Ferràndez Cañadell

"És sa meua presó, sa meua llibertat, on totes les fronteres són cel, arena i mar.

Tan gros aquest petit món meu, té un riu per a creuar els seus ponts.

I jo que som natiu, aquí sa meua vida hi viu fent niu."

ILLA

Projecte Mut

Del poema "illa" de Ben Clark

"El coneixement és el regal més preuat que et podem donar

i que ningú et podrà prendre mai"

Ma mare

A la meva família, en especial a n'Alís, i als amics

Agraïments

Semblava que el final d'aquesta tesi no arribava, però la insistència i la força de voluntat per part de tots ha permès treure-la endavant. Ha estat un projecte emocionant, ple de sorpreses i d'alguns contratemps. Sense cap dubte ha estat una aventura que quedarà ben gravada en la meva memòria, i que tant sols representa un primer tast d'aquest especial jaciment mallorquí, que de ben segur encara amaga secrets que volen ser escoltats.

Ara voldria agrair a tots aquells que d'una o d'altra manera han participat en la realització d'aquets ambiciós projecte.

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No vull deixar d'esmentar totes les persones que a un moment o un altre han col·laborat amb jo (o jo he col·laborat amb ells!) per a la realització dels treballs. Així, vull agrair a tots els co-autors dels mateixos la seva participació, ajuda, i direcció. També vull fer palès el meu agraïment més sincer a les persones que ja he esmentat als capítols d'agraïment dels diferents treballs, molt especialment a: Dr Juan Pleguezuelos (Granada), Dr Johannes Müller (Berlin), Miquel Trias (Palma), Dr Javier Aramburu (Palma), Dr Mark van Strydonck (Brussel·les), Mathieu Boudin (Brussel·les), Dr Harald Pieper (Schwentinental), Dr Rainer Hutterer (Bonn),... així com als revisors dels diferents treballs. També d'una manera especial vull agrair a l'Institut Mediterrani d'Estudis Avançats (CSIC-UIB) haver-me acollit i facilitat el meu treball durant el període anterior a la meva incorporació al present Programa de Doctorat.

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Abans d'entrar en el present Programa de Doctorat em vaig beneficiar (i ho agraeixo!) d'un contracte de 4 anys associat al Subprograma de formación del personal investigador (FPI; BES-2013-062867) del Ministerio de Economía y Competitividad, englobat al Projecte de Recerca CGL2012-38087 (IP: Dr

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Resum

La present Memòria tracta de l'estudi de vertebrats fòssils post-messinians de les Illes Balears fins ara desconeguts. La investigació s'ha centrat principalment en el registre fòssil de vertebrats del Pliocè basal obtingut a Na Burguesa-1 (NB-1) i del jaciment del Pleistocè-Holocè des Pouàs a Eivissa. La troballa de nous tàxons en aquests jaciments ha permès avaluar l'origen paleobiogeogràfic de les faunes post-messinianes de les Illes Balears, explorar les condicions que poden haver influït en el procés de colonització, valorar la possible existència de tàxons relictes pre-messinians i analitzar el procés d'extinció dels llinatges faunístics post-messinians.

Els fòssils de NB-1 es van recuperar d'unes bretxes mitjançant un llarg tractament químic. Aquest procediment va permetre obtenir c. 7400 fòssils pertanyents a 4 espècies diferents d'anurs, unes 13 espècies de rèptils, 6 espècies de mamífers i almenys una dotzena d'espècies d'ocells. Totes aquestes espècies, la majoria pertanyents a llinatges filètics registrats per primera vegada a l'illa de Mallorca, ens ofereixen una visió més precisa de l'estoc inicial que va arribar a les Illes Balears durant la Crisi salina del Messinà (MSC).

La Memòria inclou la descripció de *Paraethomys balearicus*, una nova espècie insular de múrid obtinguda a NB-1, amb dents hipsodontes de mida mitjana. El m1 mostra els seus trets més distintius: la hipsodòncia, la presència d'un cíngol anterior inusual, un cíngol labial ben desenvolupat, cúspides labials accessòries elevades que s'assemblen al patró d'*Apodemus* i una fosseta entre c1 i l'hipocònid. *Paraethomys balearicus* conserva trets propers als presents a les primeres poblacions de *P. meini* del Turolià superior, el seu presumpte avantpassat continental. La relació entre el nou tàxon i el seu avantpassat directe continental dóna un suport addicional a un origen messinià per a l'anomenada fauna de *Myotragus*. L'absència de *Paraethomys* en tots els altres jaciments mallorquins més recents suggereix que la seva extinció probablement es va produir en un moment indeterminat durant el Pliocè.

També s'inclou la caracterització del conjunt paleornitològic obtingut a NB-1, compost per *Tyto* sp.1, *Tyto* sp. 2, *Otus* sp., un Phasianidae, una espècie de Charadriiformes i almenys cinc passeriformes. La depredació per almenys *Tyto* sp. 1 i *Otus* sp. va permetre generar la rica tafocenosis de NB-1, que englobaria el rang de mides de les presumptes preses detectades al dipòsit.

D'altra banda, s'ha observat que un nou glírid obtingut a NB-1, del qual deriva el llinatge filogenètic d' *Hypnomys*, es relaciona amb un avantpassat que es localitzaria al Miocè mitjà-final. En contrast amb la hipòtesi més acceptada, l'elevada complexitat dental del glírid NB-1 exclou la relació directa del llinatge d'*Hypnomys* amb *Eliomys*, el qual es caracteritza per un patró dental molt més senzill.

La revisió del material obtingut a es Pouàs va permetre detectar c. 6000 fòssils que documenten la presència d'un escurçó nan endèmic d'Eivissa, V*ipera latastei ebusitana*, probablement relacionada amb un possible escurçó més gran del jaciment de la cova de Ca na Reia. L'anàlisi filogenètica indica que *V. l. ebusitana* deriva probablement d'una població de *V. lastei* del nord-est peninsular. Les diferències morfològiques entre *V. l. ebusitana* i les poblacions ibèriques de *V. latastei* suggereixen que es tracta d'un nou tàxon nan resultat de processos evolutius insulars, que es va extingir poc després de l'arribada dels primers pobladors humans a aquesta illa fa uns 4000 anys.

La presència d'*Apocricetus darderi* i *Paraethomys balearicus* a Mallorca ha permès datar l'arribada d'un estoc faunístic continental del Turolià tardà a l'illa durant el MSC. Aquests tàxons, juntament amb *Alytes* aff. *muletensis* de NB-1 i *Debruijnimys* sp. del Pliocè de ses Fontanelles a Eivissa, situa la regió d'origen de la dispersió faunística principalment al SE de la península Ibèrica, quan les Bètiques i les Balears es van connectar a través del Promontori Balear durant la màxima caiguda del nivell del mar. A més, els corredors riparians podrien haver facilitat l'arribada de tàxons altament dependents d' hàbitats humits, com l'ancestre del ferreret *Alytes* i *Discoglossus*. D'altra banda, les anàlisis moleculars suggereixen que la separació de l'escurçó nan d'Eivissa de les poblacions ibèriques de *V. latastei* es va produir fa menys de 1,3 milions d'anys. Aquestes dades suggereixen que *V. l. ebusitana* seria el primer vertebrat terrestre que arribà a les Illes Balears per via ultramarina.

La millora del coneixement del registre fòssil dels vertebrats balears revela quatre episodis d'extincions faunístiques post-messinianes, els quals van afectar cadascuna de les illes de manera diferencial en els darrers 5 milions d'anys. En alguns casos, sembla que l'extinció va afectar a tot l'arxipèlag, mentre que en altres episodis només va afectar algunes de les illes. Les causes de les extincions s'han relacionat amb canvis en les condicions ambientals, factors de competitivitat interespecífica i, finalment, amb l'arribada dels humans i les espècies introduïdes per aquests

Summary

The present report deals with previously unknown post-Messinian fossil vertebrates of the Balearic Islands. The research mainly focused on the basal Pliocene vertebrate fossils recovered at Na Burguesa-1 (NB-1), and at the Pleistocene-Holocene site of Es Pouàs in Eivissa. The discovery of new taxa at both sites has enabled to refine the paleogeographical origin of the post-Messinian faunas of the Balearic Islands, assess the conditions that could have influenced the colonization process, explore the possible existence of pre-Messinian relict taxa in the archipelago and analyze the process of extinction of the post-Messinian faunal lineages.

The fossils from NB-1 were recovered through a long chemical treatment from a breccia discovered in 2012. This procedure allowed the recovery of c. 7400 items belonging to 4 different species of anurans, about 13 species of reptiles, 6 species of mammals, and at least a dozen species of birds. These taxa mostly belong to phyletic lineages not previously recorded in the island of Mallorca, and provide an accurate picture of the initial vertebrate faunistic stock that reached the Balearic Islands during the Messinian Salinity Crisis (MSC).

The report includes the description of *Paraethomys balearicus*, a new insular species of murid with medium-sized hypsodont teeth that was recovered at NB-1. The m1 presents the most distinctive traits of this new taxon: hypsodonty; high occurrence of an unusual anterior cingulum; well-developed labial cingulum; high accessory labial cuspids resembling the *Apodemus* pattern; and presence of a funnel between c1 and the hypoconid. *Paraethomys balearicus* preserves traits close to those present in the earliest populations of *P. meini* from the upper Turolian of the Iberian Peninsula, its assumed mainland ancestor. The relationship between the new taxon and its direct mainland ancestor gives additional support to a Messinian origin for the so-called *Myotragus* fauna, which became isolated on the islands after the refilling of the Mediterranean Sea (5.33 Ma). The absence of *Paraethomys* from all subsequent Mallorcan sites known to date suggests that it became extinct most probably at an indeterminate time during the Pliocene.

The report also includes the characterization of the paleornithological assemblage found at NB-1, which includes three nocturnal birds of prey (*Tyto* sp.1, *Tyto* sp. 2 and *Otus* sp.), a representative of the Phasianidae, a species of Charadriiformes, and at least five Passeriformes. Predation exerted by at least *Tyto* sp. 1 and *Otus* sp. is on the basis of the composition of the NB-1 taphocenosis, which covers the entire, wide range of prey sizes detected to be present in the deposit.

Furthermore, a new glirid discovered in NB-1 seems to be on the origin of the *Hypnomys* phylogenetic lineage and is related to a Middle-Late Miocene ancestor. Contrary to previous accepted assumptions, the high dental complexity of the new NB-1 glirid discards a sister, direct relationship of the *Hypnomys* and *Eliomys* lineages since the latter is characterized by the display of a much simpler dental pattern.

The review of the material obtained at es Pouàs site on the years 1989-1994 allowed the detection of c. 6000 fossils that document the presence of a new dwarf endemic viper, *Vipera latastei ebusitana*, probably related to a large snake tentatively identified as a viper present at Ca na Reia site. Phylogenetic analyses indicate that *V. l. ebusitana* most probably derived from a northeast Iberian population of *V. lastei*. The morphological differences between *V. l. ebusitana* and the Iberian populations suggest that it is a new dwarf taxon resulting from insular evolutionary processes; it became extinct shortly after the first human arrival to the island about 4000 years ago.

The endemic *Apocricetus darderi* and *Paraethomys balearicus* suggest the arrival to the island of a continental faunal stock of late Turolian age during the MSC. These taxa, together with *Alytes* aff. *muletensis* from NB-1 and *Debruijnimys* sp. from the Pliocene of ses Fontanelles (Eivissa), point out to SE Iberia as the source region of the faunal newcomers. The colonization of the islands was enabled by the establishment of a

direct land connection between the Betic mountains and the Balearics through the Balearic Promontory during the maximum MSC sea level fall. In addition, riparian corridors could have played a role facilitating the arrival of taxa highly dependent on humid habitats, such as the midwife toad *Alytes* and the painted frog *Discoglossus*. On the other hand, analyses using molecular clocks suggest that the separation of the Eivissan dwarf viper from the Iberian populations of *V. latastei* occurred around one million years ago. This fact makes it the first (and the only one known) case of terrestrial vertebrate that reached the Balearic Islands though overseas dispersal.

The study of all the above-mentioned material has revealed that the vertebrate fossil record of the Balearic Islands has passed through four different faunal extinction episodes during the post-Messinian, each one affecting the islands in a different way. In some cases, extinction seems to have affected the whole of the archipelago, while in others it seems to be restricted to some islands only. Extinction causes might be related to changes in environmental conditions, interspecific competition and, especially to the arrival of humans and of their accompanying species to the archipelago.

Resumen

La presente Memoria tiene como objeto temático el estudio de vertebrados fósiles post-mesinienses hasta ahora desconocidos de las Islas Baleares. La investigación se ha centrado principalmente en el registro fósil de vertebrados del Plioceno basal obtenido en el depósito de Na Burguesa-1 (NB-1) en Mallorca, y del yacimiento del Pleistoceno-Holoceno des Pouàs en Eivissa. El hallazgo de nuevos taxones en estos yacimientos ha permitido evaluar el origen paleobiogeográfico de las faunas post-mesinienses de las Islas Baleares, explorar las condiciones que pueden haber influido en el proceso de colonización, valorar la posible existencia de taxones relictos pre-mesinienses y analizar el proceso de extinción de los linajes faunísticos post-mesinienses.

Los fósiles de NB-1 se recuperaron a partir de las brechas descubiertas en el 2012 mediante un largo tratamiento químico. Este procedimiento permitió obtener c. 7400 fósiles pertenecientes a 4 especies diferentes de anuros, unas 13 especies de reptiles, 6 especies de mamíferos y al menos una docena de especies de aves. Todos estos taxones, la mayoría pertenecientes a linajes filéticos registrados por primera vez en la isla de Mallorca, nos ofrecen una visión más precisa de la fauna inicial que llegó a las Islas Baleares durante la Crisis salina del Messiniense (MSC).

La Memoria incluye la descripción de *Paraethomys balearicus*, una nueva especie insular de múrido obtenida en NB-1, con dientes hipsodontos de tamaño medio. El m1 muestra sus rasgos más distintivos: la hipsodoncia, una frecuencia elevada de un cíngulo anterior poco habitual en el género, un cíngulo labial bien desarrollado, cúspides labiales accesorias elevadas que se asemejan al patrón de *Apodemus* y una foseta entre c1 y el hipocónido. *Paraethomys balearicus* conserva rasgos cercanos a los presentes en las primeras poblaciones de *P. meini* del Turoliense superior, su presunto antepasado continental. La relación entre el nuevo taxón y su antepasado directo continental confiere un apoyo adicional a un origen mesiniense para la llamada fauna de *Myotragus*. La ausencia de *Paraethomys* en el resto de yacimientos más recientes mallorquines conocidos sugiere que su extinción probablemente se produjo en un momento indeterminado durante el Plioceno.

También se incluye la caracterización del conjunto paleornitológico obtenido a NB-1, compuesto por *Tyto* sp.1, *Tyto* sp. 2, *Otus* sp., un Phasianidae, una especie de Charadriiformes y al menos cinco Passeriformes. La depredación por al menos *Tyto* sp. 1 y *Otus* sp. permitió generar la rica tafocenosis de NB-1, que englobaria el rango de tamaños de las presumibles presas detectadas en el depósito.

Por otra parte, se ha observado que un nuevo glírido obtenido a NB-1, del que deriva el linaje filogenético de *Hypnomys*, se relaciona con un antepasado que se localizaría en el Mioceno medio-final. En contraste con la hipótesis más aceptada inicialmente, la elevada complejidad dental del glírido NB-1 excluye la derivación directa del linaje de *Hypnomys* a partir de *Eliomys*, el cual se caracteriza por un patrón dental mucho más sencillo.

La revisión de material obtenido de es Pouàs permitió detectar c. 6000 fósiles que documentan la presencia en el Pleistoceno superior y el Holoceno de una víbora enana endémica de Eivissa, *Vipera latastei ebusitana*, probablemente relacionada con una posible víbora más grande del yacimiento de la cova de Ca na Reia. El análisis filogenético indica que *V. l. ebusitana*, deriva probablemente de una población ibérica de *V. latastei* del nordeste de la península Ibérica. Las diferencias morfológicas entre *V. l. ebusitana* y las poblaciones ibéricas de *V. latastei* sugieren que se trata de un nuevo taxón enano resultado de procesos evolutivos insulares, que se extinguió poco después de la llegada de los primeros pobladores humanos a esta isla hace unos 4000 años.

La presencia de Apocricetus darderi y Paraethomys balearicus en Mallorca ha permitido datar la llegada de un stock faunístico continental del Turoliense tardío en la isla durante la MSC. Estos taxones, junto con

Alytes aff. muletensis de NB-1 y Debruijnimys sp. del Plioceno de ses Fontanelles en Eivissa, permiten localizar la región de origen de la dispersión faunística principalmente en el SE de la Península Ibérica, cuando la Cordillera Bética y las Baleares se conectaron a través del Promontorio Balear durante la máxima caída del nivel del mar. Además, corredores ribereños podrían haber facilitado la llegada de taxones altamente dependientes de los hábitats húmedos, tales como el ancestro del ferreret y Discoglossus. Por otra parte, los análisis moleculares sugieren que la separación de la víbora enana de Eivissa de las poblaciones ibéricas de V. latastei se produjo hace menos de 1,3 millones de años. Estos datos sugieren que V. l. ebusitana sería el primer vertebrado terrestre que alcanzó las Baleares por vía ultramarina.

La mejora del conocimiento del registro fósil de los vertebrados baleares revela cuatro episodios de extinciones faunísticas post-mesinienses en los últimos 5 millones de años, los cuales afectaron cada una de las islas de manera diferencial. En algunos casos, parece que las extinciones afectaron a todo el archipiélago, mientras que en otros sólo afectaron algunas de las islas. Las causas de las extinciones se han relacionado con cambios en las condiciones ambientales, factores de competitividad interespecífica y, finalmente, con la llegada de los humanos y las especies introducidas por estos.

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10. **Torres-Roig E**., Agustí J., Bover P. i Alcover J.A. 2019. A new giant cricetine from the basal Pliocene of Mallorca (Balearic Islands, western Mediterranean). *Historical Biology*, 2: 559-573.

Annex 3. Article relacionat amb la present Tesi, que es troba dins del Programa de Doctorat de Ciències de la Terra de la UB, però que forma part de la Tesi Doctoral d'un altre coautor 265-273

11. Hennekam, J.J., Benson, R.B.J., Herridge, V.L., Jeffery, N., **Torres-Roig, E**., Alcover, J.A. i Cox, P.G. (in press). Morphological divergence in giant fossil dormice: predicted shape analyses of insular gigantism. *Proceedings of the Royal Society of London*, series B

PART 1. INTRODUCCIÓ GENERAL

CAPÍTOL 1. Presentació.

1.1. Justificació

L'interès sobre la fauna vertebrada fòssil post-messiniana (això és, del Pliocè, Pleistocè i Holocè) de les Balears s'inicià l'any 1909, amb la descoberta i descripció de *Myotragus balearicus* per Dorothea Bate. Des de llavors s'ha avançat considerablement en l'estudi de les faunes vertebrades de les Balears pre-humanes. D'una banda, s'han descrit nombroses espècies de vertebrats d'aquestes faunes, principalment de jaciments del Pleistocè superior i Holocè, però també d'altres èpoques anteriors. S'han pogut estudiar nombrosos aspectes de l'evolució morfològica, del cicle vital i de la genètica d'aquestes espècies, s'han establert models zoogeogràfics del poblament i s'ha avançat notablement en el coneixement paleogeogràfic de les Balears. No obstant, encara queden moltes incògnites sobre aquestes faunes. Aquesta Tesi es centra en l'estudi d'aspectes prèviament desconeguts de les faunes vertebrades fòssils post-messinianes de les Balears, les illes més aïllades de la Mediterrània. L'interès científic per aquestes faunes s'ha centrat en diferents objectius que constitueixen els d'aquesta Tesi i dels treballs previs a la mateixa. En primer lloc, en l'estudi de les faunes inicials que donaren origen a les espècies que varen trobar els primers pobladors humans a les Balears. El seu coneixement és incomplet, com demostren els resultats presentats en aquesta Memòria. En segon lloc, s'ha intentat entendre les cronologies i causes de les extincions de les espècies endèmiques de vertebrats de les Balears. Finalment, s'han avaluat els processos evolutius que han sofert aquestes espècies. Per raons logístiques (possibilitat d'accés a materials) els estudis realitzats s'han centrat a Mallorca i a Eivissa. A la primera illa, s'han realitzat treballs sobre les faunes del Zancleà i sobre els mamífers del Pleistocè. Els primers profunditzen en el coneixement de la fauna del Zancleà, amb la identificació de tàxons prèviament desconeguts (e.g., Anura, Aves, Rodentia), i el seu significat biogeogràfic, ecològic i evolutiu. Els segons han abastat l'extinció de *Myotragus* i aspectes de l'evolució d'*Hypnomys*. A Eivissa, les aportacions s'han centrat en la descripció d'un tàxon nou per a la ciència i l'anàlisi del seu origen i la seva extinció.

1.2. Objectius i estructura de la Tesi

En la present Tesi Doctoral es dóna a conèixer l'existència de nous micro-vertebrats provinents del jaciment mallorquí de Na Burguesa-1 del Pliocè basal i dels jaciments clàssics eivissencs de l'avenc des Pouàs i Ca na Reia situats al Pleistocè-Holocè i Pleistocè inferior, respectivament. Cal mencionar que el gruix principal de material disponible per realitzar l'elaboració d'aquesta Memòria i dels treballs previs provè del jaciment de Na Burguesa-1. D'aquest dipòsit s'han detectat i estudiat representats d'anurs, escatosos (encara en vies d'estudi), aus i mamífers (algunes espècies, pendents d'estudi). D'altra banda, sobre materials excavats durant els anys 80-90 dels jaciments eivissencs, s'han identificat restes fòssils inèdites atribuïbles a un ofidi endèmic de reduïdes dimensions. L'estudi de tots aquest materials han permès cobrir els següents objectius:

a. Millora en el coneixement sobre la composició de vertebrats del Pliocè basal de Mallorca i del Pleistocè-Holocè d'Eivissa.

b. Descripció nous tàxons i presentació de les seves implicacions paleobiogeogràfiques i paleoecològiques.

c. Avaluació de la possible existència de tàxons heretats de faunes pre-messinianes o arribats després de la inundació zancleana.

d. Avaluació de les possibles causes d'extinció de diferents tàxons durant el Pliocè de Mallorca i l'Holocè d'Eivissa.

La Tesi es presenta com a un compendi d'articles. Per optar al títol de Doctor es presenten quatre d'aquests treballs publicats a revistes indexades al *Science Citation Index* de la *Web of Knowledge*. Per a la discussió global i les conclusions s'han tengut en compte aquests quatre treballs, així com també altres treballs realitzats amb anterioritat a aquest programa de doctorat, que aporten informacions que s'integren a l'assoliment dels objectius generals de la Tesi.

La Memòria s'estructura en quatre parts que inclouen cinc capítols, la bibliografia i els annexos. La primera part inclou una amplia introducció general. La segona part correspon als resultats globals recolzats sobre quatre treballs publicats a revistes indexades al JCR (adjuntats a l'annex 1) i per material que es troba en estudi (rèptils i Gliridae). Aquestos constitueixen el cos principal de la Tesi. Els dos primers tracten sobre la fauna del jaciment de Na Burguesa-1 (Palma, Mallorca) i inclouen l'estudi del múrid i la descripció de la fauna ornítica del jaciment. En el primer treball es descriu una nova espècie de múrid de transcendència biogeogràfica, altament informativa sobre l'edat del jaciment i l'origen de la fauna. El segon té transcendència tafonòmica, ja que identifica, entre altres tàxons, les espècies que originaren el depòsit. El tercer treball consisteix en la descripció d'un vipèrid obtingut als nivells del Pleistocè superior i l'Holocè des Pouàs (Sant Antoni de Portmany, Eivissa). S'estableix l'origen d'aquesta espècie i les causes de la seva extinció. El quart treball és un estudi de les relacions d'un dels endemismes teriològics de les Gimnèsies, i rere l'aproximació genètica amb els seus parents vivents, explora els seus ancestres més probables, d'acord amb el testimoni dels fòssils. En la tercera part es presenta una discussió global. Per a la realització d'aquesta discussió s'han tingut en compte tant els articles presentats a la segona part, com els treballs realitzats prèviament a la incorporació del doctorant al Programa de Doctorat de Ciències de la Terra de la Universitat de Barcelona (annex 2). Finalment, la quarta part correspon a les conclusions globals de la Tesi Doctoral.

CAPÍTOL 2. Història geo-estructural i faunes de vertebrats de les Balears

2.1. Marc geològic de l'arxipèlag Balear

Actualment les Illes Balears constitueixen la part emergida de l'anomenat Promontori Balear, un relleu que s'estén aproximadament uns 400 km al NE de la Península Ibèrica i que es troba delimitat al NO pel solc de València o conca Catalano-Balear, al SE per la conca Algeriana i al NE per la conca Liguro-Provençal. Topogràficament correspon a la prolongació nord-oriental de les serralades Bètiques. El conjunt d'aquestes serralades conformen el Sistema Bètico-Balear, que juntament amb els relleus muntanyosos que conformen el Rif del nord d'Àfrica i les mars adjacents que els connecten, donen lloc al segment occidental de l'Orogen Alpí Peri-mediterrani. Aquest orogen és el resultat d'una complexa evolució geodinàmica regida pel moviment relatiu de les plaques euroasiàtica i africana amb la participació de plaques menors, com la ibèrica (e.g., Cohen, 1980; Durand-Delga, 1980; Dercourt et al., 1986). L'estructuració del Sistema Bètico-Balear es caracteritza per la superposició durant el Cenozoic de dos etapes deformatives principals (Fontboté et al., 1989, 1990; Roca, 1996; Ayala et al., 2015): a) una etapa compressiva desenvolupada des de l'Oligocè superior al Miocè mitjà (Fig. 1A-D); i b) una etapa distensiva, des del Miocè mitjà a l'actualitat (Fig. 1E-F).

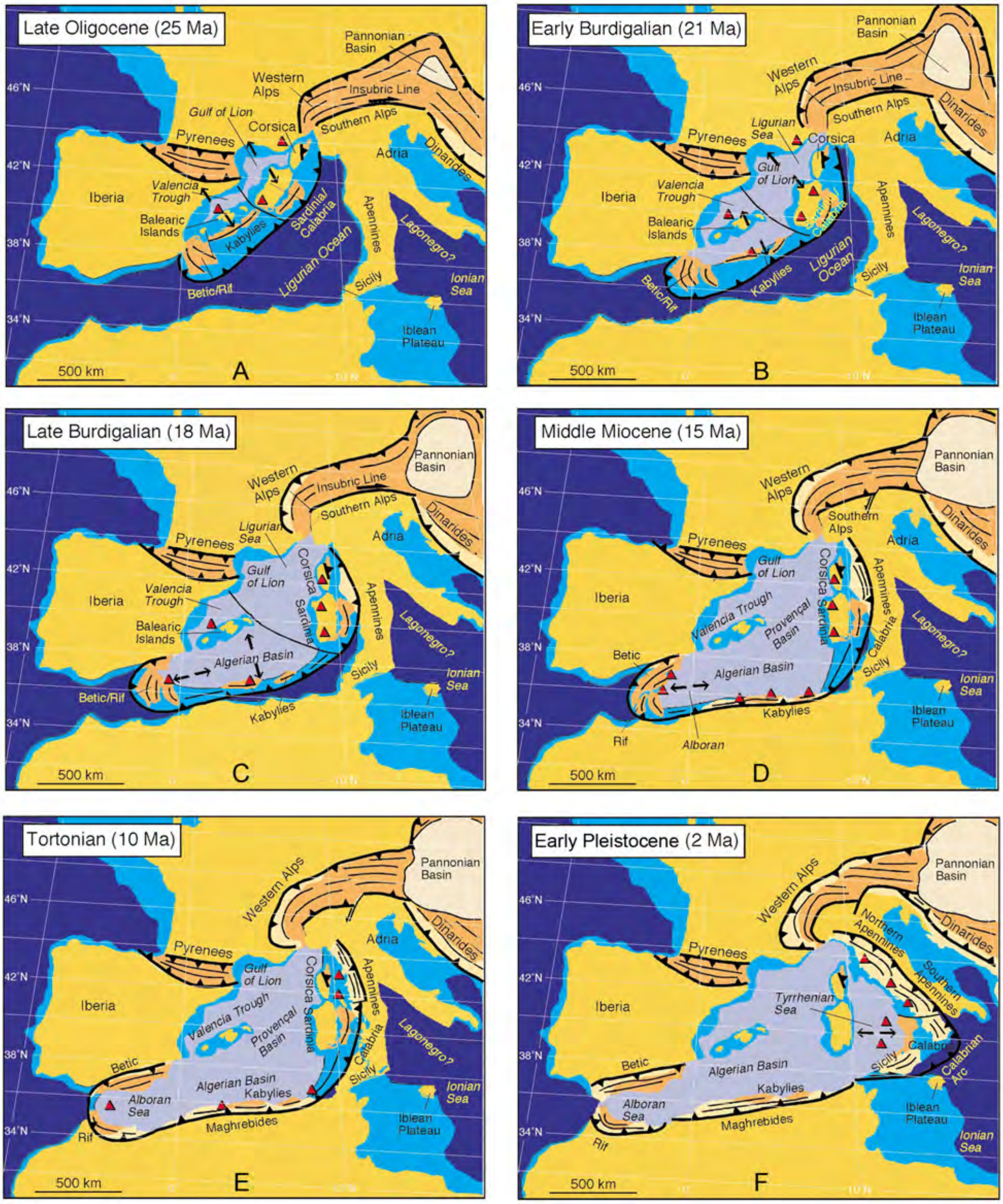


Figura 1: Evolució paleogeogràfica de la Mediterrània occidental des de l'Oligocè superior fins al Pleistocè. Modificat de Rosenbaum et al. (2002).

Fase compressiva

Es desenvolupa predominantment a l'Oligocè superior i acaba al Langhià-Serraval·lià (Ramos-Guerrero et al., 1989). Durant aquest període va tenir lloc la col·lisió entre les plaques africana i euroasiàtica (amb la placa ibèrica ja soldada a la euroasiàtica) i la consegüent formació d'un sistema de plecs i d'encavalcaments d'orientació NE-SO i vergents cap al NO. Paradoxalment, dintre d'aquest context, en el marge ibèric oriental, entre València i Provença, va tenir lloc un procés d'aprimament de l'escorça que va tendir a separar la vora on ja s'havia elevat l'edifici alpí que comunicava el Sistema Bètico-Balear amb els Alps. Entre aquest relleu i el continent el moderat procés d'aprimament no va permetre la formació d'escorça oceànica, però un progressiu enfonsament del fons marí creat entre el Golf de València, sud de Catalunya i nord de les Balears, va donar lloc al solc de València. S'han reconegut evidències d'aquest episodi extensiu a Menorca (Bourrouilh, 1973, 2016; Sàbat et al., 2018) i recentment a Eivissa (Etheve et al., 2016). En canvi, a Mallorca s'ha remarcat el caràcter compressiu d'aquest episodi (Ramos-Guerrero et al., 1989; Gelabert et al., 1992; Sàbat et al., 2011). Tot i això, el règim tectònic predominant al Promontori Balear durant aquesta fase es troba en discussió (Etheve et al., 2016; Sàbat et al., 2011; 2018). Al NE del solc de València l'escorça continental va arribar a la ruptura, amb la consegüent formació d'escorça oceànica (Burrus et al., 1987). Aquest fet va provocar que la microplaca de Còrsega i Sardenya, que originàriament quedava prop de Catalunya, el Llenguadoc i Provença, migrés cap al SE en un moviment de rotació antihorari (Rehault, 1981; Burrus, 1984). L'edat i magnitud d'aquesta rotació, juntament amb l'obertura de la Conca Liguro-Provençal, es va determinar a partir de l'anàlisi paleomagnètica de roques volcàniques de Sardenya (Edel, 1980; Montigny et al., 1981). D'aquesta anàlisi es conclou que la microplaca va rotar uns 25-30° en un lapse de temps que es troba al voltant de 3 milions d'anys (Ma), en el límit Aquitanià-Burdigalià. Abans que es produís aquest desplaçament, una part del massís cirno-sard formava part de l'estructura de l'orogen Bètico-Balear que enllaçava amb els Alps sense interrupció. Aquesta part se troba al NE de l'illa de Còrsega (Fig. 2) i la resta es troba submergida en la conca Liguro-Provençal i a l'Est de Sardenya (Gueguen et al., 1998). La interrupció amb el proto-Promontori Balear es va donar amb la formació d'una gran falla direccional destra d'orientació NO-SE, la falla de Paul Fallot, situada al N de Menorca. Aquesta falla va permetre el lliscament cap al SE de la microplaca cirno-sarda (Vergés i Sàbat, 1999).

Fase distensiva

Iniciada al Langhià-Serraval·lià (Fallot, 1922; Colom, 1975, Pomar et al., 1983; Álvaro et al., 1984). En aquest context el Promontori Balear és sotmès a un règim tectònic distensiu que originà un sistema de horst i grabens d'orientació NE-SW limitats per falles normals. S'interpreta que el pas d'un context contractiu a un extensiu es va donar per: a) la migració cap al sud de la subducció de la placa africana sota la placa euroasiàtica, traslladant el desenvolupament del solc de València i la conca Liguro-Provençal a la formació de la conca Algeriana (Roca et al., 1990); i b) el col·lapse de l'orogen com a resposta a la compensació isostàtica degut al ràpid aixecament sofert durant la col·lisió entre Àfrica i Ibèria (Dewey, 1988). A aquesta fase s'associa una certa activitat volcànica submarina, que s'estén des del Miocè superior fins a l'actualitat (Martí et al., 1992), procedent de magmes originats en un marc de tectònica extensional. Les manifestacions volcàniques més remarcables s'han desenvolupat al llarg del sistema de falles NO-SE que limita el solc de València amb la conca Liguro-Provençal i al límit meridional del Promontori Balear, on es localitza la muntanya submarina Emile Baudot i el Camp Volcànic del SO de Mallorca (Acosta et al., 2004a i b).

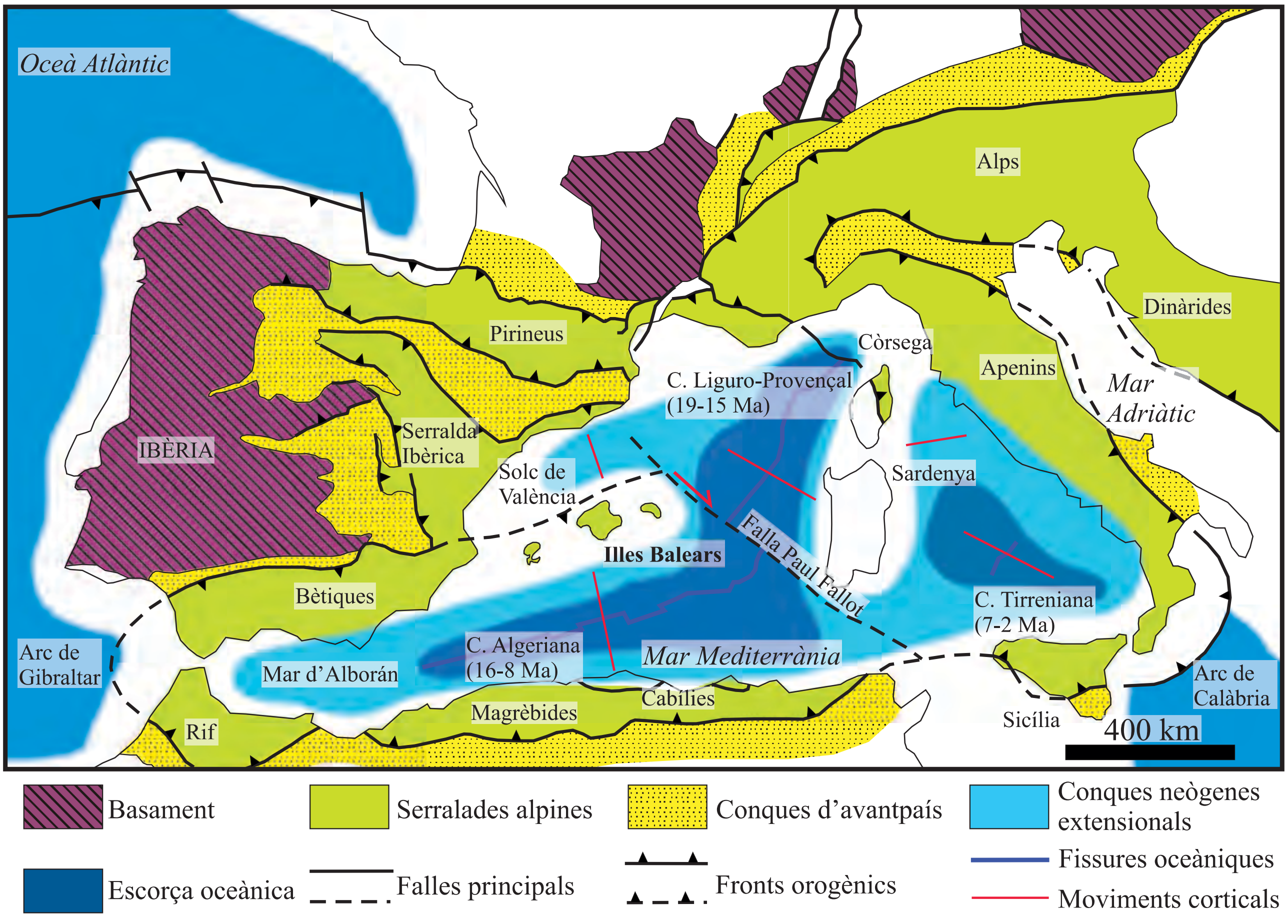


Figura 2: Mapa tectònic actual de la Mediterrània occidental amb els principals cinturons orogènics i conques d'avantpaís. Modificat a partir de Vergés i Sàbat (1999) i Carminati et al. (2012).

La problemàtica de l'illa de Menorca

La situació actual de Menorca a l'extrem oriental del Sistema Bètico-Balear, juntament amb el registre estratigràfic i l'estructura geològica que presenta respecte la resta de les Illes Balears, ha conduit a la postulació de diverses hipòtesis sobre la seva evolució neògena en relació al desenvolupament de les Bètiques (Fallot, 1945). Segons Roca (1992), aquestes hipòtesis es poden agrupar en: a) les que interpreten Menorca com una part del Sistema Bètico-Balear, i b) les que consideren que Menorca no pertany al Sistema Bètico-Balear, sinó que correspondria a un microbloc de la placa ibèrica amb una posició comparable a la que tenia Sardenya abans de la migració cap al SE.

Segons el primer grup d'hipòtesis, la inclusió de l'illa de Menorca dintre del Sistema Bètico-Balear, ve donada per la presència d'estructures contractives alpines correlacionables amb les de Mallorca i per suposades semblances estratigràfiques del Paleozoic i Mesozoic de Menorca amb el sud de la Península Ibèrica (la unitat bètica interna dels Malàguides) i les Serres de Llevant de Mallorca (Fallot, 1948; Bourrouilh, 1970; 2016). Aquestes suposades similituds entre l'estratigrafia de Menorca amb alguns sectors de l'orogen bètic es contradiuen amb el que conclouen diversos autors (e.g., Azéma et al., 1974; Fourcade et al.,1977). Segons aquests, les fàcies mesozoiques i paleozoiques de Menorca únicament són correlacionables amb les de Sardenya i amb les Cadenes Costaneres Catalanes. En canvi, Sàbat et al., (2018) consideren que únicament les fàcies mesozoiques de Menorca són correlacionables amb les de Sardenya, a excepció dels sediments triàsics.

El fet que els anys 70 no s'hagués descrit cap material paleozoic a la resta de les Balears portà a la defensa del segon grup d'hipòtesis. A més, a favor d'aquestes, Mauffret et al. (1972), Mauffret (1976) i Mauffret et al. (1978) detecten en les àrees submergides de Menorca la presència de falles NW-SE i un registre estratigràfic continu del rebliment neogen (Burdigalià-recent) de la conca Liguro-Provençal adossada a l'Est de l'illa de Menorca (Hsü et al., 1978). L'absència de deformacions contractives en els perfils sísmics del mateix sector descartaria la fase compressiva bètica sobre Menorca (Bizon et al., 1978).

En contraposició al segon grup d'hipòtesis, els estudis paleomagnètics realitzats a Balears (e.g., Freeman et al., 1989; Parés et al., 1992) mostren que, amb posterioritat al Burdigalià inferior, Menorca i Mallorca han estat rotades en sentit horari, mentre la microplaca de Còrsega i Sardenya va tenir una rotació antihoraria desenvolupada durant l'Aquitanià-Burdigalià inferior (Montigny et al., 1981; Burrus, 1984). A més, la descripció d'un petit aflorament del Carbonífer a la costa N de Mallorca (Rodríguez-Perea i Ramos-Guerrero, 1984) debilità l'argument de la presència de materials paleozoics restringida exclusivament a Menorca. Tot i així, Sàbat et al. (2018) consideren que les diferencies estratigràfiques de Menorca amb qualsevol altra de les Illes Balears són significativament importants. Segons Gelabert (1998) aquestes diferències estratigràfiques podrien ser degudes a una paleogeografia pre-miocena diferent respecte les altres illes, tot i que estarien englobades dins de l'orogen bètic. D'altra banda, Bourrouilh (1973) i Roca (1992) suggerien que la bona correlació estructural neògena existent entre Menorca i Mallorca, derivada de les dues fases deformatives, és incongruent amb les hipòtesis que recolzen la pertinença de l'illa de Menorca a la microplaca cirno-sarda. Recentment Sàbat et al. (2018) arriben a la conclusió de que la estructura contractiva de Menorca respecte a la resta de les Balears i Sardenya presenta una geometria i edat diferent, qualificant Menorca com una "illa exòtica" que forma part del Promontori Balear, com a resultat del seu major desplaçament durant l'obertura del solc de València.

2.2. Les faunes pre-messinianes de les Balears: els primers vertebrats insulars

L'Eocè-Oligocè de Mallorca

La primera menció d'un vertebrat fòssil de les Illes Balears correspon a la troballa d'unes restes d'un suposat lagomorf (*Lagomys?*) provinents d'unes bretxes situades a la base del puig del Castell de Bellver, Mallorca (de la Marmora, 1835). Actualment es desconeix la ubicació de les restes i la localització del jaciment, fet que no permet comprovar la seva validesa taxonòmica, ni l'edat, ni la seva relació amb les faunes insulars ben definides.

Els dipòsits lacustres del Paleogen de Mallorca, àmpliament explotats per a l'obtenció de lignits, han lliurat una gran quantitat de restes fòssils aïllades, tant de petits com grans vertebrats. Actualment es troben escampats a diferents col·leccions i no han estat estudiats en detall des de fa molts d'anys. Haime (1855) mencionà l'existència d'unes restes d'un queloni fòssil que Bouvy havia recollit de les mines de Selva-Binissalem (Mallorca) i Hermite (1879) cità restes de cocodril d'aquesta mateixa localitat. L'any 1857, Cristoforo Bellotti obtingué una mandíbula d'*Anthracotherium* d'alguna localitat lignítica mallorquina i la dipositá al Museo Civico di Storia Natural de Milano, però posteriorment es va perdre. Posteriorment, noves restes d'*Anthracotherium* procedents d'una mina de carbó de Sineu obtingudes per Olfield Thomas foren estudiades per Forsyth Major (1904). Ramos-Guerrero i Álvarez-Ramis (1990) identifiquen aquest jaciment com el del Puig des Bou. Vidal (1917) esmenta haver trobat *Anthracotherium* als lignits de Sineu. Deperet i Fallot (1920) manifesten haver trobat *Plagiolophus fraasi* a la Mina de can Mirall (Selva) i comenten que Gómez Llueca va venir a Mallorca i va trobar a la mateixa mina més dents de *Plagiolophus* i restes de *Trionyx*. També diuen que als lignits de Sineu surten *Anthracotherium* i *Amphitragulus* cf. *gracilis,* i que Gómez Llueca també ha trobat restes d'*Anthracotherium* a Sineu. Stehlin (1930) esmenta haver identificat un *Plagiolophus* al Museo Civico di Storia Natural de Milano, que semblava procedir de les col·lectes de Bellotti a Mallorca.

Cap d'aquests vertebrats presentava indicis d'haver evolucionat en condicions d'insularitat. Posteriorment a aquest autors, les troballes de restes de vertebrats fòssils dels depòsits de l'Eocè superior (Bartonià i Priabonià; Biniamar, Lloseta, Selva) i de l'Oligocè (Rupelià i Catià; Sineu, Peguera I, Peguera II, Binissalem) s'incrementaren considerablement, tant de mamífers grans (*Lophiotherium*, *Paloplotherium*, *Anoplotherium*, *Diplobune*, *Palaeochoerus* i *Amphitragulus*) com de petits, i de rèptils (Bauzà, 1946, 1958; Colom, 1975). El conjunt és heterocrònic (Eocè tardà - Oligocè; Hugueney i Adrover, 1982) i es troba relacionat amb les faunes europees (Colom, 1975). Segons de Bruijn et al. (1978), aquesta varietat de formes suggereix que Mallorca: a) formava part del continent, o b) estava tant pròxima al continent com per permetre una migració constant de mamífers terrestres. Aquests mateixos autors defineixen una nova espècie de rosegador (*Pseudoltinomys gliriformis*, Theridomyidae) provinent de Biniamar (Selva, Eocè tardà o Oligocè inferior). A partir d'aquesta espècie endèmica interpreten que Mallorca podria no haver estat connectada al continent o que simplement aquest tàxon estava associat a un biòtop especial.

El descobriment de dos conjunts faunístic de l'Oligocè inferior/mitjà (Rupelià superior) de Peguera (Peguera I i Peguera II; Adrover i Hugueney, 1975; Adrover et al., 1977; Hugueney, 1997; Martín-Closas i Ramos, 2005) va donar a conèixer una fauna que presentava una composició de tàxons tant d'origen europeu (Cricetidae, Gliridae, Theridomyidae, Pseudosciuridae, Insectívors s.l., Carnivora indet., Cainotheriidae, Didelphidae) com d'origen africà (Phiomyidae –posteriorment atribuïts a Thryonomidae, també d'origen africà- i, d'una manera temptativa -posteriorment mai confirmada- Ctenodactylidae). Els representants d'alguns d'aquest grups, com *Sacaresia moyaeponsi* [descrit com a Thryonomidae, be que s'ha suggerit que no pertany a aquesta família sinó que hauria de pertànyer a una família pròpia; López-Antoñanzas et al, 2004], *Moissetia paguerensis* [Gliridae], *Bransatoglis adroveri* [Gliridae] i *Tetracus daamsi* [Erinaceidae] (Hugueney i Adrover, 1991; 1995; 2003 respectivament), mostren clars indicis d'un cert grau d'aïllament. Inicialment Adrover i Hugueney (1975) varen suggerir la possibilitat d'una connexió bètico-rifenya per explicar l'arribada de la fauna africana, però aquesta hipòtesi va ser qüestionada per de Bruijn et al. (1978) en no trobar-se cap evidència de grups africans a cap altra regió europea, a excepció d'Oschiri, Sardenya (de Bruijn i Rümke, 1974) i de Sicília (Kotsakis 1984). A més, de Bruijn et al. (1978) consideren que durant una gran part del Cenozoic Mallorca ja era una illa. Mentre, Hugueney (1997) conclou que la presència de tàxons endèmics durant l'Oligocè fa pensar que la regió es trobava parcialment aïllada dels continents, tant de l'euroasiàtic com de l'africà.

El darrer conjunt faunístic premiocènic de Mallorca s'atribueix a l'Oligocè superior (Catià superior; Martin-Closas i Ramos, 2005). Aquesta fauna, d'origen euroasiàtic, correspon al conjunt de Sineu (Hugueney i Adrover, 1990). Es tracta d'una fauna formada predominantment per cricètids: *Pseudocricetodon incertus*, P. aff. *thaleri* i *Paracricetodon* aff. *cadurcensis*; un glírid amb una estructura dental complexa definit inicialment com a *Vasseuromys moyai* i transferit posteriorment al gènere *Oligodyromys* per Freudenthal i Martín-Suárez (2007); un eòmid, *Eomys* aff. *molassicus*; i un teridòmid. Únicament *Oligodyromys moyai* sembla estar relacionat amb un taxó present als jaciments de Peguera (*O. planus*). La resta són exclusius de cada un dels dipòsits, sense relació aparent. Hugueney i Adrover (1982) consideren que el conjunt de Sineu no és una fauna insular i que cadascuna de les successions observades des de l'Eocè superior fins a l'Oligocè superior sembla ser el resultat de diverses onades migratòries (de Bruijn et al., 1978). Freudenthal i Martín-Suárez (2007), en la mateixa línia, consideren que cap element dels diferents conjunts faunístics mostren adaptacions derivades de l'aïllament insular. En canvi, Matamales-Andreu et al. (2018), en base a les associacions faunístiques de rosegadors i gasteròpodes, suggereixen que Mallorca va quedar definitivament aïllada a partir de l'Oligocè superior.

El Miocè mitjà de Mallorca i Menorca

Les primeres faunes inequívocament insulars varen ser descobertes a un jaciment pròxim a la població de Sta. Margalida (Adrover et al., 1977). Es tracta d'un dipòsit d'origen lacustre, molt pobre en quant al nombre d'espècies i amb un elevat grau d'endemicitat. Aquesta fauna inclou un ocotònid (*Gymnesicolagus gelaberti*) i tres glírids (*Carbomys sacaresi*, *Margaritamys llulli* i *Peridyromys ordinasi*). Tots aquests micromamífers, a excepció de *Peridyromys*, mostren clars indicis de gegantisme, increment de la hipsodòncia i augment del gruix de les crestes (Mein i Adrover, 1982). Adrover et al. (1985) documenten l'existència d'una segona localitat fossilífera en les proximitats de la població de St. Llorenç, que conté una fauna idèntica a la de Sta. Margalida. Aquesta fauna inclou també un mamífer de mida gran que no ha pogut ser identificat (Köhler i Moyà-Solà, 2011).

Quintana i Agustí (2007) descriuen les restes fòssils d'un ocotònid, amb trets molt semblants a *Gymnesicolagus gelaberti*, procedents dels jaciments menorquins de Punta Nati 2 i es Cul de Sa Ferrada, alhora que descriuen una nova espècie de *Margaritamys*, *M. adroveri*, procedent del primer d'aquests jaciments. La presència de trets més arcaics en *M. adroveri* respecte *M. llulli* de Mallorca porta a pensar als autors que l'illa de Menorca presentava una associació endèmica, o alternativament, que les faunes de Menorca podrien estar estretament relacionades amb les faunes mallorquines, però en un context temporal més antic. D'altra banda, suggereixen que la troballa d'un fragment de mandíbula de *G.* aff. *gelaberti* en sediments marins d'es Cul de sa Ferrada (Tortonià inferior) representa la datació més recent de l'associació faunística de Sta. Margalida-St. Llorenç, sense fer cap menció a la possibilitat de que la peça hagi pogut estar reelaborada. En el jaciment de Punta Nati 2, del Miocè mitjà, Bailon et al. (2002) documenten l'existència d'un vipèrid indeterminat. Prèviament Quintana (1999) esmenta al mateix jaciment restes de tortuga i d'un o més rèptils de petita talla.

Una altra fauna fòssil insular de la mateixa època es troba actualment al sud de la Península Ibèrica, a la regió de Las Murchas (Granada). La fauna trobada indica que aquesta zona era una illa al Miocè mitjà (Martín-Suárez et al., 1993). Aquest conjunt es troba compost per descendents insulars de *Pseudodryomys* i *Peridyromys*, aparentment relacionats amb les faunes de *Gymnesicolagus* de Mallorca i Menorca (Martín-Suárez et al., 1993; Quintana i Agustí, 2007; Bover et al., 2008).

L'arribada d'aquest conjunt de faunes (St. Margalida, St. Llorenç, Punta Nati-2, es Cul de sa Ferrada i Las Murchas) s'associa a una connexió de les illes amb el continent durant la regressió del Langhià-Serraval·lià del Miocè mitjà (Riba, 1981), possiblement lligada a la darrera etapa de l'estructuració compressiva del Promontori Balear, que finalitzà en aquest moment (Álvaro et al., 1984). Segons Martín-Suárez et al. (1993), els tàxons que composen aquest conjunt de faunes insulars deriven d'uns ancestres comuns d'origen centreeuropeu. A partir del Serraval·lià s'inicià el període distensiu en el Promontori Balear relacionat amb la formació de la mar d'Alboran (Álvaro et al., 1984).

Possiblement a partir d'aquest moment les faunes quedaren totalment aïllades i s'inicià el procés d'evolució insular. Les causes i el moment de la desaparició d'aquestes faunes són desconegudes, encara que no es descarta que la transgressió que va tenir lloc durant el Tortonià (Bourrouilh, 1973; Roca, 1992) hi tingués algun efecte. Gràcia et al (2000) i Bover et al (2014) esmenten restes de tortugues terrestres als jaciments, presumiblement tortonians, de la cova de Cala Varques B i a la cova des Coll.

2.3. La Crisi de salinitat del Messinià

La Crisi Salina del Messinià (d'aquí endavant, MSC en la seva abreviatura anglesa) és un esdeveniment geològic clau per entendre l'evolució paleobiogeogràfica de la Mediterrània. Va tenir lloc al final del Miocè, entre 5,97-5,33 Ma (Krijgsman et al., 1999; Manzi et al., 2013). Aquest esdeveniment va consistir principalment en el progressiu aïllament i dessecació de la Mediterrània, fet que donà lloc al dipòsit d'un gran volum d'evaporites (guixos i sals) a les diverses subconques del Mediterrani (Hsü et al., 1973, 1977). La restricció de la comunicació entre l'Atlàntic i el Mediterrani està relacionada amb l'evolució tectònica de la regió de l'arc de Gibraltar – Corredor Bètic – Corredor del Rif, que va deixar ambdues masses d'aigua completament aïllades (Krijgsman et al., 1999; García-Castellanos i Villaseñor, 2011). Entre els 5,60-5,53 Ma es produí la davallada màxima del nivell del mar (CIESM, 2008) amb una caiguda pròxima als 1500 m respecte el nivell actual (Clauzon et al., 1996). El fons de les conques es convertiren en unes extenses salines i els marges dels continents es trobaren exposats als sistemes de drenatge dels grans rius, com el Roine o el Nil, on s'excavaren importants valls erosives i es produïren grans col·lapses als marges continentals (Clauzon, 1973; 1982; Cameselle i Urgeles, 2017). Durant aquest curt període de temps s'establiren comunicacions terrestres entre Euràsia i Àfrica, un fet que va promoure una dispersió faunística entre els dos continents (e.g., Agustí et al., 2006; van der Made et al., 2006) i la colonització de les illes mediterrànies, que en aquell moment teòricament estarien parcialment envoltades d'un desert salí que podria haver actuat com a una barrera biogeogràfica selectiva (Alcover, 1987). L'obertura de l'estret de Gibraltar a l'inici del Pliocè inferior (Zancleà), fa 5,33 Ma, propicià la reinundació de la Mediterrània i el posterior restabliment de les condicions marines normals. Des de llavors, el conjunt faunístic aïllat a les Illes Balears va evolucionar sota condicions d'insularitat (e.g., van der Made et al., 2006; Bover et al., 2008).

A finals de la MSC i abans de la reinundació marina definitiva de la Mediterrània, tingué lloc un episodi d'inundació denominat *Lago Mare* (Hsü et al., 1977, 1978). Durant aquest episodi s'establí un ambient dominat per aigües salobres o pràcticament dolces que quedà registrat a tota l'àrea Mediterrània (Pierre et al., 2006). Aquest episodi ha estat detectat tant a les conques perifèriques com a les conques profundes per sobre les evaporites fini-messinianes, just abans de la gran reinundació zancleana que establí les condicions marines normals. Segons Flecker (2008), l'establiment de les condicions salobres a la conca Mediterrània por ser explicada per dos fenòmens: a) aportacions sobtades d'aigües salobroses/dolces del Paratethys relacionats amb la dinàmica geoestructural; i b) increments de les aportacions hídriques dels sistemes de drenatge dels continents relacionats amb l'evolució climàtica de la regió.

Actualment la MSC ha estat interpretada en base a dos models contraposats: 1) el model inicial i més àmpliament acceptat, considerat el paradigma de la MSC, sosté que la conca mediterrània era profunda amb aigües de poca profunditat (*shallow-water deep-basin or deep dessicated basin*), fet que implica grans oscil·lacions en el nivell del mar (més de 1500 m) del Mediterrani fins a la seva dessecació per obtenir els dipòsits de sals existents (Hsü et al., 1973), i 2) el model alternatiu d'aigües profundes en un context sense dessecació que contempla una baixada moderada del nivell del mar (*deep-water non-dessicated scenario*; de Benedetti, 1976; Schmalz, 1991; entre altres). Segons Roveri et al. (2016), aquest model és possible i té les següents implicacions: a) hi hauria aigües permanents durant tota la durada de l'esdeveniment, amb importants restriccions amb l'Atlàntic, que generarien la precipitació d'evaporites; i b) existiria un vincle genètic entre el desenvolupament de salmorres profundes i l'erosió dels marges continentals (Roveri et al., 2014).

La principal crítica al primer model es centra en les implicacions que tenen les evaporites clàstiques àmpliament distribuïdes per fenòmens de fluxos gravitacionals en aigües profundes i que havien passat desapercebudes en estudis previs (Lugli et al., 2015). D'altra banda, el segon model no permet explicar els fenòmens de dispersió faunística entre Euràsia i Àfrica, així com a illes mediterrànies, durant l'esdeveniment fini-messinià.

2.4. Les faunes insulars post-messinianes: estat dels coneixements fins l'any 2014

La MSC és l'esdeveniment clau que marca l'inici del darrer episodi faunístic registrat a les Illes Balears. Tot i que el registre fòssil ha millorat considerablement en els darrers anys (sobretot a Mallorca), fins fa poc encara no s'havia pogut trobar cap evidència paleontològica que permetés establir una relació directa entre els tàxons insulars i els seus ancestres continentals en el moment de la colonització, ni establir l'origen geogràfic d'aquesta. Tampoc s'havia documentat l'arribada de cap vertebrat terrestre posterior a la MSC.

Aquest episodi s'inicià amb la culminació de la reinundació zancleana fa 5.33 Ma i s'estén fins a l'Holocè. A partir d'aquest moment, Mallorca, Menorca i les Pitiüses inicien un període d'aïllament que durant el Pliocè es caracteritza pel desenvolupament de tres conjunts paleofaunístics ben diferenciats (Bover et al., 2008). Des d'aquest període es registren una sèrie d'episodis d'extinció que acaben determinant la composició faunística final al Pleistocè mitjà-final, la qual es veu truncada amb l'arribada dels primers pobladors humans, que comporta un nou episodi d'extinció.

Fins a finals de la dècada dels 90, el registre paleontològic de vertebrats terrestres no voladors de Mallorca i Menorca estava compost per 3 llinatges de mamífers (e.g., Alcover et al., 1981): un bòvid (*Myotragus*), un glírid (*Hypnomys*) i un sorícid (*Nesiotites*), juntament amb un lacèrtid del gènere *Podarcis* (Pleistocè inicial-Holocè), i els amfibis alítids *Alytes* (Pleistocè inferior-Holocè) i *Discoglossus* (Pleistocè inferior). El registre fòssil dels 3 llinatges de mamífers és notablement complet al llarg del Pliocè-Holocè a Mallorca i Pleistocè-Holocè a Menorca (Alcover et al., 1981, Agustí i Moyà-Solà 1990; Moyà-Solà et al., 1999). D'altra banda, al Pliocè de Menorca es registrà una peculiar fauna composta per un glírid (*Muscardinus cyclopeus*), un lepòrid (inicialment identificat com a cf. *Alilepus* sp.) i un testudínid de mida gran (*Cheirogaster gymnesica*) (Bate 1914; Pons-Moyà et al., 1981; Agustí et al., 1982). Pel que respecta a Eivissa, s'observà una successió faunística particular. Per una banda la fauna pliocena es va considerar que estava composta per 2 bòvids (Caprinae i Antilopinae), un gerbíl·lid (*Protatera* sp.), un glírid (*Eliomys* sp.), un lepòrid (*Trichizolagus* o *Alilepus*), un insectívor, un lacèrtid i un testudínid (Moyà-Solà et al., 1984, 1999, Agustí i Moyà-Solà 1990). Durant el trànsit Pliocè-Pleistocè la fauna terrestre únicament estava composta per 2 glírids (*Eivissia canarreiensis* i *Hypnomys* sp.), un testudínid (*Cheirogaster* sp.) i un lacèrtid (*Podarcis* sp.) (Kotsakis 1981; Alcover i Agustí 1985; Bour 1985). Finalment, els dipòsits del Pleistocè superior-Holocè de les illes Pitiüses no mostraven cap registre de mamífers terrestres fòssils, sinó que únicament hi apareixien ocells, quiròpters i *Podarcis pityusensis* (Florit et al., 1989).

2.4.1. Les faunes de Mallorca

Mallorca és l'illa balear que presenta la continuïtat més completa i detallada en la composició de la seva fauna vertebrada terrestre des del Pliocè fins a l'Holocè. L'any 2004 es coneixien 140 jaciments de *Myotragus* a Mallorca (Bover i Alcover, 2005); en l'actualitat es pot estimar que el seu nombre se situa entorn als 160. Els mamífers terrestres presents en el moment de l'arribada dels humans són els descendents directes d'uns llinatges que varen arribar a la illa durant el Messinià (Bover et al., 2008). A començaments d'aquest mil·lenni es considerava que la fauna mencionada anteriorment estava composta exclusivament per tres mamífers (*Myotragus*, *Hypnomys* i *Nesiotites*), un lacèrtid (*Podarcis*) i dos amfibis (*Alytes* i *Discoglossus*). Tots ells semblaven haver estat els únics llinatges evolutius que havien colonitzat l'illa durant el Messinià. D'acord amb els coneixements que es tenien, se suposava que *Discoglossus* s'havia extingit durant un moment indeterminat del Pleistocè, mentre que els restants tàxons havien subsistit fins l'arribada dels humans. El descobriment dels dipòsits del Caló den Rafelino i de Na Burguesa-1, han posat de manifest que l'estoc faunístic que arribà a les Balears durant la MSC era molt més divers.

El jaciment del Caló den Rafelino

A partir de l'any 2007, com a resultat d'unes intenses prospeccions de bretxes fossilíferes antigues per part de Josep Quintana i Pere Bover, es descobrí un nou jaciment que produí un canvi radical en el coneixement de les faunes pliocenes de Mallorca (Bover et al., 2007). Aquest jaciment, pròxim al Caló den Rafelino (Manacor) i denominat sota el mateix nom, es troba constituït per una bretxa fossilífera molt pobre. Els sediments reblien una antiga cavitat que es desenvolupà sobre la plataforma del Complex d'Esculls del Miocè superior (Pomar et al., 1990; Fornós, 1998). Abans del descobriment del dipòsit del Caló den Rafelino (a partir d'ara CdR), la fauna més antiga que es coneixia procedia dels jaciments de cala Morlanda i de sa Penya Roja (Moyà-Solà i Pons-Moyà, 1982). La fauna d'aquest darrers jaciments estava composta per *Myotragus pepgonellae* i restes molt fragmentàries d'*Hypnomys* i *Nesiotites*.

El jaciment del CdR ha permès documentar la presència de cinc mamífers diferents (Fig. 3). Aquests inclouen els representants més antics dels llinatges clàssics (*Myotragus*, *Hypnomys* i *Nesiotites*) i dos tàxons nous que no havien estat detectats a cap altre jaciment. D'aquesta localitat s'ha descrit *Myotragus palomboi*, l'espècie antecessora de *M. pepgonellae* del dipòsit de cala Morlanda (Bover et al., 2010), *Nesiotites rafelinensis* (el tàxon més controvertit dels descrits: veure Rofes et al., 2012; Furió i Pons-Monjo 2013; Rofes et al., 2013) i les restes atribuïdes a un *Hypnomys* sense identitat específica degut a l'escassetat de les restes fòssils (Bover et al., 2014). D'altra banda, els dos llinatges descoberts per primer cop a Mallorca corresponen a un cricètid i un lepòrid. El primer, *Tragomys macpheei*, és una espècie de gran mida caracteritzada per presentar una dentició amb un patró remarcablement selenodont i un elevat grau d'hipsodòncia. Aquest cricètid es va relacionar temptativament amb el gènere continental *Apocricetus* (Agustí et al., 2012). El segon va ser descrit per Quintana et al. (2010) com a *Hypolagus balearicus*. S'inclou a un gènere força abundant i àmpliament distribuït en el continent durant el Miocè superior i el Pliocè.

Aquest jaciment destaca a més per l'aportació d'un nou conjunt d'escamosos composat per una varietat inesperada de tàxons. S'hi han trobat unes poques restes d'un testudínid de gran mida (Bover et al., 2014). S'han descrit les restes d'un gran lacèrtid, *Maioricalacerta rafelinensis*, caracteritzat per unes mandíbules curtes i molt robustes amb una dentició ambliodonta (Bailon et al., 2014). El primer registre a Mallorca d'un ànguid atribuït a *Dopasia/Ophisaurus*, així com les primeres restes fòssils d'ofidis pliocens, amb restes corresponents a un tipus de Colubrinae (Bover et al., 2014), una sèrie de vèrtebres d'un gran escurçó atribuït a *Vipera* sp. pertanyent al Complex d'Escurçons Orientals (sigles en anglès: OVC) (Bailon et al., 2010) i vèrtebres d'un petit escurçó semblant a *Vipera natiensis* de Menorca (Bover et al., 2014: annex 2).

L'edat del dipòsit, com la de la majoria en el conjunt de les illes, s'ha estimat indirectament en funció dels caràcters primitius d'alguns dels tàxons de la fauna que presenta i del context geològic en el que es va formar el dipòsit. Es pot establir que el jaciment es posterior a la calcària escullosa que data del Tortonià superior-Messinià, segons Bizon et al. (1973). A més, en base als trets més arcaics de *M. palomboi* que els de *M. pepgonellae* i les característiques derivades de *T. macpheei* respecte el seu suposat ancestre continental, es pot atribuir el depòsit al Pliocè inferior, anterior al jaciment de cala Morlanda (suposadament del final del Zancleà o de començaments del Piasencià) i posterior al Messinià.

El jaciment de Na Burguesa-1

L'any 2012 membres del grup espeleològic Speleo Club Mallorca varen descobrir el jaciment de Na Burguesa-1 (d'aquí endavant, NB-1). Les primeres restes recuperades ja van mostrar una clara relació amb els tàxons descoberts al Caló d'en Rafelino (Bover et al., 2014). El major nombre d'espècies fòssils així com el seu menor grau d'evolució insular, han permès situar NB-1 en un moment molt proper, en termes geològics, a l'episodi de colonització de les illes. Una extensa bibliografia atribueix un origen Messinià a aquests tàxons insulars (e.g. van der Made et al., 2006; Bover et al., 2008), però en cap cas s'havien trobat evidències directes a l'illa de Mallorca. Per tant, es tracta d'un jaciment clau per comprendre l'origen dels vertebrats post-messinians de Balears. Una part de la fauna d'aquest depòsit va ser estudiada per l'autor d'aquesta Tesi abans d'estar inscrit al Programa de Doctorat de la UB. Aquests treballs publicats prèviament s'han inclòs als annexes. La present Tesi incideix en l'estudi i interpretació del significat de diferents tàxons de la fauna vertebrada d'aquest depòsit, que (com s'ha dit prèviament) fins a la data és coneguda encara d'una forma incompleta, ja que encara ara hi ha molts de tàxons pendents d'estudi.

Les successions faunístiques del Plio-Quaternari de Mallorca

Una part important del conjunt faunístic del dipòsit del CdR és absent als jaciments posteriors coneguts. La desaparició de *T. macpheei*, *H. balearicus* i de tots els escamosos registrats al jaciment, posen de manifest l'existència d'un important episodi d'extinció durant el Pliocè que es desconeixia prèviament. Les causes concretes d'aquestes desaparicions romanen desconegudes.

A partir del moment de la deposició dels materials al jaciment de cala Morlanda fins a l'Holocè (amb l'excepció de la fauna herpetològica) el registre fòssil és força continu, documentant una evolució anagenètica dels tres llinatges de mamífers (*Myotragus*, *Hypnomys* i *Nesiotites*), amb un desenvolupament progressiu de la seva eficiència biològica en unes condicions d'insularitat de llarga durada. Tot sembla indicar que la seva desaparició es troba completament lligada a l'arribada dels primers pobladors humans a l'arxipèlag Balear, fa c.4300 anys (Bover i Alcover, 2003, 2008; Bover et al., 2016; Fig. 3).

· *Myotragus*

El tàxon més estudiat i millor conegut d'aquesta fauna és *Myotragus*. El seu llinatge va evolucionar d'una manera molt peculiar, i es considera una espècie clau per entendre la paleoecologia de Mallorca (Alcover et al., 1999). Fins ara, s'han descrit sis cronoespècies del seu llinatge: *Myotragus palomboi* del CdR (Pliocè inferior; Bover et al., 2010), *M. pepgonellae* de cala Morlanda (final del Pliocè inferior; Moyà-Sola i Pons-Moyà, 1982), *M. antiquus* del Cap Farrutx (Pliocè superior; Pons-Moyà, 1977), *M. kopperi* de sa Pedrera de s'Ònix (Pleistocè inferior, 1,8 Ma; Moyà-Solà i Pons-Moyà, 1981; Pons-Moyà et al., 1979), *M. batei* de sa Pedrera de Gènova (Pleistocè Mitjà; Crusafont i Angel, 1966) i *M. balearicus* de la cova de Ca na Barxa (espècie tipus, Pleistocè Superior-Holocè; Bate, 1909). Els principals canvis morfològics registrats durant la seva evolució han estat associats a la millora de l'eficiència energètica en unes condicions d'insularitat. Aquest canvis han afectat a l'aparell masticatori (e.g., reducció progressiva del nombre de dents incisiviformes i premolars, l'augment del grau d'hipsodòncia, l'adquisició d'un parell d'incisius de creixement continu, l'increment de les crestes d'inserció muscular relacionades amb la masticació, l'escurçament del rostre del crani que donà com a resultat la frontalització dels ulls), al sistema locomotor (e.g., escurçament dels metapodis, la fusió progressiva dels ossos tarsals, canvi en l'estructura de la pelvis), a la seva mida corporal (amb una clara tendència al nanisme), a la mida cervell i òrgans dels sentits (reducció del cervell, reducció del sistema visual i olfactiu) i a aspectes sobre el cicle vital (*life history*: longevitat, creixement, edat de maduresa sexual, metabolisme).

L'adquisició d'un aparell masticatori més potent li va permetre ampliar el ventall de recursos disponibles, i s'ha pogut documentar que podia consumir plantes amb grans continguts d'alcaloides, com el boix, *Buxus balearica* (Alcover et al., 1999). Per altra banda, els canvis en l'aparell locomotor comportaren l'adquisició d'una locomoció de marxes curtes (*slow gear locomotion*; Sondaar, 1977), reduint la seva capacitat tant per córrer com per saltar i fer moviments de ziga-zaga en absència de depredadors terrestres (e.g. Leinders i Sondaar, 1974; Moyà-Solà, 1978). L'estudi d'aquest tàxon ha permès avançar significativament sobre el coneixement de la paleobiologia de mamífers insulars. La limitació de recursos i l'absència de depredadors són els factors que més repercuteixen sobre l'evolució de les espècies en els ecosistemes insulars. En conseqüència, la despesa energètica pot ser reduïda adoptant modes de locomoció més eficients i una fisiologia que permeti maximitzar els recursos disponibles. En aquest sentit, Köhler i Moyà-Solà (2004) realitzaren un estudi sobre el cervell i òrgans dels sentits de *Myotragus balearicus* on demostraren que la mida del cervell està reduïda respecte al que s'esperaria d'un bòvid del seu pes, així com una disminució de la sensibilitat dels òrgans dels sentits, especialment la reducció del còrtex visual. Anteriorment, Dechaseaux (1961) realitzà una descripció detallada de l'endocrani de *Myotragus* i Crusafont i Angel (1966) ja insinuen que l'aplanament dels frontals podria estar relacionat amb una reducció de l'encèfal. A més, Dechaseaux (1961) esmenta uns bulbs olfactius petits i Bover i Tolosa (2005) observen que la làmina cribosa de la cavitat nasal de *M. balearicus* es troba poc desenvolupada, afectant el sentit de l'olfacte. Tota aquesta pèrdua de la sensibilitat dels òrgans dels sentits així com la reducció del cervell s'interpreta com una adaptació a la reducció de la despesa energètica sota condicions d'insularitat. En la mateixa línia, Köhler i Moyà-Solà (2009) avaluen la història vital de *M. balearicus* a partir de dades histològiques i conclouen que presentava un creixement extremadament lent i un metabolisme baix, amb l'adquisició tardana de la maduresa sexual. Jordana et al. (2011) documenten, en base a la microestructura de l'esmalt dentari i la histologia, que *Myotragus* tenia un evident retràs de la senescència i un augment de la esperança de vida. Aquest augment del cicle vital es relaciona posteriorment amb l'elevat desenvolupament de la hipsodòncia (Köhler, 2010; Jordana et al., 2012; 2014).

Les relacions filogenètiques de *Myotragus* amb el seu presumpte avantpassat continental encara no són ben conegudes. Les darreres evidències apunten que *Aragoral* (Vallesià superior, MN10; Alcalá i Morales, 1997) o *Norbertia* (límit Turolià-Ruscinià, MN13/14; Köhler et al., 1995) podrien ser els avantpassats directes de *Myotragus*, però les relacions filogenètiques de *M. palomboi* amb el seu presumpte avantpassat continental no són concloents (Bover et al., 2010). També s'ha tractat d'estudiar les relacions filogenètiques de *Myotragus* a partir de l'obtenció d'ADN antic. El primers treballs (Lalueza-Fox et al., 2000, 2005a, 2005b) el relacionaren amb *Ovis*, però les darreres anàlisis apunten a que aquest resultat sigui el producte de seqüències quimèriques (P. Bover, com. pers.), i els estudis més recents apunten cap a *Budorcas* com el parent vivent més proper de *Myotragus* (Bover et al., 2019).

· *Hypnomys*

A Mallorca fins a la data s'han descrit tres cronoespècies del llinatge d'*Hypnomys*: (1) *H. waldreni*, contemporani amb *M. antiquus* (Reumer, 1979); (2) *H. onicensis*, descrit de sa Pedrera de s'Ònix (Reumer, 1994), la localitat tipus de *M. kopperi*; i (3) *H. morpheus* que va conviure amb *M. balearicus* (Bate, 1918). Tot i que s'han trobat restes fòssils més antigues a dipòsits com el de cala Morlanda o CdR, l'escassetat del material obtingut no ha permès establir els trets diferencials que els distingeixin de la resta d'espècies.

El patró evolutiu principal observat en el llinatge d'*Hypnomys* consisteix en l'adquisició progressiva d'una gran mida, l'augment de la hipsodòncia, el retràs en la erupció del premolar definitiu, l'adquisició d'una superfície oclusiva plana dels molars com a resposta a una alimentació basada en vegetació xeròfila i una elongació del zigopodi i eixamplament de la part distal de l'húmer i el fèmur en comparació amb *Eliomys quercinus* (Alcover i Roca, 1975; Bover et al., 2010). Segons Mills (1976), *H. morpheus* probablement tenia un comportament menys arborícola que *Eliomys*. Bover et al. (2010) a partir de l'estudi d'esquelets complets i en articulació d'*H. morpheus*, avaluaren el comportament locomotor d'aquest tàxon insular indicant que era més terrestre i que presentava unes majors habilitats excavadores que *E. quercinus*. Contràriament, Quintana i Moncunill-Solé (2014) a partir de l'estudi de diverses espècies d'*Hypnomys*, consideren que presenten grans similituds amb espècies arbòries, grimpadores i planejadores. A més, no accepten que hagi hagut una elongació del zigopodi i indiquen que les habilitats grimpadores i excavadores estaven més desenvolupades en *Hypnomys* que no pas en *E. quercinus*.

Els recents estudis histològics dels ossos llargs d'*H. onicensis* revelen que *Hypnomys* presentava una excepcional longevitat i una historia vital alentida en relació a la seva mida corporal (Orlandi-Oliveras et al., 2016). Segons aquests autors algun dels trets observats de la histologia suggereixen que *H. onicensis* presentava un augment del període de creixement, així com una taxa de creixement diferent d'*E. quercinus*.

S'ha suposat que *Hypnomys* descendia d'una forma continental d'*Eliomys*, segons la morfologia general de la seva dentició (Bate, 1918; Agustí, 1980; Zammit-Maempel i de Bruijn, 1982; Alcover i Agustí, 1985; Agustí 1986). Tot i així, la relació de parentiu no està definitivament constatada. Reumer (1982) va observar una tendència a la simplificació del patró dental en el llinatge d'*Hypnomys*, sent més complex en les espècies més antigues. Aquesta observació entra en contradicció amb la proposta inicial, ja que s'hauria d'observar una tendència a l'augment de la complexitat del patró si es considerés a *Eliomys* com la forma ancestral d'*Hypnomys*.

· *Nesiotites*

El llinatge es troba composat actualment per tres cronoespècies a Mallorca: *Nesiotites rafelinensis*, coexistent amb *M. palomboi* (Rofes et al., 2012), *N. ponsi*, procedent de dipòsits que contenen *M. antiquus* (Reumer, 1979) i *N. hidalgo*, coetani amb *M. balearicus* i *H. morpheus* (espècie tipus; Bate, 1944). A més, s'ha trobat una forma intermèdia en el dipòsit de sa Pedrera de s'Ònix, que quedà descrita amb una terminologia taxonòmica oberta com a *Nesiotites* aff. *ponsi* (Alcover et al., 1981) o *N.* ex. interc. *ponsi-hidalgo* (Reumer, 1981). En altres dipòsits, com podria ser el de cala Morlanda, s'han obtingut restes de *Nesiotites* sense atribució específica per la falta de material adequat (Pons-Moyà, 1990). El principal patró evolutiu observat al llarg de llinatge de *Nesiotites* és l'augment de la mida corporal.

Generalment estava força acceptat que l'avantpassat més probable de *Nesiotites* era el gènere *Episoriculus* (Reumer, 1980). Hutterer (1994) va transferir els *Episoriculus* fòssils europeus al gènere *Asoriculus*, i Reumer (1998) va considerar a *Episoriculus* com a subgènere de *Soriculus*, diferenciant-lo d'*Asoriculus*. El consens va arribar amb els primers anàlisis morfològics que relacionaven a *Nesiotites* amb *Asoriculus* (Alcover et al., 1981; Pons-Monjo et al., 2010, 2012; Rofes i Cuenca-Bescós, 2006, 2009), tot i que la seva posició filogenètica no quedava ben resolta (Rofes et al., 2012). A partir d'un genoma mitocondrial pràcticament complet de *N. hidalgo*, Bover et al. (2018) realitzen el primer anàlisi filogenètic molecular d'aquest tàxon i conclouen que el seu parent actual més proper és *Soriculus nigrescens* de l'Himàlaia i combinant les dades moleculars i les morfològiques confirmen la seva estreta relació amb *Asoriculus gibberodon*. A més, el rellotge molecular i les estimacions de divergència entre *N. hidalgo* i el seu parent actual són congruents amb la colonització messiniana.

· *Podarcis*

Les restes de sargantanes s'han anat trobat recurrentment des del Pleistocè inferior fins a l'Holocè en l'illa principal. Actualment sobreviuen, com a testimonis del passat, només als illots que envolten Mallorca i Menorca. Les restes més antigues, del Pleistocè inferior (Kotsakis, 1981), s'atribueixen a *Podarcis* sp. i les restes trobades a partir del Pleistocè mitjà fins a l'actualitat són atribuïdes a *Podarcis lilfordi* (Bailon, 2004).

· *Alytes i Discoglossus*

El registre fòssil de Mallorca documenta l'existència de dos anurs als jaciments pleistocènics. *Alytes muletensis*, el ferreret, ha estat identificat en dipòsits que van des del Pleistocè inferior fins a l'Holocè (Sanchiz i Adrover, 1979). Mayol i Alcover (1981) documentaren la supervivència d'algunes poblacions a torrents de difícil accés de la Serra de Tramuntana. Actualment el ferreret es considera el darrer vestigi dels vertebrats terrestres originals de la illa que viu a Mallorca, i es troba sota la màxima protecció amb plans de recuperació impulsats pel Govern de les Illes Balears. El segon anur descrit és un alítid de gran mida, *Discoglossus* sp., obtingut a la Pedrera de s'Ònix (Pleistocè inferior). No s'ha trobat cap altra resta d'aquest anur en jaciments d'edat posterior (Alcover et al., 1981).

2.4.2. Les faunes de Menorca

A l'illa de Menorca es documenten dues faunes post-messinianes successives amb clars efectes d'una evolució sota condicions d'insularitat (baixa diversitat d'espècies, disharmonia i casos de gegantisme). La primera fauna se situa dins del Pliocè i la segona es documenta a partir del Pleistocè (Quintana, 1999; Alcover et al., 1999).

La primera fauna es troba registrada a diferents petits jaciments localitzats, predominantment, a la zona de Punta Nati-cala's Pous (Quintana, 1999). Els components faunístics terrestres que poden presentar són: un testudínid gegant *Cheirogaster gymnesica*, un glírid gegant *Muscardinus cyclopeus* i un lepòrid, que inicialment fou atribuït a cf. *Alilepus* sp., i posteriorment fou descrit com *Nuralagus rex* (Bate, 1914; Agustí et al., 1982; Quintana et al., 2011; Fig. 3). A més, als mateixos jaciments es detectaren restes fòssils de serps: un escurçó endèmic descrit com *Vipera natiensis* i restes atribuïdes a *Coluber* (Bailon et al., 2002, 2005). També cal destacar la documentació de les primeres restes de les Balears atribuïdes a *Gekkota* (Bailon et al., 2005), *Blanus* sp. (García-Porta et al., 2002), i a un alítid de gran mida atribuït a *Latonia* sp. (Quintana et al., 2005). Dintre dels jaciments d'aquest episodi faunístic s'ha esmentat també *Podarcis* aff. *lilfordi* (Bailon, 2004).

Tot aquest conjunt faunístic es denominat *fauna de Nuralagus*. Aquest lepòrid es considerat el vertebrat fòssil més singular de Menorca. Les estimes del pes corporal suggereixen una mitjana de 12 kg, presentava un cap relativament petit en relació al cos, extremitats proporcionalment més curtes que la dels conills actuals, una condició plantígrada i una columna vertebral fortament arquejada (Quintana, 2005; Quintana et al., 2011). A més, presentava una sèrie de característiques observades a algunes espècies insulars, com podria ser *Myotragus*, relacionades amb la reducció de l'encèfal i d'alguns òrgans dels sentits (Quintana et al., 2011).

Al final del Pliocè-inicis del Pleistocè tingué lloc l'inici del segon episodi faunístic registrat a Menorca. Fins a l'actualitat, no s'ha trobat cap indici de la *fauna de Nuralagus* en dipòsits del Pleistocè, excepte *Podarcis*, la qual cosa suggereix que la gran majoria de components d'aquesta fauna desapareix de la illa abans d'aquesta data. Als dipòsits menorquins de Pleistocè-Holocè únicament es registra la fauna de *Myotragus*. Es pensa que l'arribada a Menorca d'aquesta fauna pot estar relacionada amb l'inici dels períodes glacials, els quals generaven caigudes del nivell del mar que permetien la unió recurrent entre Mallorca i Menorca. La ciclicitat d'aquests esdeveniments complicà la diferenciació entre les poblacions mallorquines i les menorquines (Cuerda, 1975; Bover, 2004; Bover et al., 2008).

Dins d'aquest darrer episodi faunístic també es documenta l'existència de *Podarci*s, l'únic tàxon heretat de la fauna de *Nuralagus* (Bailon, 2004). El seu llinatge evolutiu es pot rastrejar a Menorca fins a l'època dels romans (Reumer i Sanders, 1984). Actualment, com passa a Mallorca, l'espècie només sobreviu als petits illots perifèrics de l'illa principal.

Es coneix *Alytes talaioticus* a partir de materials obtinguts a dipòsits holocènics (Sanchiz i Alcover, 1982). Actualment està atribuït a *Alytes muletensis* de Mallorca (Sanchiz, 1998). Finalment, es coneix una espècie encara no descrita de *Discoglossus* procedent d'uns pocs jaciments del Pleistocè inferior (Barranc de Binigaus, sa Segonya i Punta Esquitxador; Alcover et al., 1981; Quintana, 1999).

2.4.3. Les faunes de les Pitiüses

El coneixement dels vertebrats fòssils del Neogen de les Pitiüses és un dels que menys aportacions noves ha rebut des dels estudis inicials. Això es degut, per una banda, a la escassetat de jaciments paleontològics trobats, i per altra, a una manifesta pobresa de restes fòssils, així com al estat de conservació deficient que presenten. Les darreres novetats s'han donat a partir del reanàlisi de les restes fòssils ja conegudes.

La fauna insular més antiga d'Eivissa prové del jaciment de ses Fontanelles (Sant Antoni de Portmany; Moyà-Solà et al., 1984; Fig. 3). En aquest jaciment es registra la diversitat màxima de vertebrats fòssils terrestres de l'illa. La fauna que conté inclou un bòvid (Moyà-Solà, comunicació personal), dos rosegadors, *Protatera* sp. (que posteriorment passà al gènere *Debruijnimys*; Castillo i Agustí, 1996) i *Eliomys* sp., un insectívor indeterminat, un lepòrid inicialment atribuït a *Trichizolagus-Alilepus* i posteriorment assignat a *Hypolagus balearicus* (Quintana i Moncunill-Solé, 2014), un lacèrtid i un testudínid de gran mida (Moyà-Solà et al., 1984, 1999). La presència dels dos rosegadors suggerí que aquest dipòsit es podria atribuir al Messinià (Agustí i Moyà-Solà, 1990), ja que aquests tàxons també s'han registrat en dipòsits del Miocè tardà i del Pliocè inicial de la Península Ibèrica.

El registre de vertebrats fòssils d'un moment indeterminat atribuït al Pliocè superior-Pleistocè inferior es troba representat a Eivissa a la cova de Ca na Reia (Santa Eulària des Riu) i, tal volta, a la Pedrera de Can Bessora (Sant Antoni de Pormany). El primer dipòsit conté les restes de dos glírids, els darrers mamífers endèmics d'Eivissa (*Eivissia canarreiensis* i *Hypnomys* sp., Alcover i Agustí 1985), un testudínid de mida mitjana atribuït a *Cheirogaster* (Bour, 1985) i un lacèrtid que coincideix amb *Podarcis* (Kotsakis, 1981). També s'hi han detectat restes de quiròpters, així com, d'ocells, sent la localitat tipus de *Puffinus nestori*, el presumpte avantpassat de *Puffinus mauretanicus/yelkouan* (Alcover, 1989).

A Eivissa i Formentera es coneixen vuit jaciments del Pleistocè tardà. Aquests dipòsits han lliurat desenes de milers de restes de vertebrats. La fauna coneguda fins ara consistia exclusivament en aus, quiròpters i un lacèrtid (*Podarcis pityusensis*). El jaciment més destacable de tots és es Pouàs (Sant Antoni de Portmany), que constitueix un dels millors registres de la fauna paleornitològica del Pleistocè i Holocè de la Mediterrània occidental (Guerra, 2015). En els nivells inferiors únicament s'enregistra l'existència d'una testudínid de mida mitjana, per aquesta raó es pensa que aquests nivells poden estar relacionats amb el conjunt faunístic de la Cova de Ca na Reia. En els nivells superiors s'ha documentat una fauna ornitològica molt peculiar, ecològicament paral·lela a la fauna paleornitològica de Hawaii (Seguí i Alcover, 1999). Una de les espècies d'aquesta fauna és *Rallus eivissensis*, l'únic rascló endèmic descrit fins ara d'una illa mediterrània (McMinn et al., 2005).

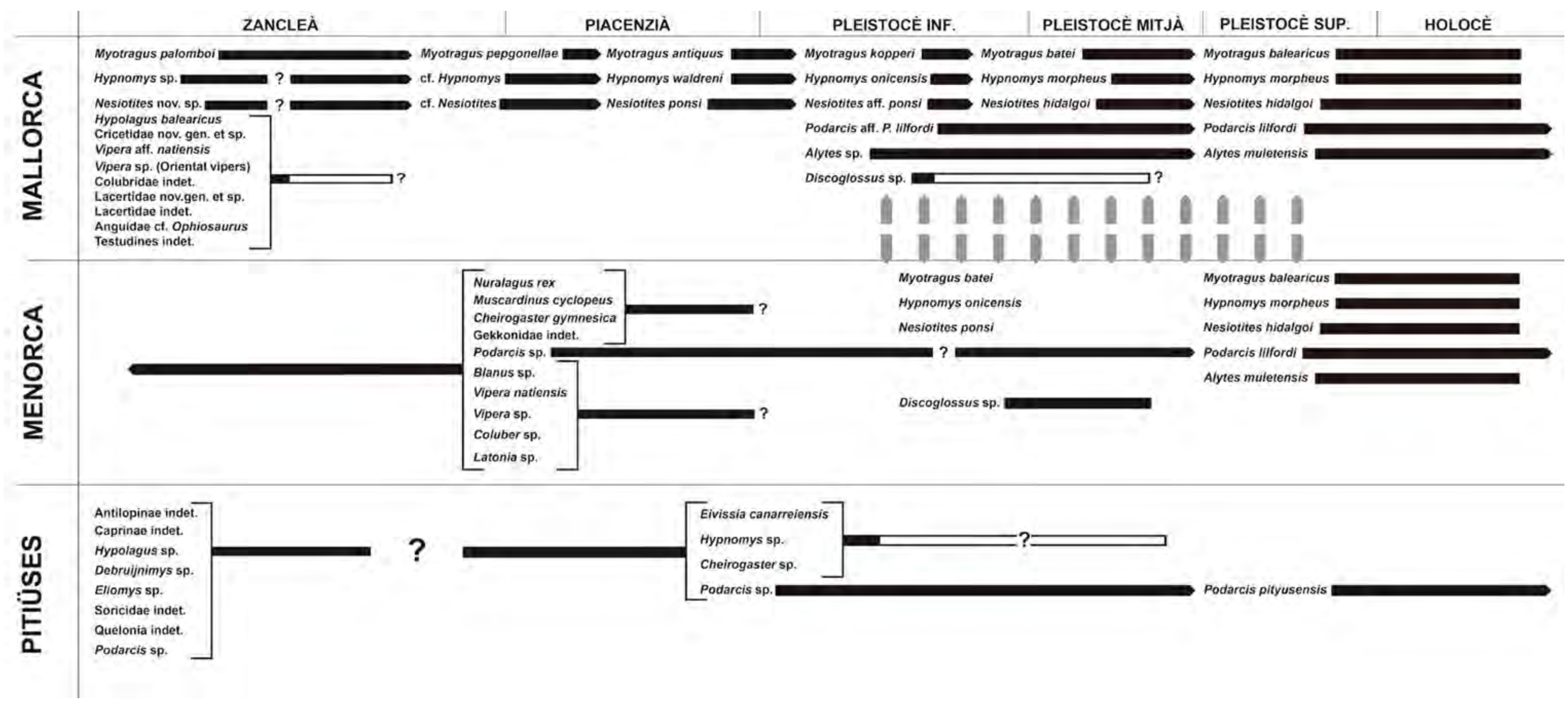


Figura 3: Síntesi de les successions de vertebrats terrestres del Pliocè-Holocè de les Illes Balears d'acord amb els coneixements disponibles abans de 2014. Les fletxes grises remarquen el contacte entre Mallorca i Menorca durant les glaciacions. Extret de Bover (2011).

CAPÍTOL 3. Context geològic i geogràfic dels principals jaciments fossilífers de procedència dels materials estudiats.

3.1. Na Burguesa-1 (Mallorca).

El jaciment va ser descobert de manera fortuïta l'abril de 2012 pels espeleòlegs Damià Vicens, Damià Crespí i Antelm Ginard, del Speleo Club Mallorca. El dipòsit es troba a la part sud-occidental de la Serra de Tramuntana, a la Serra de na Burguesa (municipi de Calvià), a uns 160 m s.n.m., prop de la carretera que va cap al monument situat al cim del Puig des Caragol, a les proximitats de Palma (Fig. 4). El dipòsit va ser denominat amb el mateix nom de la serra seguit del número 1 per diferenciar-lo d'altres possibles futures descobertes. La ubicació original precisa del jaciment es desconeix, ja que les troballes es realitzaren sobre una sèrie de blocs extrets i que s'utilitzaren per facilitar l'accés a una petita construcció de la empresa municipal d'aigua de Palma (EMAYA), però hi ha pocs dubtes de que aquests blocs que contenen els materials fòssils procedeixin de l'emplaçament on es realitzà la construcció de la companyia municipal.

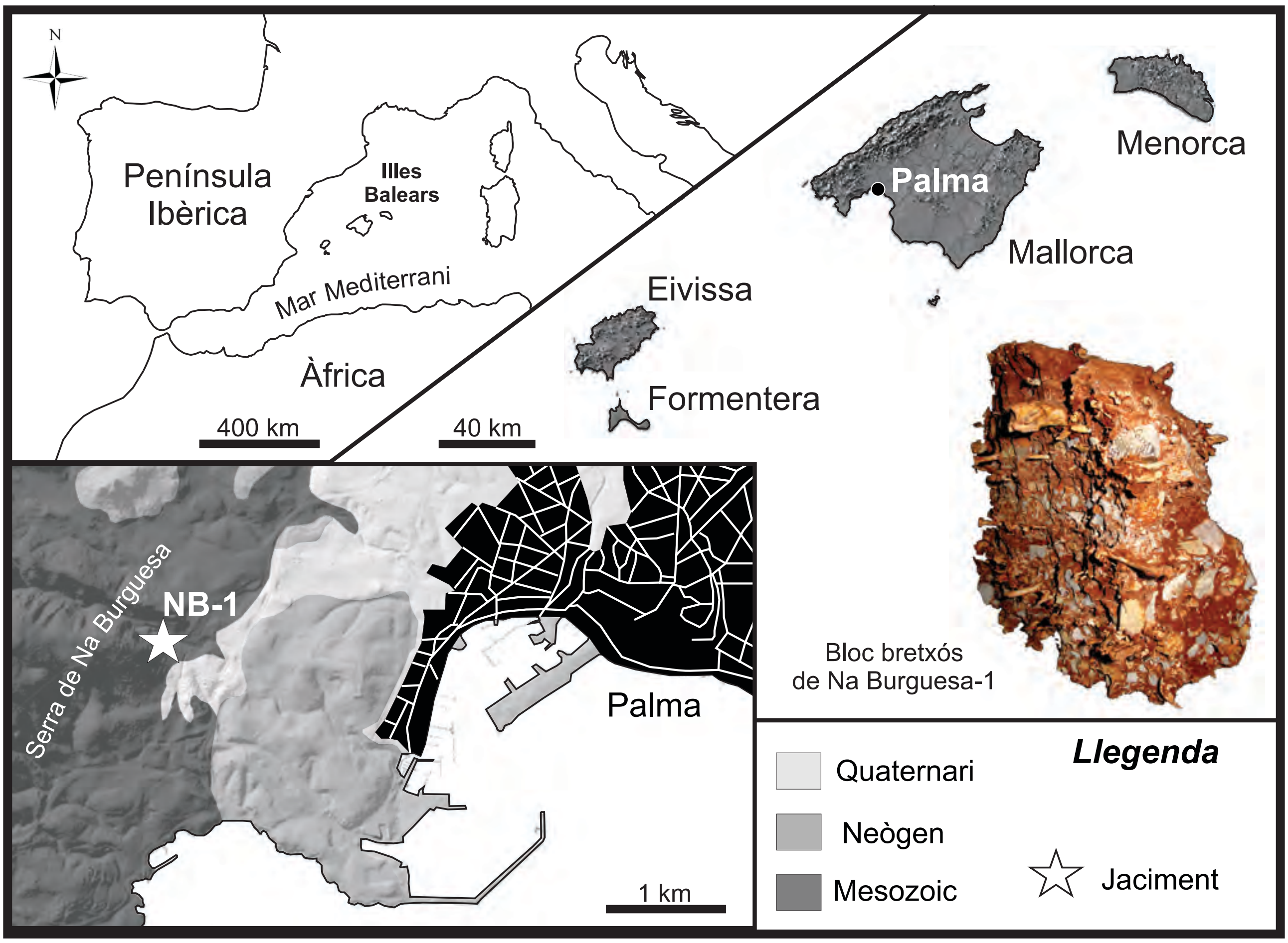


Figura 4: Localització del jaciment de NB-1, Mallorca (Illes Balears). Els blocs es troben constituïts per una bretxa composta de clastes predominantment calcaris i en menor proporció per clastes d' espeleotemes i d'unes altres bretxes més antigues resedimentades, aparentment estèrils. Ocasionalment, alguns blocs presenten restes d'espeleotemes (colades càrstiques) que formarien part del sostre o de la base del bloc bretxós. Tots aquests es troben inclosos en una matriu de llims vermells fortament cimentats per calcita. Als blocs es poden distingir capes de concentració de petits vertebrats i, en menor mesura, closques de gasteròpodes pulmonats (Fig. 5). El dipòsit correspon al rebliment d'una antiga cavitat (cova o fissura) excavada sobre les calcàries i dolomies grises del Lias que conformen els relleus més importants de la zona.

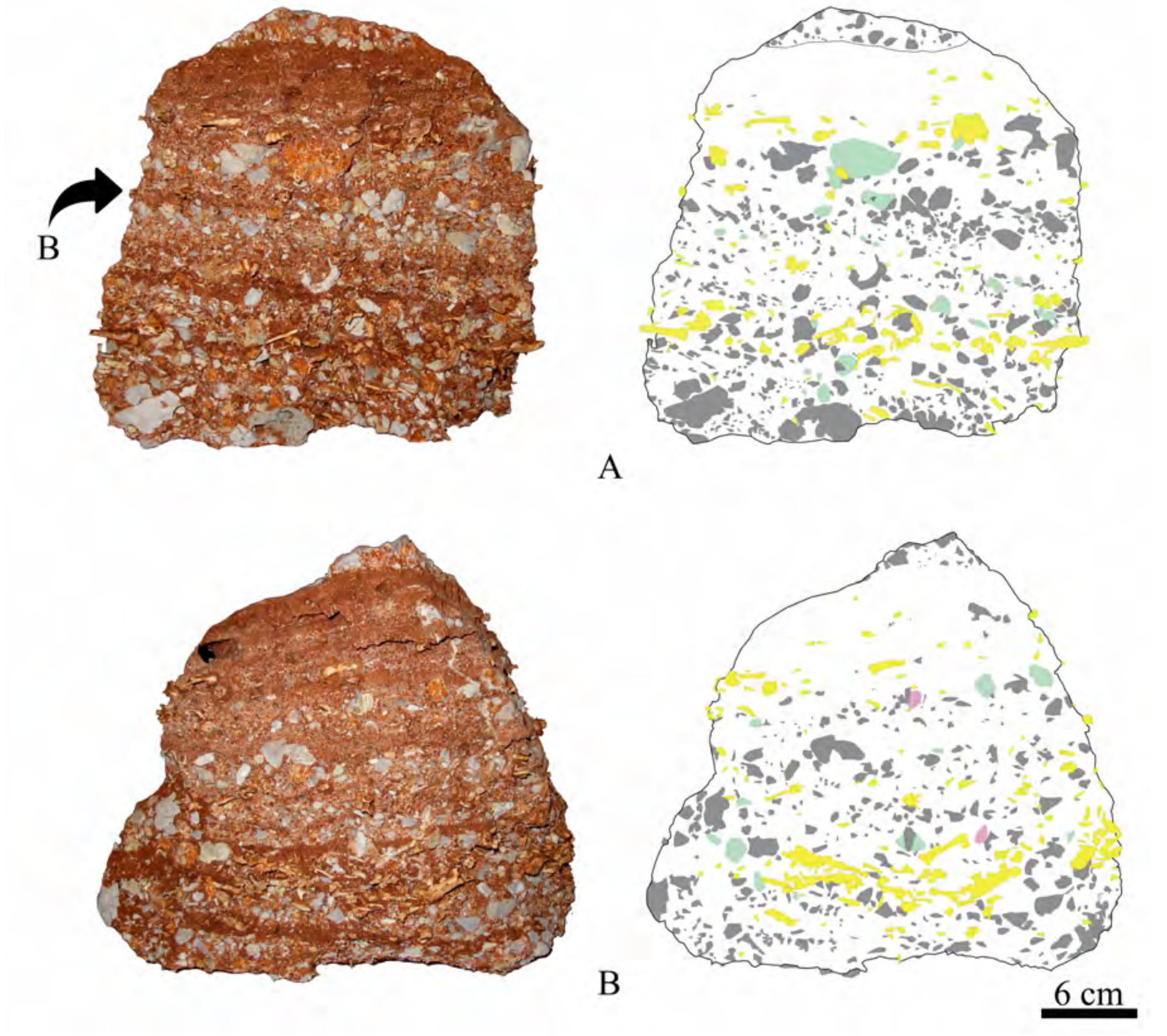


Figura 5: Bloc en els estadis inicials del seu tractament on s'identifiquen directament els diferents elements que l'integren, així com la seva distribució espacial. Parell A corresponents al costat 1; parell B corresponents al costat 2 del mateix bloc. En groc es remarquen els diferents elements ossis, en gris els clastes de calcàries, en verd els clastes de bretxa resedimentada i en rosat els clastes espeleotèmics. Imatge realitzada el dia 15-05-2014.

Després d'informar a la Comissió Insular de Patrimoni del Consell de Mallorca, la brigada del Consell de Mallorca va recuperar diversos blocs i els va traslladar a les dependències de l'IMEDEA al Campus de la UIB amb la finalitat de processar-los i extreure'n la major quantitat possible de material fòssil per ser posteriorment estudiat. Les primeres obtencions de vertebrats fòssils ja mostraven un estat de conservació superior als obtinguts al CdR, així com una elevada riquesa tant de tàxons com d'elements ossis.

El predomini d'un registre de petits mamífers amb una clara selecció de mides, juntament amb la recuperació de les restes d'una olibassa de gran mida (*Tyto* sp.) i falanges pedals atribuïbles a un altre estrigiforme de petita talla, permet concloure que es tracta d'un dipòsit originat predominantment per bioacumulació que, de manera ocasional, ha incorporat algunes restes de vertebrats de mida major (e.g., restes de bòvid, testudínid gran, etc.). Com s'ha mencionat anteriorment, la major part de les restes mostren un estat de conservació molt bo, sense indicis de retreballament ni de transport per fluxos d'aigua energètics que produïssin el trencament d'ossos o una selecció espacial de les restes, ja fos per diferències de densitat com hidrodinàmiques. Únicament s'ha pogut observar que alguns elements han patit fractures, amb lleus desplaçaments com a resultat de la compactació del sediment (Fig. 6A), i una certa orientació paral·lela entre diferents elements llargs. D'altra banda, una petita part de les restes mostren marques d'arrels (Fig. 6B) o senyals d'osteofàgia per rosegadors presents en el registre del jaciment (Fig. 6C) i ocasionalment presenten mineralitzacions de morfologia dendrítica d'òxids de manganès o impregnacions totals de l'element ossi per aquest mineral (Fig. 6D). En conclusió, l'antiga cavitat d'on procedeixen les restes era una zona tancada que afavoria l'acumulació tant del sediment com de les restes òssies produïdes com a resultat de la depredació per estrigiformes. Aquesta relació entre el tipus d'agent bio-acumulador i restes produïdes és congruent amb el bon grau de preservació que presenten aquestes, ja que en els casos de dipòsits bio-acumulats per mamífers o accipitriformes les restes mostrarien importants patrons de trencament (Andrews, 1990). Posteriorment aquestes restes quedaven exposades temporalment en el fons de la cavitat on eren afectades ocasionalment per l'activitat dels petits rosegadors que arribaven a l'interior de la cavitat. Durant moments d'intenses pluges les restes eren sepultades per una barreja de llims i clastes calcaris de l'àrea circumdant. Les restes que es trobaven més pròximes al nivell superficial es podien veure afectades per desenvolupament de comunitats vegetals que hi creixien a l'interior.

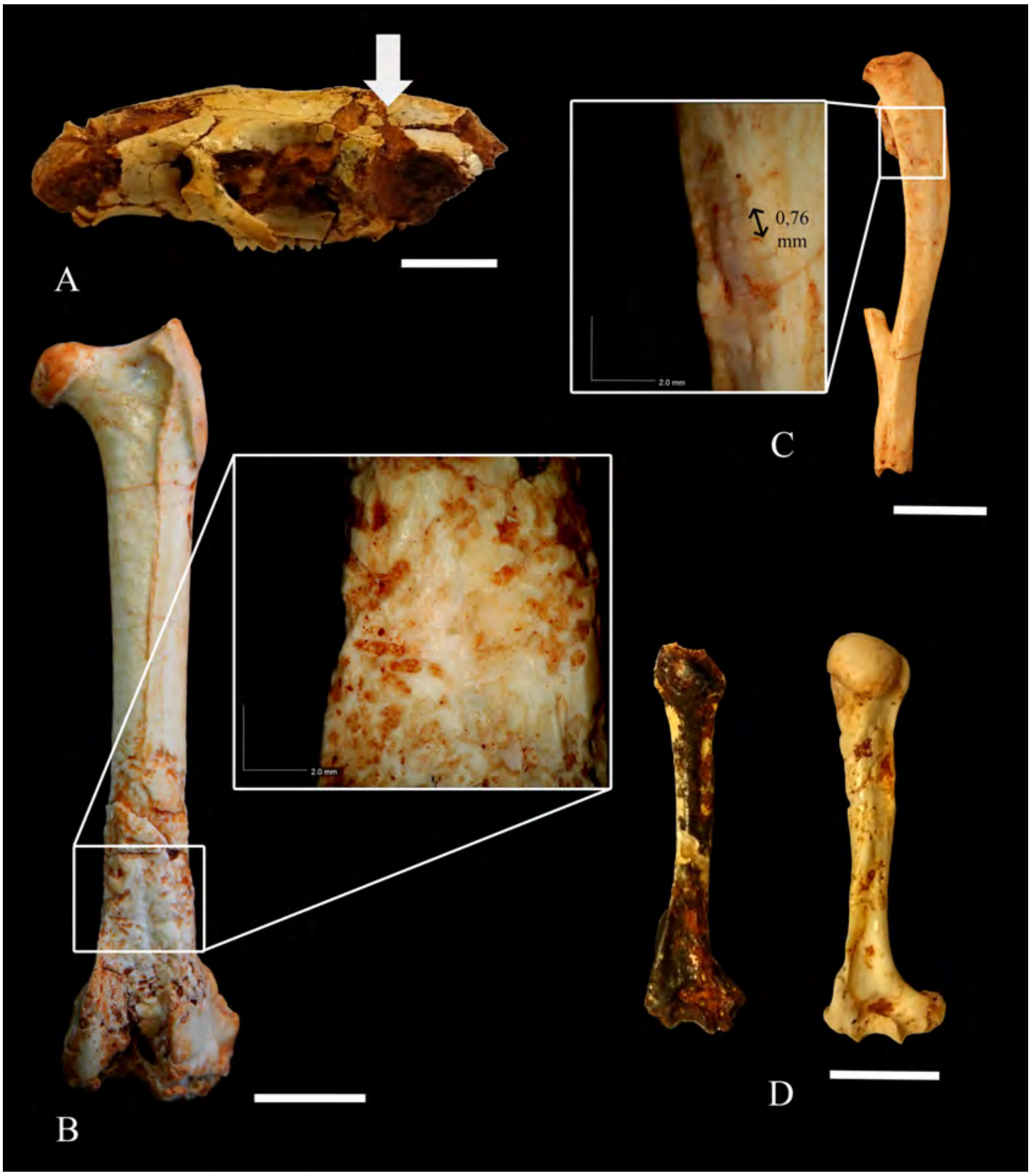


Figura 6. Elements ossis de NB-1 afectats per diferents processos tafonòmics. A, crani del cricètid (IMEDEA 104796) en norma dorso-lateral on es poden apreciar diverses fractures (fletxa blanca) en la caixa craniana com a resultat de la compactació diferencial. B, fèmur esquerra del titònid gegant (IMEDEA 106330) en norma cranial on s'hi pot observar el desenvolupament de marques d'arrels en la seva meitat inferior. C, tíbia esquerra del cricètid (IMEDEA 104144) amb marques d'osteofàgia en el marge medial. La marca més ben definida presenta una amplada que és coincident amb amplada de la incisiva superior del múrid recuperat al mateix jaciment. D, húmers esquerres del cricètid en norma caudal amb mineralitzacions d'òxids de manganès (IMEDEA 94752) i sense mineralitzacions (IMEDEA 104647). Escales: 1 cm.

L'edat del dipòsit, així com la dels dipòsits precedents, s'ha estimat indirectament a partir dels caràcters d'alguns dels tàxons recuperats respecte als d'altres jaciments coneguts. Les primeres restes obtingudes atribuïdes a un cricètid gegant, mostraven clars caràcters arcaics respecte *Tragomys mapcheei* del CdR, situant el jaciment de NB-1 entre el Messinià i el Pliocè més basal (Bover et al., 2014). Els patrons de gegantisme que exhibeix el cricètid, suggereix una cronologia pliocènica molt primerenca com l'edat més probable.

3.2. Es Pouàs i cova de Ca na Reia (Eivissa)

El jaciment d'es Pouàs es localitza a uns 265 m. s.n.m., a la perifèria oriental del pòlie de Corona, pròxim a la població de Santa Agnès de Corona, pertanyent al municipi de Sant Antoni de Portmany, nord-oest de l'illa d'Eivissa (Fig. 7). Es tracta d'un avenc obert sobre calcàries urgonianes, amb una boca de 7 m de diàmetre i 19 m de fondària, que comunica amb una sala de planta allargada de direcció E-W que fa 32 x 15 m (Trias, 1983). La cavitat es troba reomplerta per una barreja homogènia de materials clàstics grollers i fins (Thomas i Montoriol 1953; Trias 1983; Fig. 8).

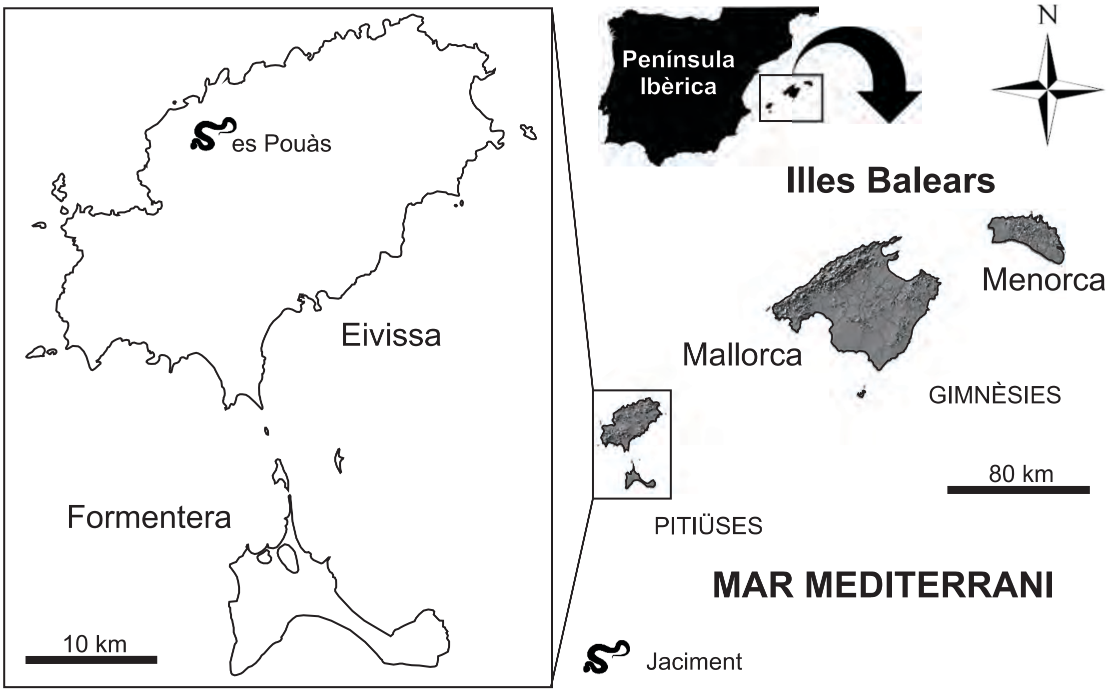


Figura 7: Localització del jaciment de l'avenc des Pouàs, Eivissa (Illes Balears). A l'interior de l'avenc hi havia un dipòsit arqueològic pre-púnic del que en l'actualitat tan sols es conserven algunes restes a les parets de la sala. La resta d'aquest dipòsit va ser destruït pels propietaris del terreny, que van buidar uns 2 m de sediments per dur a terme la construcció d'una discoteca dins de la cavitat (Trias, 1982; Florit et al., 1989).

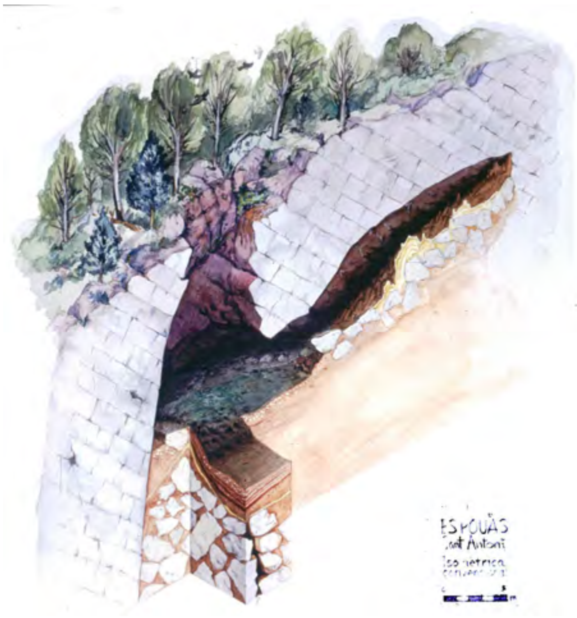


Figura 8: Secció des Pouàs on es detalla la estructura del rebliment de la cavitat. Il·lustració realitzada per Miquel Trias.

Per sota dels nivells arqueològics va aparèixer un conjunt faunístic extremadament peculiar, previ a l'arribada dels humans a Eivissa, estimada en fa 4150-4350 anys (Alcover 2008). Aquest conjunt destaca per l'absència de mamífers terrestres. Aquest fet convertia les Pitiüses, durant el Pleistocè superior i Holocè, en el major territori no desèrtic de la regió mediterrània mancat de mamífers terrestres (Florit et al., 1989). Aquesta anomalia faunística va condicionar el desenvolupament d'unes comunitats ornítiques de similituds ecològiques amb l'ornitofauna pre-humana de les illes Hawaii (Seguí i Alcover 1999).

Rere les diverses campanyes d'excavacions realitzades entre 1988-1994, el jaciment paleontològic ha proporcionat més de 120.000 elements ossis, predominantment restes atribuïbles a ocells, sargantanes i gasteròpodes i, en menor proporció, ratapinyades i miriàpodes (Alcover, 2003; Guerra, 2015). Així mateix, en els nivells tal volta corresponents al Pleistocè mitjà, s'han obtingut les restes d'un testudínid de gran mida (*Cheirogaster* sp.?). Probablement una forma descendent de la descrita per Bour (1985), trobada a la cova de Ca na Reia.

El dipòsit de la cova de Ca na Reia va ser descobert pel naturalista Nèstor Torres abans de l'any 1981. Aquesta cavitat es troba situada al vessant meridional del puig des Guixer a 120 m s.n.m., dintre del municipi de Santa Eulària des Riu, sud-est de l'illa d'Eivissa (Fig. 9). Es tracta de la cova més evolucionada de tot un sistema de cavitats relacionades amb la formació d'un dolina d'esfondrament d'aproximadament 25 m de diàmetre (Trias, 1982). La cavitat està desenvolupada sobre calcàries del Triàsic i està formada per una sala de 13 x 7 x 6 m, amb una petita cambra annexa (Fig. 10). Al fons d'aquesta, constituint el rebliment d'una diàclasi, es localitza el dipòsit fossilífer constituït per una bretxa poc cimentada formada per llims sorrencs que inclouen blocs de calcària (Gasull i Alcover, 1982).

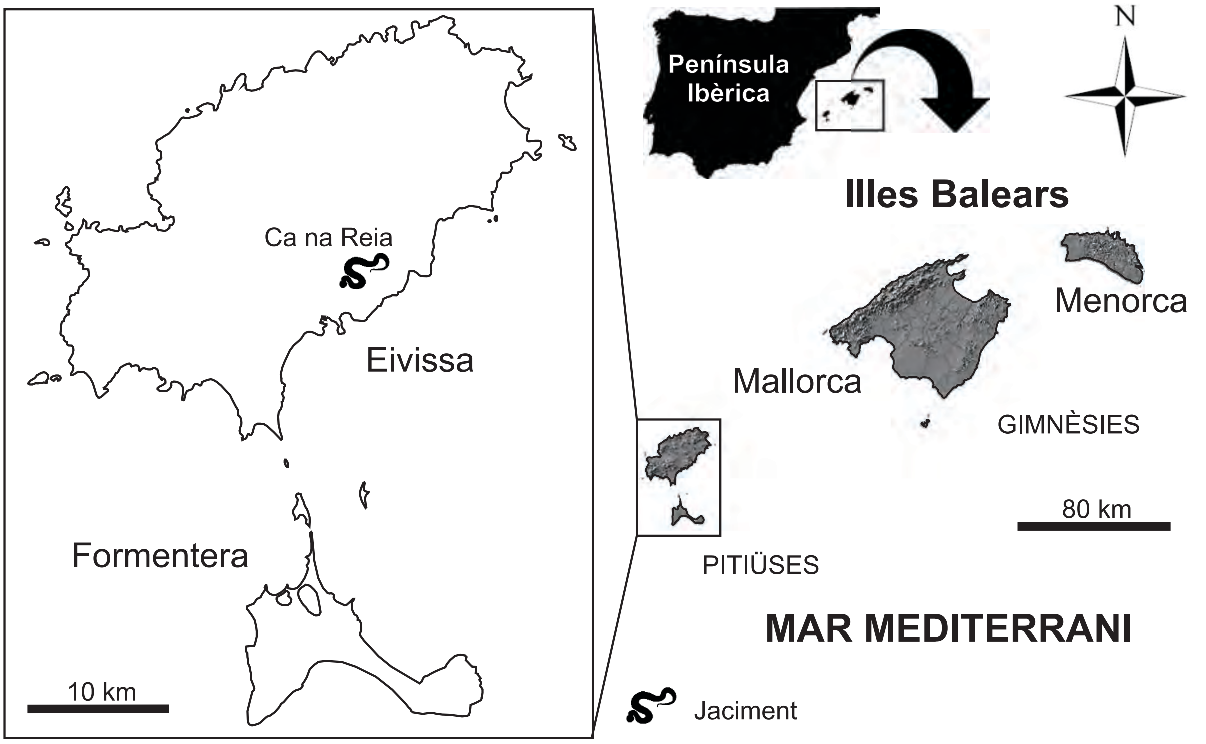


Figura 9: Localització del jaciment de Ca na Reia, Eivissa (Illes Balears). Aquest cova va ser un dels primers dipòsits que van proporcionar vertebrats prehumans de l'illa d'Eivissa. Tot i que no destaca per la quantitat de material fòssil que ha lliurat, documenta la presència d'un testudínid de talla mitjana atribuït a *Cheirogaster* sp. (Bour, 1985), restes de sargantanes (Kotsakis, 1981), quiròpters i diferents espècies d'ocells (Moyà-Solà et al., 1984). D'aquest jaciment es descriu *Puffinus nestori* (Alcover, 1989) i els glírids *Eivissia canarreiensis* i *Hypnomys* sp. (Alcover i Agustí, 1985).

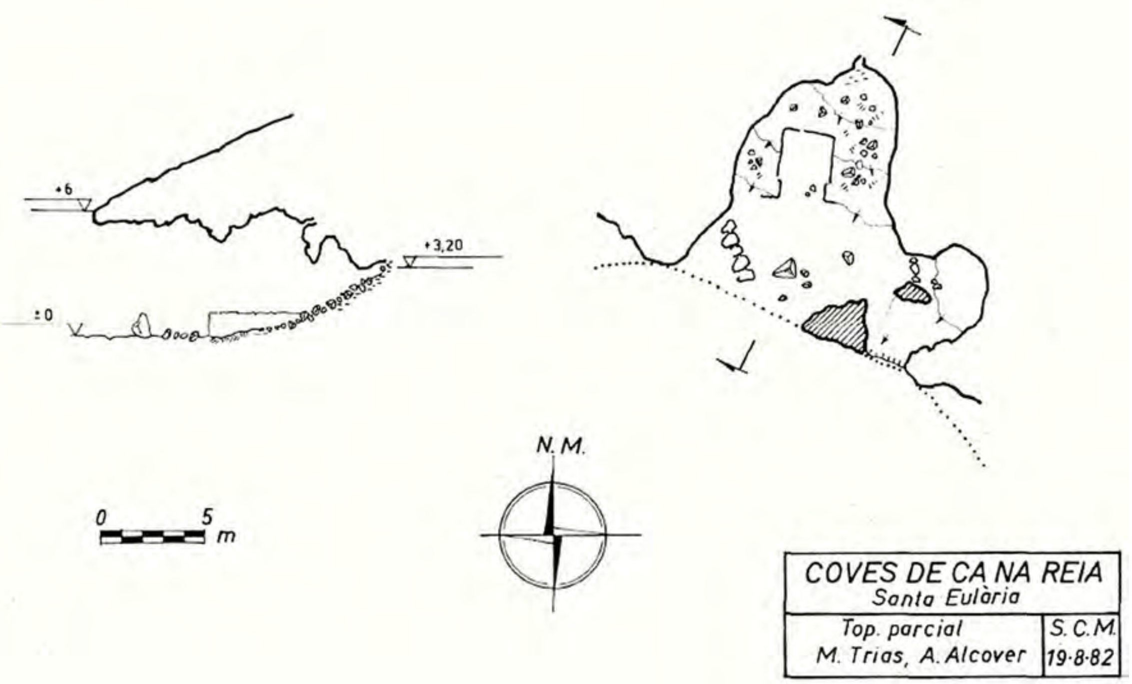


Figura 10: Planta (dreta) i tall (esquerra) del dipòsit de la cova de Ca na Reia. Extret de Trias (1982).

La presència d'un bon registre malacològic, amb una fauna comparable a la descoberta per Paul (1982) a cala Salada (Eivissa), va permetre situar el dipòsit al Pleistocè inicial (Torres i Alcover, 1981; Gasull i Alcover, 1982; Paul, 1984).

CAPÍTOL 4. Materials i mètodes.

4.1. Extracció, preparació, siglat, registre, conservació i dipòsit de les mostres

El jaciment de NB-1 correspon a un dipòsit format per unes bretxes fossilíferes molt riques, amb una matriu de llims vermells cimentats per carbonat de calci. Per poder iniciar l'estudi de les restes fòssils ha estat necessari realitzar un tractament químic per extreure-les, un procés que es va perllongar durant dos anys i mig.

D'altra banda, les restes fòssils recuperades des Pouàs i de la cova de Ca na Reia es trobaven parcialment triades sense identificació i únicament ha calgut revisar materials que es troben conservats a la col·lecció de l'IMEDEA. En el cas des Pouàs les restes fòssils provenen de les excavacions realitzades entre els anys 1989 i 1994 i fins a l'actualitat s'han identificat prop de 6000 restes òssies pertanyents a un petit vipèrid. En canvi, en la revisió del material conservat de la cova de Ca na Reia únicament s'ha recuperat una vèrtebra caudal, presumiblement pertanyent a una forma més antiga d'aquest escurçó.

Extracció del material fòssil de NB-1

Després de recollir una sèrie de blocs del jaciment i portar-los al laboratori, es seleccionaren aquells que mostraven una major riquesa de restes òssies. Abans d'iniciar l'atac amb àcid es va reduir la mida dels blocs majors mitjançant la injecció de ciment expansiu a l'interior de perforacions realitzades prèviament amb un trepant. Les mides finals dels blocs han de ser adequades per a la seva manipulació i trobar-se ajustades a la capacitat dels recipients. Es molt important assolir un equilibri entre la mida del bloc, concentració de restes òssies i la mida d'aquests. En funció d'aquest paràmetres les restes es recuperaran més o menys completes i hauran patit un major o menor nombre d'atacs químics. Per tant, prèviament a l'atac amb àcid és summament important conèixer, mitjançant una inspecció visual superficial del bloc, el contingut potencial de les restes fòssils (mides, distribució, orientació, etc.) per poder planificar acuradament l'extracció i garantir al màxim la recuperació de les restes.

La metodologia utilitzada consisteix bàsicament en processar diverses mostres a la vegada seguint un cicle composat per quatre passos:

1. <u>Consolidació dels fòssils exposats</u>. Abans d'iniciar l'atac amb àcid es protegeixen totes aquelles restes que estiguin exposades mitjançant una resina acrílica termoplàstica (Paraloid B-72) àmpliament utilitzada com a consolidant, adhesiu o vernís tant en la preparació d'espècimens fòssils, com en la conservació d'obres d'art. Es tracta d'una de les fases més importants del cicle ja que l'objectiu d'aquest es minimitzar el seu efecte sobre els fòssils. Sense aquest recobriment els ossos perdrien una gran quantitat del carbonat de calci que contenen tant en la seva estructura, com el que ha precipitat durant el procés de fossilització. La dissolució d'aquest carbonat de calci reduiria considerablement les probabilitats de recuperació de les restes òssies, arribant fins tot a la seva destrucció total.

   El paraloid-B72 se sol diluir amb acetona, toluè, xilè, etc., en una concentració del 10%, encara que està en funció de la penetrabilitat que es desitgi. Es pot donar una primera impregnació amb pinzell o xeringa al 10% per garantir una bona penetrabilitat cap a l'interior de la resta òssia i una segona al 15% per protegir les parts més exposades. Abans d'iniciar el tractament amb àcid es deixen eixugar les restes consolidades durant dues d'hores o més si la mostra s'ha impregnat significativament.

2. <u>Atac amb àcid</u>. L'àcid acètic (CH_3-COOH) o l'àcid fòrmic (HCOOH) són àcids orgànics dèbils àmpliament utilitzats en l'extracció de restes fòssils de composició fosfàtica incloses en roques calcàries. En aquest cas s'han realitzat immersions amb àcid acètic dissolt al 10-15% durant 48h, una concentració més elevada o una exposició prolongada de la mostra podria fer-la mal bé o destruir-la

per complet. A grans trets les reaccions que es produeixen són les següents:

a. Dissolució de l'àcid acètic amb aigua, que produeix anions d'acetat i protons.

$$CH_3\text{-}COOH + H_2O \rightarrow CH_3\text{-}COO^- + H_3O^+$$

b. A l'afegir la mostra a la solució el carbonat de calci reacciona amb els anions d'acetat donant com a resultat acetat de calci i diòxid de carboni en forma de gas.

$$CH_3\text{-}COO^- + H_3O^+ + CaCO_3 \rightarrow (CH_3\text{-}COO)_2Ca + H_2O + CO_2$$

Durant l'atac químic és molt important que les roques estiguin completament submergides per evitar la cristal·lització de l'acetat de calci sobre la mostra. Un cop finalitzada la immersió amb àcid es podrà apreciar una lleugera reducció de la roca, deixant exposades parts de les restes òssies que anteriorment no es veien, així com noves restes que no afloraven. A més, durant aquest procediment l'argila es desprèn de la roca per la descalcificació, acumulant-se al fons del recipient. Es molt important rentar i tamisar aquest sediment per recuperar possibles restes fòssils despreses durant el procés. La seva detecció es pot realitzar amb l'ajuda d'un binocular quan és necessari.

3. Neutralització. Un cop l'àcid ja actuat sobre la mostra és imprescindible acabar de neutralitzar-lo, així com eliminar les sals dissoltes (acetat de calci) generades durant el procés. La cristal·lització d'aquestes sals a l'interior dels fòssils poden causar fractures per expansió o el col·lapse total d'aquest. Per neutralitzar l'àcid i eliminar l'acetat de calci es varen submergir els blocs i les restes òssies despreses en una solució aquosa durant uns dies, canviant periòdicament l'aigua fins a la desaparició de l'àcid i les sals. Si durant l'assecat, els fòssils mostraven signes de cristal·litzacions blanquinoses o una lleugera pàtina blanca es tornaven a submergir en aigua fins que s'eliminaven les sals per complet.

4. Assecat. Aquesta és la darrera fase del cicle. Les mostres es deixaven assecar de manera natural evitant una radiació directe del Sol, ja que podria ocasionar fractures a les restes òssies per elevats contrastos tèrmics. Un cop els blocs es troben secs, abans d'iniciar el procés de consolidació s'ha d'eliminar els sobrants de paraloid de l'anterior sessió que quedin sobre les argiles cimentades mitjançat un pinzell lleugerament banyat amb acetona i un bisturí fi per garantir la penetrabilitat de la nova sessió de consolidació i avançar el procés de preparació final de les restes fòssils.

Preparació

Un cop es disposa de les restes fòssils aïllades de la matriu es procedeix a la seva preparació definitiva garantint la seva conservació i unes condicions adequades per al seu posterior estudi.

El primer pas en la preparació dels espècimens recuperats és l'eliminació dels excedents de consolidant barrejats amb argiles formades durant la fase de consolidació del procés d'extracció. Aquesta neteja es realitza afegint acetona amb un pinzell petit per a que dissolgui parcialment les capes de consolidant brutes i poder retirar-les acuradament amb l'ajuda d'unes pinces entomològiques i bisturí. Si la capa de consolidant no és gaire gruixuda es pot retirar directament amb el pinzell prèviament humit amb acetona. Alguns espècimens poden presentar restes de la matriu que s'han de retirar amb molta precaució amb l'ajuda del bisturí.

El segon i darrer pas consisteix en consolidar definitivament l'espècimen per immersió total en el consolidant (paraloid + acetona). Si es tracta d'una peça molt fràgil es pot anar consolidant amb un pinzell o una xeringa. Hi ha que tenir molta precaució amb la immersió total perquè el consolidant intern que manté l'estructura de l'espècimen es podria dissoldre amb l'acetona provocant el col·lapse o la fragmentació de l'espècimen.

Materials recuperats

Després de processar c. 100 kg de bretxa, i amb una elevada dosi de paciència, s'han recuperat milers de restes fòssils de diversos taxons. Els mamífers terrestres són el millor grup representat amb un total de 5928 restes. D'aquestes, 2748 corresponen a un mínim de 50 individus d'un glírid de proporcions corporals semblants a Eliomys.

Seguidament, s'han recuperat 2174 restes corresponents a un mínim de 55 individus d'un cricètid de grans dimensions (713 registres a la col·lecció de vertebrats de l'IMEDEA; d'aquí endavant IMEDEA-VER). I en menor quantitat s'han recuperat 470 restes atribuïbles a un mínim de 16 individus, predominantment d'exemplars juvenils, d'un lepòrid (103 registres a IMEDEA-VER), 368 restes d'un mínim de 23 individus d'un sorícid (297 registres a IMEDEA-VER), 161 restes pertanyents a un mínim de 11 individus d'un múrid (127 registres a IMEDEA-VER) i únicament han aparegut 8 restes (3 registres a IMEDEA-VER), principalment fragmentàries, d'un bòvid juvenil (Fig. 11). D'altra banda, les restes corresponents a quiròpters són escasses, havent-se recuperat entorn a una trentena de restes, predominantment fragmentàries.

En l'estudi dels rosegadors s'ha comptat amb la participació del Dr Jordi Agustí, investigador de la Institució Catalana de Recerca i Estudis Avançats (ICREA) i del Dr Pedro Piñero, ambdós membres de l'Institut Català de Paleoecologia Humana i Evolució Social.

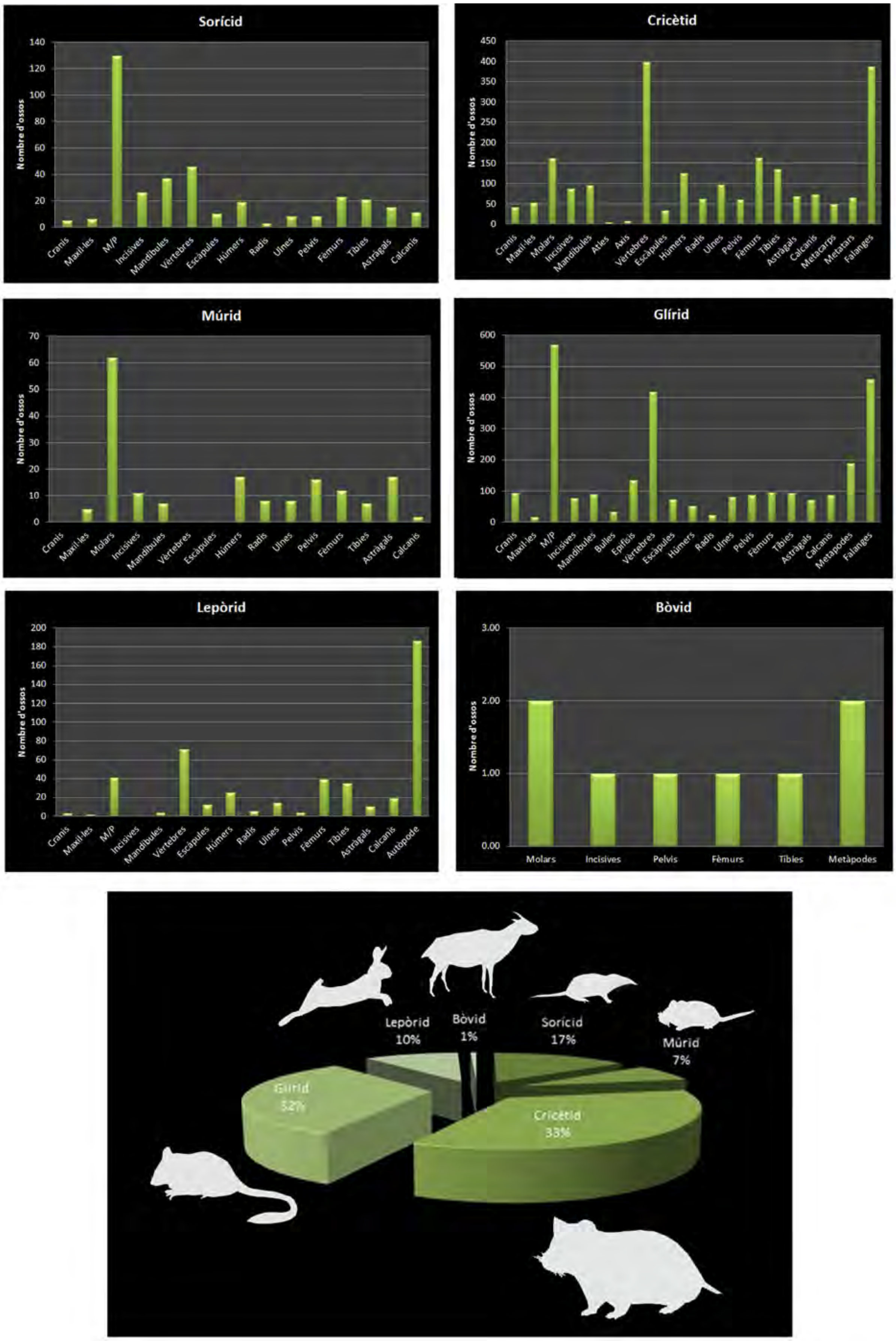


Figura 11: Nombre d'elements ossis de cada espècie de mamífer recuperats durant el tractament químic de les bretxes de NB-1 i representació percentual obtinguda en funció del nombre mínim d'individus.

El següent grup que destaca per la seva abundància i diversitat és la dels rèptils. Fins a la data s'han recuperant prop d'un milenar d'elements ossis atribuïts a un queloni, a una o dues espècies de Gekkota, una forma gran i una petita de lacèrtid, un escíncid, un ànguid, tres formes diferents de colubrins, diverses restes d'un gran escurçó atribuït al complexe d'Escurçons Orientals i unes poques vèrtebres atribuïbles a un escolecofidi i un amfisbènid.

Finalment, els ocells i dels amfibis són els grups amb menor representació en el jaciment de NB-1. El primer es troba composat per 528 elements ossis on el 87% de les restes corresponen a falanges. Tot i així, cal destacar la recuperació d'un fèmur i un coracoides complets i els fragments proximals d'un radi i d'una escàpula, tots ells atribuïts a una olibassa gegant. Pel que respecta als amfibis, s'han identificat 47 restes òssies, pertanyents a dos alítids, un bufònid i un rànid.

Durant una estada al Muséum National d'Histoire Naturelle (MNHN) de París es varen adquirir els coneixements necessaris en la identificació dels principals grups paleoherpetològics recuperats dels jaciment de NB-1, sota la supervisió de Salvador Bailon, expert en l'estudi paleoherpetològic del Pliocè i del Quaternari europeu del Centre National de Recherche Scientifique (CNRS) i membre de l'UMR 7209 i 7194.

Els materials s'han estudiant, uns abans de la realització d'aquesta Tesi (47 elements d'anurs i 211 restes *Apocricetus*) i uns altres durant la realització d'aquesta Tesi de manera completa o parcial (968 de rèptils de NB-1, 6046 restes de l'escurçó d'Eivissa, 83 restes de *Paraethomys*, 615 restes dentàries de glírid i 583 restes d'ocells), fan un total de 8553 restes òssies. Tot i així, resten materials pendents d'estudi, que també es troben inventariats (com el sorícid i el lepòrid, així com la major part del material postcranial dels mamífers). L'estudi de totes aquestes restes ha permès posar de manifest que l'estoc faunístic que va arribar duran la Crisi salina del Messinià era molt més divers del que es creia i ha permès replantejar l'origen d'aquestes faunes, el procés de colonització de les Balears i com va evolucionar la comunitat faunística des del moment de l'aïllament insular. A més s'ha pogut documentar la presència d'un escurçó autòcton a Eivissa, i s'han avaluat les causes de la seva extinció.

Siglat, registre, conservació i dipòsit

El material recuperat i preparat es troba dipositat a la col·lecció de vertebrats de l'Institut Mediterrani d'Estudis Avançats (IMEDEA, UIB-CSIC). Els espècimens de major interès i que es troben ben preservats s'han siglat individualment amb l'acrònim IMEDEA seguit de sis dígits. Seguint el mateix criteri d'identificació, aquells elements que es troben molt fracturats s'han agrupat per tipologia d'os amb una numeració comuna. Tots els espècimens siglats es troben registrats i es poden consultar a través de la plataforma web de la Infraestructura Global d'Informació en Biodiversitat (GBIF).

4.2. Material de comparació i preparació d'esquelets actuals

Per portar a terme una correcta classificació de les restes fòssils recuperades durant les tasques d'extracció, ha estat imprescindible la utilització de material de comparació d'una amplia varietat de grups de vertebrats actuals (amfibis, escatosos, mamífers i aus). Predominantment el material de comparació utilitzat prové de la Col·lecció de Vertebrats de l'IMEDEA (Esporles, Illes Balears), però s'ha disposat d'exemplars prestats pel Zoologisches Forschungsmuseum Alexander Koenig (ZFMK, Bonn, Alemanya), material prestat i consultat durant l'estada al Muséum National d'Histoire Naturelle (MNHN, París, França), materials del Museo Nacional de Ciencias Naturales (MNCN, Madrid, Espanya) que estaven en préstec al Dr Salvador Bailon (del MNHN, Paris), així com materials particulars que han permès enriquir el coneixement en anatomia osteològica dels diferents grups tractats (Taula 1). A més d'això, durant l'estudi dels anurs fòssils es va consultar recurrentment la base de dades de la plataforma Lisanfos KMS desenvolupada pel MNCN (Martín i Sanchiz, 2013), que actualment no es troba en funcionament.

Espècie	Sexe	Edat	Origen	Nº col·lecció	Institució
Cricetus cricetus	Femella	Juvenil	Alemanya	94991	IMEDEA
C. cricetus	Mascle	Juvenil	Alemanya	94992	IMEDEA
Eliomys quercinus	Indet.	Adult	Mallorca	7451	IMEDEA
E. q. ophiusae	Mascle	Adult	Formentera	7342	IMEDEA
Mesocritus auratus	Mascle	Juvenil	Captivitat	94829	IMEDEA
M. auratus	Femella	Juvenil	Captivitat	94830	IMEDEA
Phodopus roborovskii	Femella	Juvenil	Captivitat	94833	IMEDEA
P. roborovskii	Mascle	Juvenil	Captivitat	94834	IMEDEA
P. sungorus	Femella	Juvenil	Captivitat	94831	IMEDEA
P. sungorus	Mascle	Juvenil	Captivitat	94832	IMEDEA
Alytes muletensis	Indet.	Adult	Mallorca	3837	IMEDEA
Bufotes balearicus	Indet.	Adult	Mallorca	21411	IMEDEA
Pelophylax perezi	Indet.	Adult	Mallorca	s/n	IMEDEA
Hemorrhois hippocrepis	Mascle	Adult	Eivissa	90020	IMEDEA
Natrix maura	Femella	Juvenil	Mallorca	94964	IMEDEA
Rinechis scalaris	Mascle	Adult	Formentera	90025	IMEDEA
Vipera aspis	Mascle	Adult	Espanya	106926	IMEDEA
V. latastei	Femella	Adult	Espanya	106925	IMEDEA
V. seoanei	Mascle	Adult	Espanya	106927	IMEDEA
Athene noctua	Indet.	Adult	Espanya	21717	IMEDEA
A. noctua	Indet.	Adult	Catalunya?	94663	IMEDEA
Coturnix coturnix	Mascle	Adult	Mallorca	12106	IMEDEA
Otus scops	Femella	Adult	Mallorca	21902	IMEDEA
O. scops	Indet.	Adult	Eivissa	94019	IMEDEA
Tyto alba	Indet.	Adult	Mallorca	106870	IMEDEA
T. alba	Mascle	Adult	Mallorca	21884	IMEDEA
Cricetus cricetus	Femella	Adult	Alemanya	79614	ZFMK
C. cricetus	Mascle	Adult	Alemanya	79430	ZFMK
Rana temporaria	Indet.	Adult	Desconegut.	1896-399-89	MNHN
R. temporaria	Femella	Adult	Desconegut.	1966-178	MNHN
Macrovipera lebetina	Mascle	Adult	Desconegut	2002-64	MNHN
M. lebetina	Indet.	Juvenil	Marroc	s/n	MNHN
Vipera ammodytes	Femella	Adult	França	s/n	MNHN
V. aspis	Indet.	Adult	Desconegut	1967-100	MNHN
V. aspis	Indet.	Subadult	Desconegut	1967-367	MNHN
V. berus	Indet.	Juvenil	França	s/n	MNHN
V. berus	Indet.	Adult	França	s/n	MNHN
V. latastei	Mascle	Adult	Espanya	s/n	MNHN
V. monticola	Indet.	Adult	Marroc	RA-MNHN 1961-0334	MNHN
V. seoanei	Indet.	Subadult	Espanya	s/n	MNHN
V. seoanei	Indet.	Adult	Espanya	s/n	MNHN
V. ursini	Indet.	Subadult	Desconegut	1967-277	MNHN
Alytes obstetricans	Indet.	Adult	França	s/n	Col. S. Bailon
Bufo bufo	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
Bufotes viridis	Indet.	Adult	Desconegut	s/n	Col. S. Bailon

Espècie	Sexe	Edat	Origen	Nº col·lecció	Institució
Discoglossus pictus	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
D. sardus	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
Hyla arborea	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
Hemidactilus turcicus	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
Malpolon monspessulanus	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
Natrix natrix	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
Vipera ammodytes	Indet.	Adult	Desconegut	s/n	Col. S. Bailon
Discoglossus galganoi	Mascle	Adult	Desconegut	41080	MNCN
D. galganoi	Femella	Adult	Espanya	15125	MNCN
D. galganoi	Mascle	Adult	Espanya	41073	MNCN
D. jeanneae	Mascle	Adult	Espanya	41068	MNCN
D. jeanneae	Mascle	Adult	Espanya	41069	MNCN
D. jeanneae	Femella	Adult	Espanya	41074	MNCN
D. jeanneae	Mascle	Adult	Espanya	41075	MNCN
D. jeanneae	Mascle	Adult	Espanya	41076	MNCN
D. sardus	Indet.	Adults	Còrsega	41049	MNCN
D. sardus	Indet.	Adult	Còrsega	1991-1995	MNCN
D. scovazzi	Femella	Adult	Marroc	41065	MNCN
D. scovazzi	Mascle	Adult	Marroc	41066	MNCN
Hyla meridionalis	Indet.	Adult	Barcelona	2011	Col. Personal
Pelophylax perezi	Indet.	Adult	Mallorca	03/2014	Col. Personal
Hemidactylus turcicus	Indet.	Adult	Mallorca	04/2017	Col. Personal
Podarcis lilfordi	Indet.	Adult	Desconegut	2015	Col. Personal
P. pityusensis	Indet.	Juv./Adults	Eivissa	2014	Col. Personal
Tarentola mauritanica	Indet.	Adult	Mallorca	01/2016	Col. Personal
Macroprotodon mauritanicus	Indet.	Adult	Mallorca	07/2017	Col. Personal
Crocidura canariensis	Indet.	Adult	Canàries	2012	Col. Personal
C. pachyura	Indet.	Adult	Eivissa	2013	Col. Personal
Eliomys quercinus	Indet.	Adult	Mallorca	10/2012	Col. Personal
Mus musculus	Indet.	Juvenil	Canàries	2012	Col. Personal
Oryctolagus cuniculus	Indet.	Adult	Eivissa	03/2014	Col. Personal
Tyto alba	Indet.	Adult	Mallorca	2015	Col. Personal

Taula 1: Llistat dels tàxons actuals utilitzats durant les diferents etapes de l'estudi dels vertebrats de NB-1.

Preparacions osteològiques d'exemplars actuals

Tota una sèrie d'exemplars de vertebrats actuals han estat preparats durant el transcurs de la present Tesi Doctoral amb la finalitat d'adquirir els coneixements bàsics sobre l'anatomia osteològica dels grups d'interès i utilitzar-los com a elements bàsics d'anatomia comparada. La majoria dels exemplars han requerit tot un procés de preparació que pot haver trigat setmanes (*Bufotes balearicus*, *Vipera aspis*, *V. latastei*, *V. seoanei*, *Mesocricetus auratus*, *Phodopus roborovskii*, *P. sungorus* i material particular), mentre que altres s'han obtingut directament d'egagròpiles (*Crocidura canariensis*, *C. pachyura*, *Mus musculus*), les quals requereixen una neteja amb aigua i blanquejat si es desitja.

El procés de preparació de material osteològic es compon a grans trets de tres fases: neteja, desengreixament i blanquejat.

La neteja s'ha realitzat per maceració a temperatura ambiental o a baixa temperatura (40-50 ºC) amb la utilització d'una estufa (NAHITA drying oven 65 L, series 631 Plus). Es tracta de processos de putrefacció on els teixits tous s'eliminen per acció bacteriana. Aquestes tècniques son àmpliament utilitzades per anatomia comparada ja que interessa obtenir espècimens desarticulats.

Un cop es tenen el ossos sense teixit i completament desarticulats convé desengreixar-los adequadament perquè poden generar problemes de conservació al crear microambients àcids i d'estètica (coloració, textura i olor desagradable). El contingut de greix a l'interior dels ossos depèn de l'espècie, l'edat, el sexe, així com altres factors biològics. Per petits espècimens tals com rèptils, amfibis o petits ocells, el millor procediment per desengreixar es mitjançant banys en acetona durant dues setmanes aproximadament. Si es desitja, abans d'utilitzar acetona, es pot realitzar una immersió en amoníac de dues setmanes de duració. Durant aquesta fase si es perforen les epífisis es pot agilitzar el procés.

Per acabar, el blanquejat és un procés molt senzill que consisteix en donar un darrer bany a l'espècimen en peròxid d'hidrogen al 3% durant 24 h. Aquest procés a més de blanquejar desinfecta, però hi ha que anar amb precaució perquè el peròxid d'hidrogen pot ser agressiu segons l'estat dels ossos (restes que han patit una exposició perllongada a la intempèrie). Finalment si es deixa assecar al Sol el blanquejat serà més intens.

4.3. Material instrumental, nomenclatura i mesures

Durant les tasques de triatge de les restes òssies d'escala mil·limètrica s'ha utilitzat un estereomicroscopi Leica S8 APO i unes pinces entomològiques. Les fotografies s'han obtingut mitjançant una càmera digital DFC420 connectada al estereomicroscopi i per mitjà d'un microscopi digital AM7915MZT Dino-Lite Edge. Els exemplars de major interès varen ser fotografiats amb microscopi electrònic de rastreig (HITACHI S-3400N) dels Serveis Cientificotècnics de la Universitat de les Illes Balears (UIB).

El criteri de mesura i la nomenclatura utilitzats en la descripció d'ofidis segueixen el criteri utilitzat per Szyndlar (1984). La resta de rèptils segueix la nomenclatura utilitzada en Gans (1969) i Gans et al. (2008).

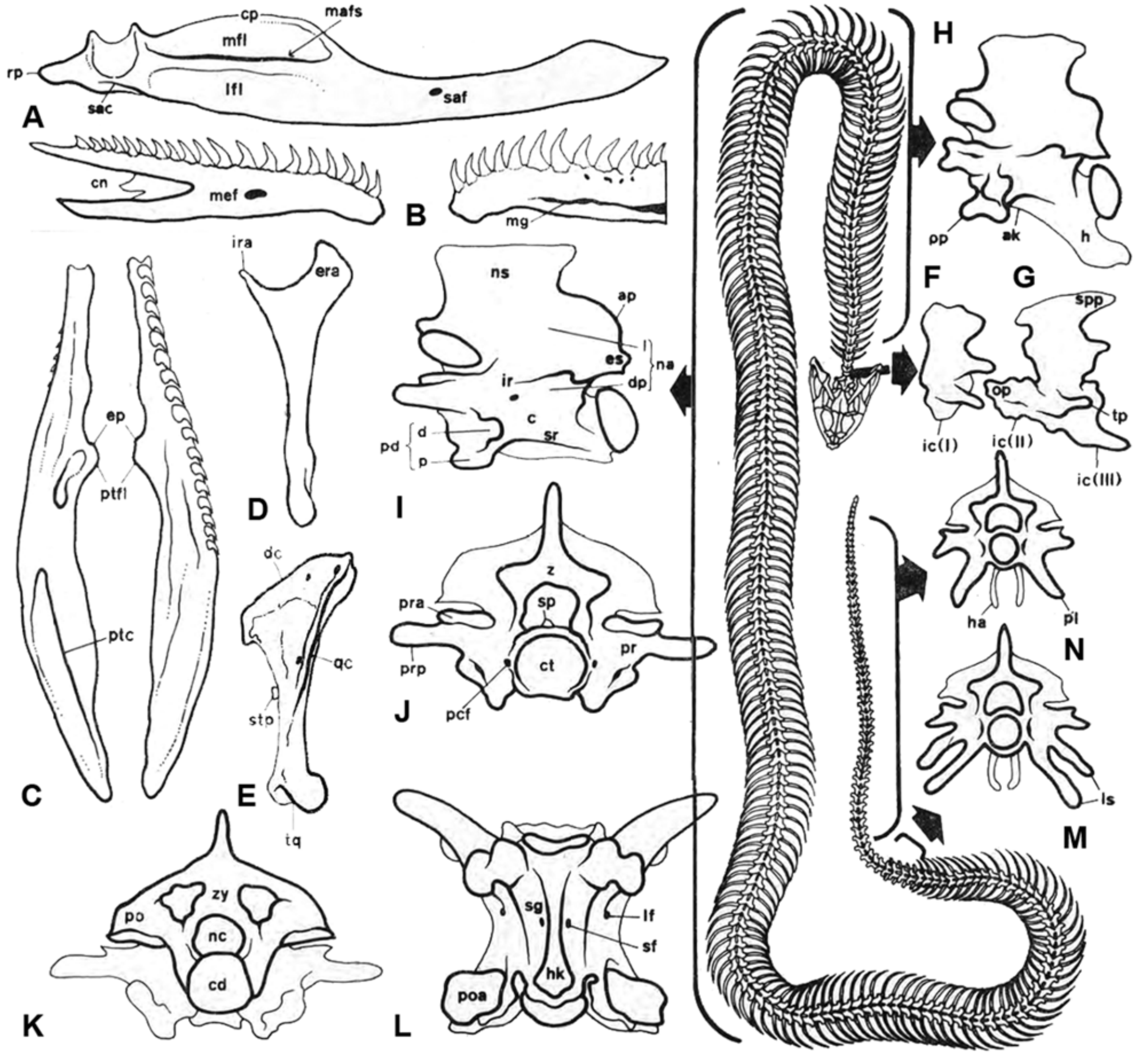


Figura 12: Nomenclatura utilitzada en els principals elements d'ofidis descrits. A, os compost en norma lateral; B, dentari en norma lateral (esquerra) i medial (dreta); C, pterigoide en norma dorsal (esquerra) i ventral (dreta); D, ectopterigoid en norma dorsal; E, quadrat en norma posterolateral; F, atles en norma lateral; G, axis en norma lateral; H, vèrtebra cervical en norma lateral; I-L, vèrtebres dorsals en norma lateral (I), anterior (J), posterior (K) i ventral (L); M, vèrtebra sacra en norma anterior; N, vèrtebra caudal en norma anterior. No es troben a escala. Modificat de Szyndlar (1984).

Abreviatures: (A) cp, procés coronoide; lfl, marge lateral; mafs, fossa mandibular; mfl, marge medial; rp, procés retroarticular; sac, cresta supraangular; saf, foramen supraangular. (B) cn, escotadura de l'os compost; mef, formane mental; mg, canal de Meckel. (C) ep, procés eptopterigoide; ptc, cresta pterigoidea; ptfl, marge pterigoideu. (D) era, ramus extern; ira, ramus intern. (E) dc, cresta dorsal; qc, cresta del quadrat; stp, procés estapedial; tq, tròclea quadrati. (F) ic I, intercentrum I. (G) ic II, intercentrum II; ic III, hipapòfisi I; op, procés odontoide; spp, procés espinal; tp, procés transversal. (H) ak, quilla anterior; h, hipapòfisi; pp, procés parapofisari. (I) ap, procés aliforme; es, espina epizigapofisària; c, centrum; d, diapòfisi; dp, part descendent de l'arc neural; ir, cresta interzigapofisària; l, laminae; na, arc neural; ns, espina neural; p, parapòfisi; pd, paradiapòfisi; sr, cresta subcentral. (J) ct, còtil; pcf, foramen paracotilar; pr, prezigapòfisi; pra, superfície articular prezigapofisària; prp, procés prezigapofisari; sp, procés subneural; z, zigosfè. (K) cd, còndil; nc, canal neural; po, postzigapòfisi; zy, zigantre. (L) hk, quilla hemal; lf, foramen lateral; poa, superfície articular postzigapofisària; sf, foramen subcentral; sg, fossa ventral. (M) ls, limfapòfisi. (N) ha, hemapòfisi; pl, pleurapòfisi.

La nomenclatura utilitzada en la descripció de les restes avianes segueix Livezey i Zusi (2006). Mentre que les mesures utilitzades segueixen els criteris proposats per von den Driesch (1976) i Mourer-Chauviré (1975).

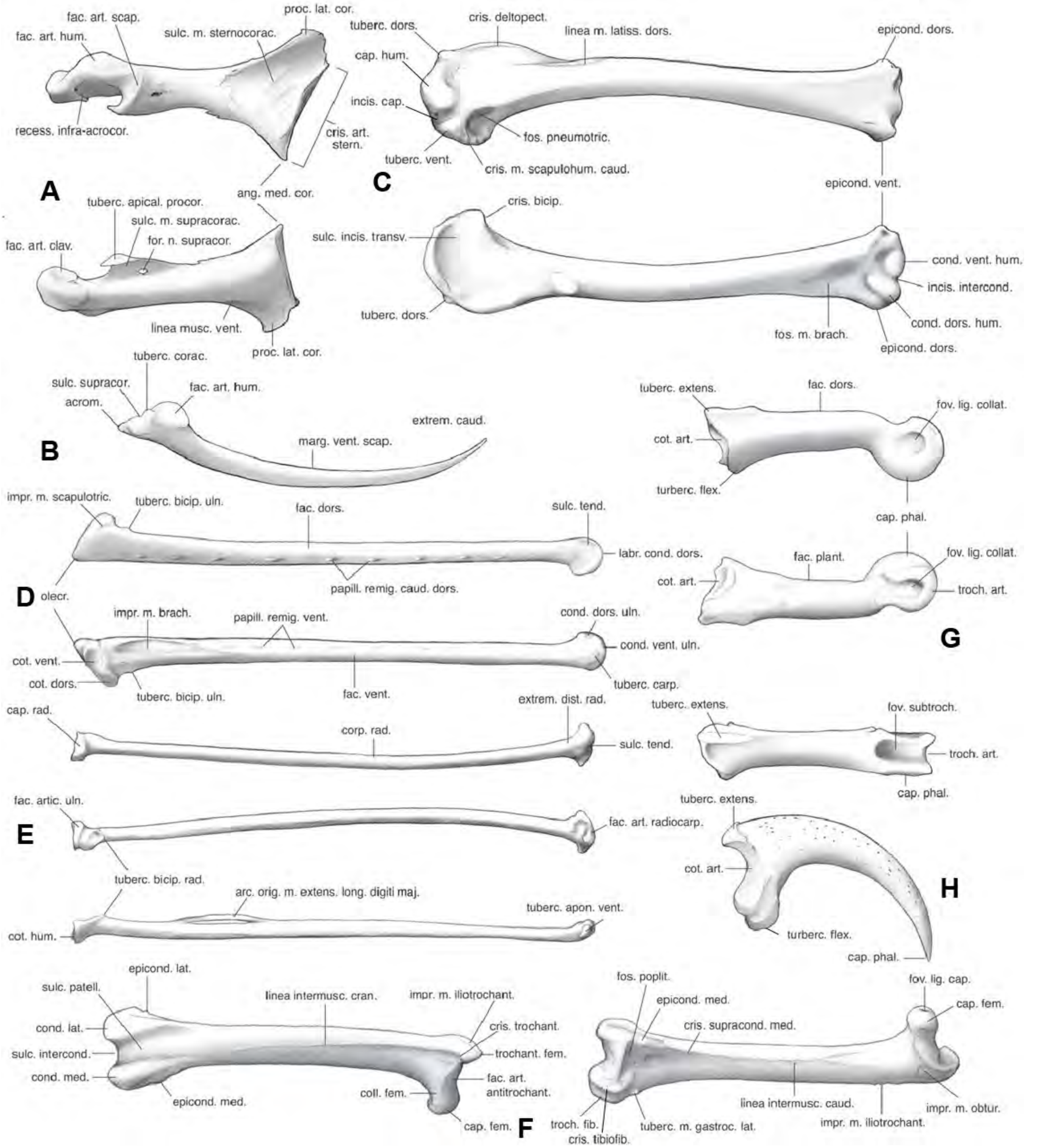


Figura 13: Nomenclatura utilitzada en els principals elements dels ocells descrits. A, coracoide en norma dorsal (superior) i ventral (inferior); B, escàpula en norma lateral; C, húmer en norma caudal (superior) i cranial (inferior); D, ulna en norma anconal (superior) i palmar (inferior); E, radi en norma dorsal (superior), ventral (intermèdia) i lateral (inferior); F, fèmur en norma cranial (esquerra) i caudal (dreta); G, falange proximal en norma lateral (superior), medial (intermèdia) i dorsal (inferior); H, falange terminal en norma lateral. No es troben a escala. Modificat de Livezey i Zusi (2006).

Abreviatures: (A) ang. med. cor., angulus medialis coracoidei; cris. art. stern., crista articularis sternalis; fac. art. clav., facies articularis clavicularis; fac. art. hum., facies articularis humeralis; fac. art. scap., facies articularis scapularis; for. n. supracor., foramen nervi supracoracoidei; linea musc. vent., linea muscularis ventralis; proc. lat. cor., processus lateralis coracoidei; recess. infra-acrocor., recessus infra-acrocoracoideus; sulc. m. sternocorac., sulcus musculi sternocoracoideus; sulc. m. supracorac., sulcus musculi supracoracoideus; tuberc. apical. procor., tuberculum apicalis procoracoidei. (B) acrom., acromion; fac. art. hum., facies articularis humeralis; marg. vent. scap., margo ventralis scapularis; sulc. m. supracorac., sulcus musculi supracoracoideus; tuberc. corac., tuberculum coracoideum; (C) cap. hum., caput humeri; cond. dors. hum., condylus dorsalis humeri; cond. vent. hum., condylus ventralis humeri; cris. bicip., crista bicipitalis; cris. m. scapulohum. caud., crista musculi scapulohumeralis caudalis; epicond. dors., epicondylus dorsalis; epicond. vent., epicondylus ventralis; fos. m. brach., fossa musculi brachialis; fos. pneumotric., fossa pneumotricipitalis; incis. cap., incisura capitis; incis. intercond., incisura intercondylaris; sulc. incis. transv., sulcus incisurae transversus; tuberc. dors., tuberculum dorsalis; tuberc. vent., tuberculum ventrale. (D) cond. dors. uln., condylus dorsalis ulnae; cond. vent. uln., condylus ventralis ulnae; cot. dors., cotyla dorsalis; cot. vent., cotyla ventralis; fac. dors., facies dorsalis; fac. vent., facies ventralis; impr. m. brach., impressio musculi brachialis; impr. m. scapulotric., impressio musculi scapulotriceps; labr. cond. dors., labrum condyli dorsalis; olecr., olecranon; papill. remig. caud. dors., papillae remigales caudales dorsales; sulc. tend., sulcus tendinis; tuberc. bicip. uln., tuberculum bicipitale ulnae; tuberc. carp., tuberculum carpale. (E) arc. orig. m. extens. long. digiti maj. arcus origo musculi extensor longus digiti majoris; cot. hum., cotyla humeralis; fac. art. radiocarp., facies articularis radiocarpalis; fac. art. uln., facies articularis ulnae; tuberc. apon. vent., tuberculum aponeurosis ventralis; tuberc. bicip. rad., tuberculum bicipitale radii. (F) cap. fem., caput femoris; coll. fem., collum femoris; cond. lat., condylus lateralis; cond. med., condylus medialis; cris. trochant., crista trochantericus; epicond. lat., epicondylus lateralis; epicond. med., epicondylus medialis; fac. art. antitrochant., facies articularis antitrochanterica; impr. m. iliotrochant., impressio musculi iliotrochantericus; linea intermusc. cran., linea intermuscularis cranialis; sulc. intercond., sulcus intercondylaris; trochant. fem., trochanter femoris. (G) cap. phal., caput phalangis; cot. art., cotyla articularis; fac. dors., facies dorsalis; fac. plant., facies plantaris; fov. lig. collat., fovea ligamenti collateralis; fov. subtroch., fovea subtrochlearis; troch. art., trochlea articularis; tuberc. extens., tuberculum extensorium; tuberc. flex., tuberculum flexorium. (H) cap. phal., caput phalangis; cot. art., cotyla articularis; tuberc. extens., tuberculum extensorium; tuberc. flex., tuberculum flexorium.

En el cas del múrid, la nomenclatura utilitzada segueix a van de Weerd (1976) i Miller (1912). Els molars inferiors es denominen com m1,2,3 i els molars superiors com M1,2,3. Les seves mesures segueixen els criteris establert per Martín Suárez i Freudenthal (1993).

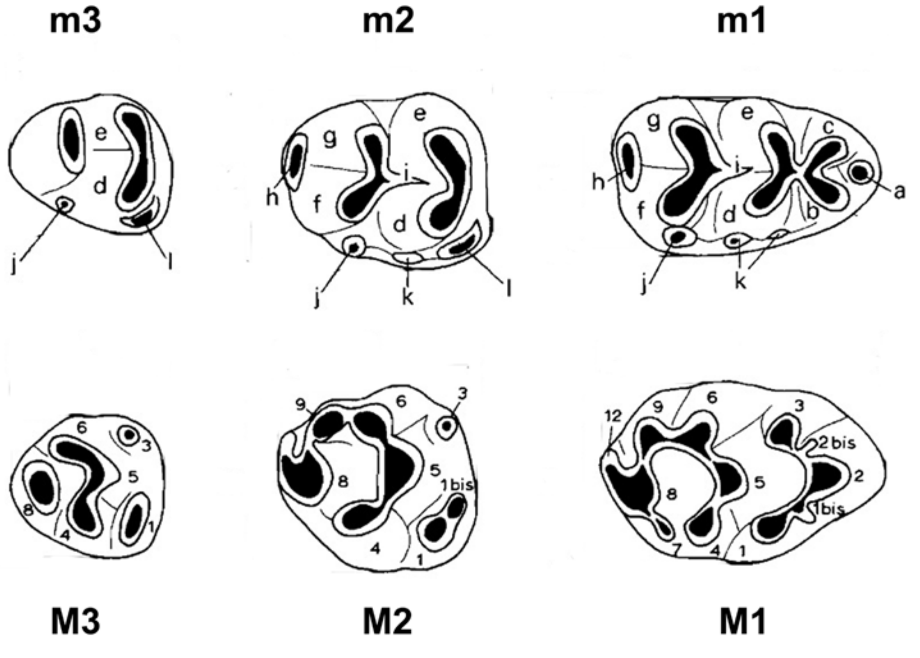


Figura 14: Nomenclatura emprada dels molars inferiors (m1, m2 i m3) i superiors (M1, M2 i M3) d'un múrid; (a) tubercle anterior mitjà o tma, (b) lòbul labial de l'anterocònid, (c) lòbul lingual de l'anterocònid, (d) protocònid, (e) entocònid, (f) hipocònid, (g) entocònid, (h) tubercle posterior, (i) cresta longitudinal, (j) cúspide accessòria posterior o c1, (k) cúspides

accessòries del cíngol labial, (l) cúspide anterolabial. Segons el criteri de Miller (1912), els molars superiors són numerats precedits d'una "t" (tubercle).

Les mesures s'han realitzat a partir d'imatges obtingudes de la càmera digital DFC420 mitjançant el programari ImageJ (Rasband, 2018), mentre que altres es varen mesurar directament amb el microscopi digital Dino-Lite. Els valors de les mesures s'expressen en mm.

4.4. Elaboració d'il·lustracions

Les il·lustracions que figuren en els treballs que s'inclouen en els annexes de la present Tesi Doctoral s'han realitzat a partir de fotografies mitjançant el programa Photoshop CS5 o manualment. En tots els casos s'ha disposat de la visualització directa de l'espècimen a figurar.

PART 2. RESULTATS GLOBALS

CAPÍTOL 5. Associació paleofaunística de vertebrats de NB-1

1. Els rèptils: identificacions preliminars

Es presenten les diagnosis taxonòmiques preliminars dels rèptils obtinguts del jaciment de NB-1. Bover et al. (2014) ja varen donar a conèixer l'existència d'una part d'aquest conjunt faunístic, tot i que no es varen il·lustrar ni descriure els fòssils. A la present Tesi Doctoral s'aporta una ampliació dels materials identificats, basada en l'estudi dels materials exhumats inicialment i de nous materials, així com una aproximació a les seves identitats taxonòmiques. Aquestes identificacions seran objecte d'una futura publicació.

Ordre TESTUDINES

Les restes que han pogut ser atribuïdes a aquest grup són molt escasses i molt fragmentaries. S'han recuperat en total 8 restes fòssils, corresponents a fragments de plaques i falanges. La gran majoria corresponen a individus juvenils i únicament s'ha trobat una falange que correspondria a un testudínid de talla mitjana.

Ordre LACERTILIA (SQUAMATA)

Subordre SAURIA

Infraordre Gekkota

Família Gekkonidae/Sphaerodactylidae

S'han identificat més d'un centenar de restes fòssils d'aquest grup. Els elements ossis més abundants corresponen a vèrtebres, alguns dentaris i maxil·les, dos frontals i un parietal. S'ha pogut observar que aquestes restes corresponen, almenys, a dues formes de gecònids, que es poden diferenciar inicialment per la seva mida. La forma gran (Gekkota sp. 1, Fig. 15) està representada per una majoria de restes cranials, mentre que la forma menor (Gekkota sp. 2, Fig. 15) està representada per vèrtebres i dentaris.

Les vèrtebres dels gecònids es diferencien fàcilment de les de la resta de lacertilis presents al jaciment. Es caracteritzen per ser amficèliques. Es tracta de l'element predominant i apareixen tant de la forma petita com de la gran. Els dentaris presenten un canal de Meckel tancat i posteriorment es bifurquen desenvolupant un procés que sobrepassa el nivell del procés coronoides. La dentició és pleurodonta de morfologia acicular i unicúspide. Les maxil·les es caracteritzen principalment per presentar una faceta prefrontal alta, una *lamina horizontalis* molt desenvolupada i una dentició com la descrita anteriorment. Els frontals dels gecònids són simples, caracteritzats per presentar la *crista cranii* fusionada, donant lloc a un conducte que tanca el sistema olfactiu. Els parietals d'aquest grup són normalment parells, units per una fina sutura. No presenten foramen pineal i la superfície dorsal s'expandeix lateralment on queda confinat el múscul adductor en la superfície ventral de l'os.

El registre fòssil dels gecònids és molt pobre i poc conegut. Al Miocè europeu únicament es troben descrites mitja desena de tàxons (*Gerandogekko arambourgi*, *G. gaillardi, Euleptes gallica, E.* sp. *i Paleogekko risgovienis*) i multitud de restes d'atribució indeterminada. Els frontals, maxil·les i dentaris són els elements ossis més comuns que s'han trobat i amb els que s'han descrit la majoria d'aquests tàxons.

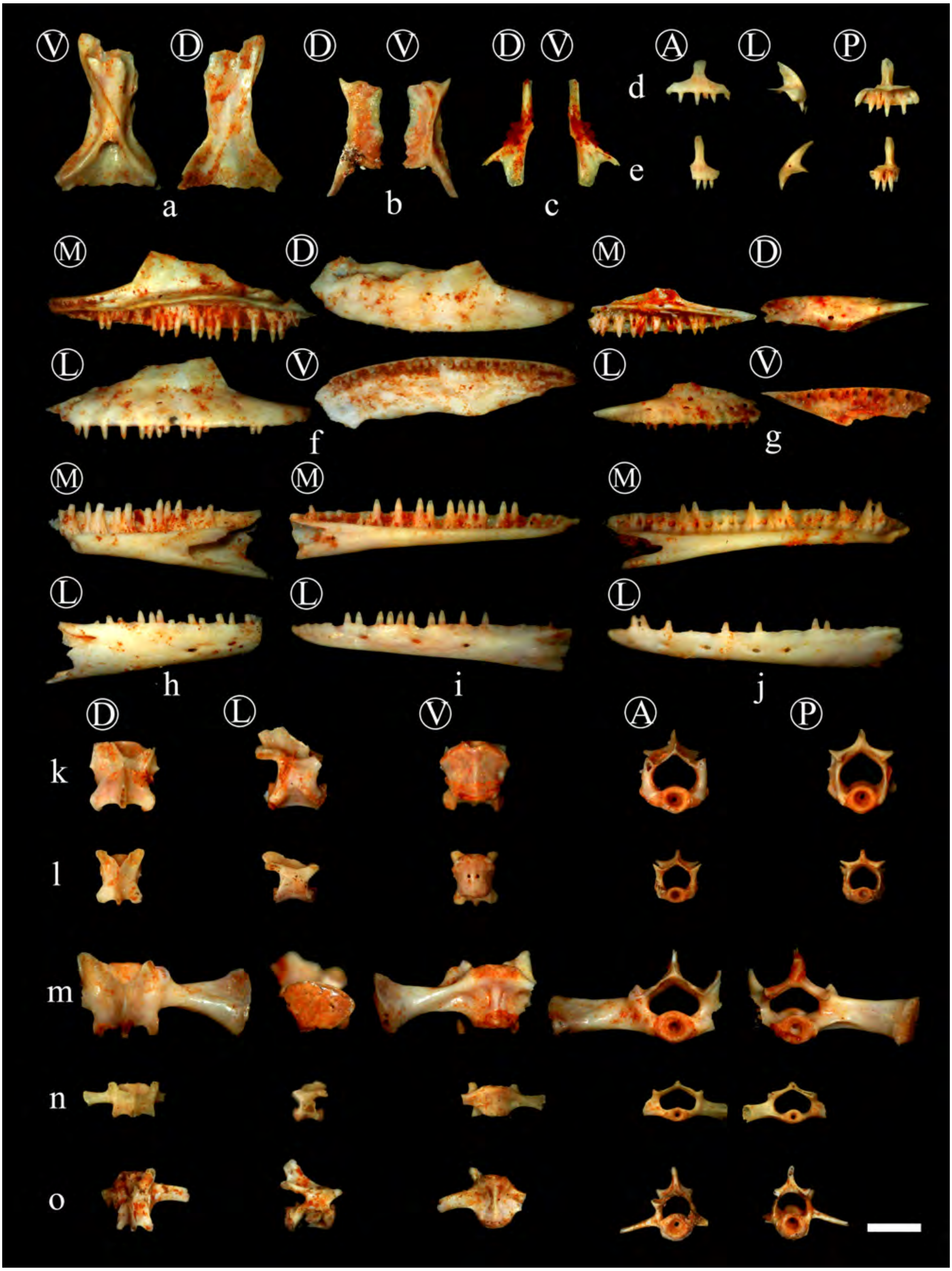


Figura 15: Restes fòssils atribuïdes a dos gecònids de NB-1. Elements de **Gekkota sp. 1**: (**a**) frontal, IMEDEA 105640; (**d**) premaxil·la, IMEDEA 105222; (**f**) maxil•la, IMEDEA 105351; (**h**) dentari, IMEDEA 105340; (**k**) vèrtebra dorsal, IMEDEA 105690; (**m**) vèrtebra sacra, IMEDEA 103070; (**o**) vèrtebra caudal, IMEDEA 103460. Elements **Gekkota sp. 2:** temptativament (**b**) parietal, IMEDEA 103250; temptativament (**c**) pterigoide, IMEDEA 103421; (**e**) premaxil·la, IMEDEA

103155; (**g**) maxil·la, IMEDEA 103428; (**i-j**) dentaris, IMEDEA 105276 i 105277; (**l**) vèrtebra dorsal, IMEDEA 105789; (**n**) vèrtebra sacra, IMEDEA 106393. A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral. Escala 2 mm.

Infraordre Scincomorpha

Família LACERTIDAE

D'aquest grup s'han identificat dos centenars de fòssils. Les restes per ordre d'abundància són vèrtebres, dentaris, maxil·les, premaxil·les, un fragment de frontal i un fragment de parietal. La majoria d'aquestes restes poden ser atribuïdes a *Podarcis*. D'altra banda també s'han identificat les restes (una premaxil·la i una vèrtebra dorsal) pertanyents a un lacèrtid de talla mitjana (Fig. 16).

Les vèrtebres dels lacèrtids es caracteritzen, igual que la majoria dels lacertilis, per presentar un còtil anterior i un còndil posterior, és a dir, una condició procèlica. El centrum vertebral presenta una superfície ventral plana. El còndil i el còtil estan relativament comprimits dorsoventralment. L'espina neural és alta i inclinada posteriorment. A més es caracteritzen per presentar unes facetes articulars suplementàries zigosfè/zigantre. Els dentaris mostren una cresta subdental poc profunda. El canal de Meckel és obert mentre el dentari no es troba articulat amb els restants ossos que formen la mandíbula inferior. Les maxil·les posseeixen un procés facial alt, curt i un procés premaxil·lar esvelt. Normalment les maxil·les no formen part de l'anell orbital perquè s'articulen amb el jugal i el lacrimal. La *lamina horizontalis* té una expansió reduïda. La dentició que presenten, tant els dentaris com les maxil·les, és pleurodonta de morfologia cilíndrica i bicuspidal, amb una cúspide central ben desenvolupada i una anterior de menor entitat. Les premaxil·les són simples i presenten un procés nasal allargat que s'estreny considerablement quan entra en contacte amb els ossos nasals. Els frontals són normalment parells, però en ocasions es troben fusionats. La *crista cranii* es troba poc desenvolupada posteriorment i en cap cas es troba fusionada. Els parietals són simples, curts, de morfologia quadrada, amb uns processos postparietals que s'estrenyen i es corben sobre la superfície occipital. Normalment són petits i presenten foramen pineal.

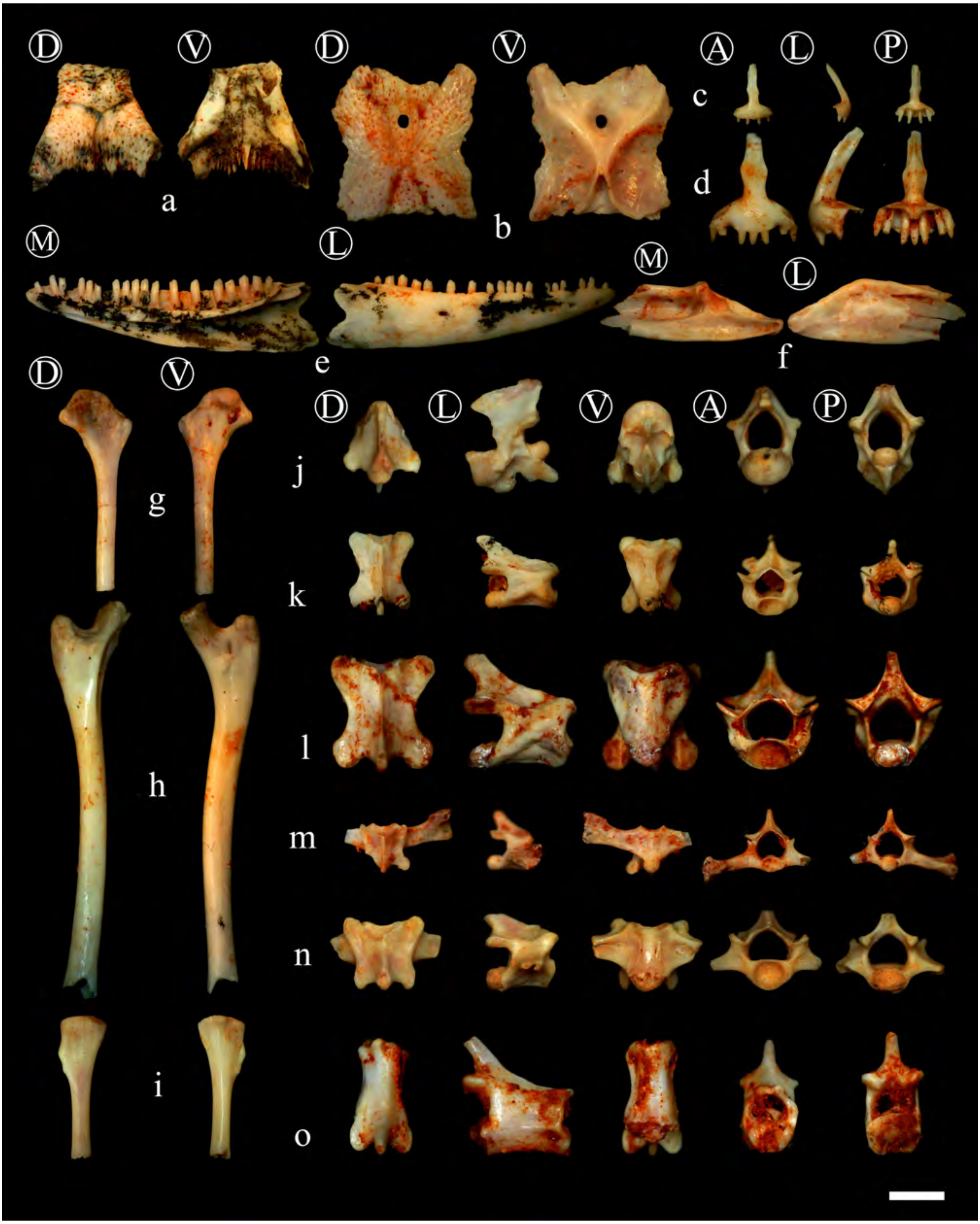


Figura 16: Restes fòssils atribuïdes a dos lacèrtids de NB-1. Elements de ***Podarcis* sp.**: (**a**) frontal, IMEDEA 105641; (**b**) parietal, IMEDEA 103160; (**c**) premaxil·la, IMEDEA 105647; (**e**) dentari, IMEDEA 105484; (**f**) articular, IMEDEA 105642; (**g**) húmer, IMEDEA 105665; (**i**) tibia, IMEDEA 105665; (**k**) vèrtebra dorsal, IMEDEA 105873; (**m**) vèrtebra sacra, IMEDEA 103211. Elements de ***Lacertidae* sp**. 2: (**d**) premaxil·la, IMEDEA 105347; (**h**) fèmur, IMEDEA 103159; (**j**) axis; IMEDEA 103085; (**l**) vèrtebra dorsal, IMEDEA 103042; (**n**) vèrtebra caudal proximal, IMEDEA 105645; (**o**) vèrtebra caudal distal, IMEDEA 105803. A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral. Escala 2 mm.

Família SCINCIDAE

Del grup dels escíncids s'han recuperat i identificat una cinquantena de restes òssies. La majoria d'aquests corresponen a vèrtebres, fragments de dentaris i fragments de maxil·les (Fig. 17). Les primeres troballes van poder ser atribuïdes a cf. *Chalcides*.

Les vèrtebres dels escíncids són molt similars a la dels lacèrtids. Són procèliques i solen presentar un cos més esvelt que la dels lacèrtids. El dentari pot presentar un canal de Meckel obert o tancat. Procés coronoide normalment molt pronunciat, dividit en una part anterior i una posterior per una destacada cresta. La maxil·la té un procés facial bastant desenvolupat. El procés posterior no sol formar part del marge de l'òrbita. Presenta una *lamina horizontalis* expandida. La dentició, tant en el dentari com en la maxil·la, és pleurodonta, cilíndrica i monocúspide amb una superfície roma on es poden apreciar estriacions.

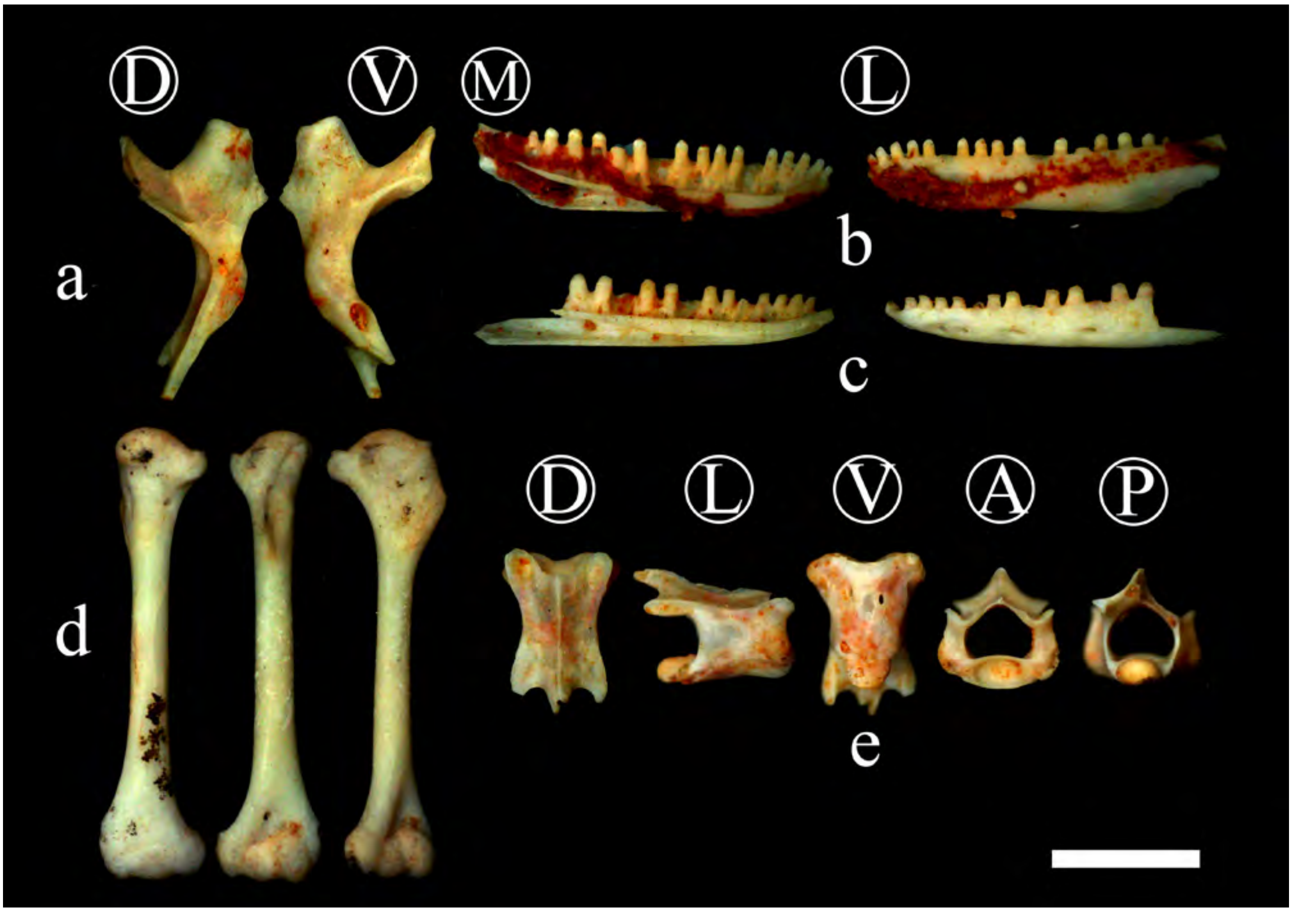


Figura 17: Restes fòssils atribuïdes a **cf. *Chalcides*** de NB-1: (**a**) pterigoide, IMEDEA 103269; (**b** i **c**) dentaris, IMEDEA 103317 i 103327; (**d**) húmer, IMEDEA 103297; (**e**) vèrtebra dorsal, IMEDEA 105750. A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral. Escala 2 mm.

<u>Infraordre Diploglossa</u>

Família ANGUIDAE

Dels les més de 350 restes atribuïdes a *Dopasia* sp., únicament cinc són fragments de dentaris i la resta són vèrtebres (toràciques, sacres i caudals). La recuperació d'un neurocrani presumiblement permetrà precisar més la determinació d'aquest tàxon (Fig. 18).

Les vèrtebres són procèliques i es caracteritzen per ser deprimides i moderadament allargades. El còtil i el còndil estan dorsoventralment comprimits i no presenten les facetes articulars suplementàries (zigosfè/zigantre). Els dentaris dels ànguids mostren una canal de Meckel obert, parcialment ocupat per l'esplecnial. Posteriorment, tenen un septe intramandibular curt que divideix el canal alveolar inferior del canal de Meckel. Dentició pleurodonta de morfologia variable a nivell genèric. A grans trets les dents són monocúspides que van des d'un aspecte molariforme fins a formes molt esmolades amb crestes tallants. Les dents poden o no presentar estriacions.

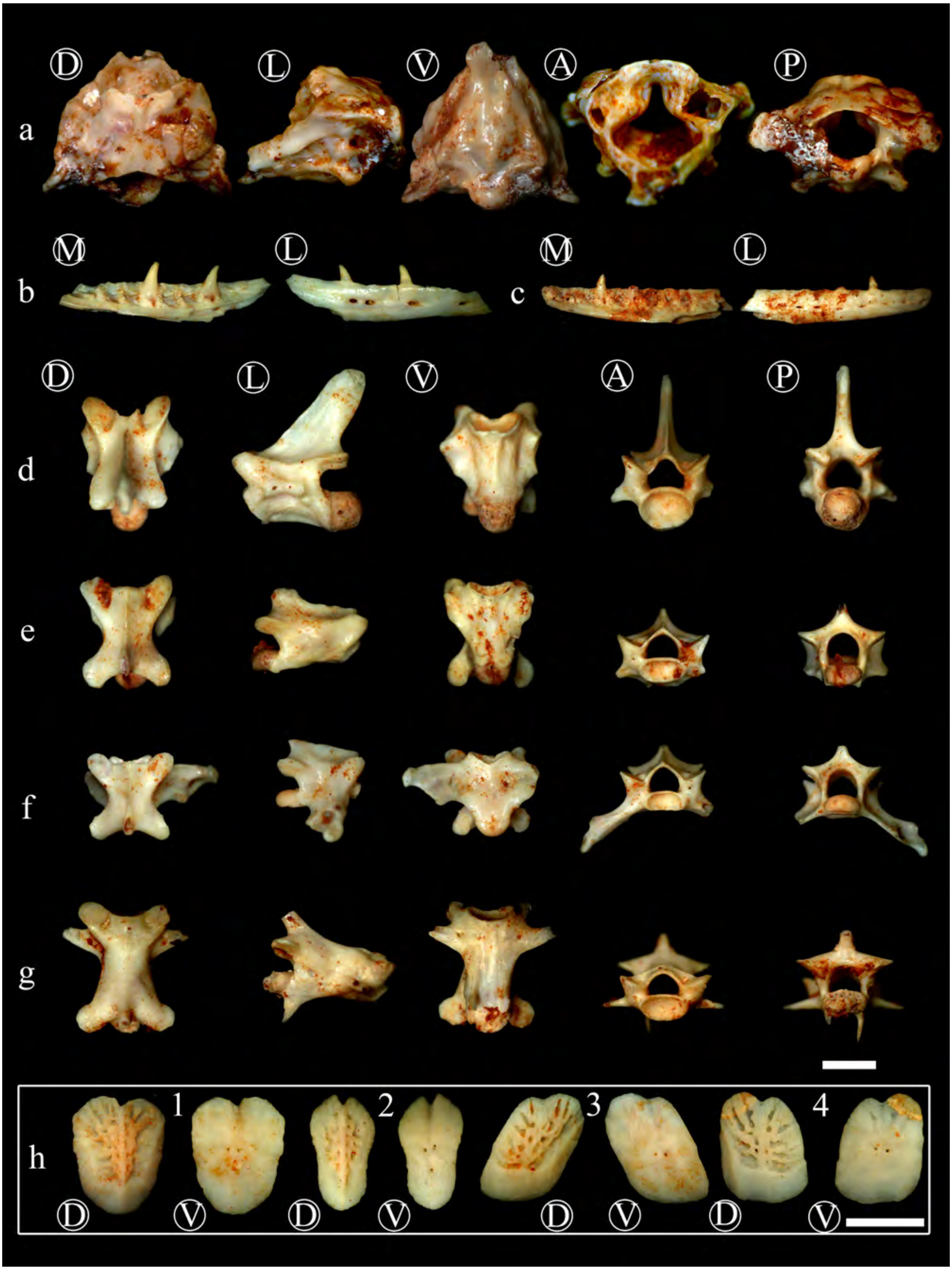


Figura 18: Restes fòssils atribuïdes a ***Dopasia* sp.** de NB-1: (**a**) neurocrani, IMEDEA 103511; (**b** i **c**) dentaris, IMEDEA 103365 i 105650; (**d**) vèrtebra dorsal anterior, IMEDEA 103391; (**e**) vèrtebra dorsal intermedia, IMEDEA 103499; (**f**) vèrtebra sacra, IMEDEA 103063; (**g**) vèrtebra caudal, IMEDEA 103026. A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral. Escala 2 mm.

Subordre AMPHISBAENIA

Primera cita d'aquest grup a l'illa de Mallorca. S'han trobat fins a la data unes 9 vèrtebres dorsals. Es tracta d'unes vèrtebres simples de mida petita (al voltant de 2 mm), ventralment són molt planes i no presenten cresta hemal i dorsalment no tenen cresta neural. Tenen un estrangulament interzigapofisari molt marcat que s'accentua en les vèrtebres més anteriors. No tenen facetes articulars tipus zigosfè/zigantre (Fig. 19).

Figura 19: Vèrtebra dorsal (IMEDEA 105326) atribuïda a un **Amphisbaenia** de NB-1. A, anterior; D, dorsal; L, lateral; P, posterior; V, ventral. Escala 2 mm.

Subordre OPHIDIA

Infraordre SCOLECOPHIDIA

Primera cita del grup a les Illes Balears. D'aquest grup de serps s'han recuperat una desena de vèrtebres dorsals. Igual que les anteriors es tracta de vèrtebres de mida molt reduïda (poc més d'1 mm). Es troben comprimides dorsoventralment, amb una morfologia típica molt simple. Es caracteritzen per presentar un arc neural pla sense espina neural, centrum estret sense cresta hemal, còndil i còtil comprimits dorsoventralment, foràmens subcentrals ben desenvolupats i absència de foràmens paracotilars. Presenten les facetes articular suplementàries zigosfè/zigantre (Fig. 20).

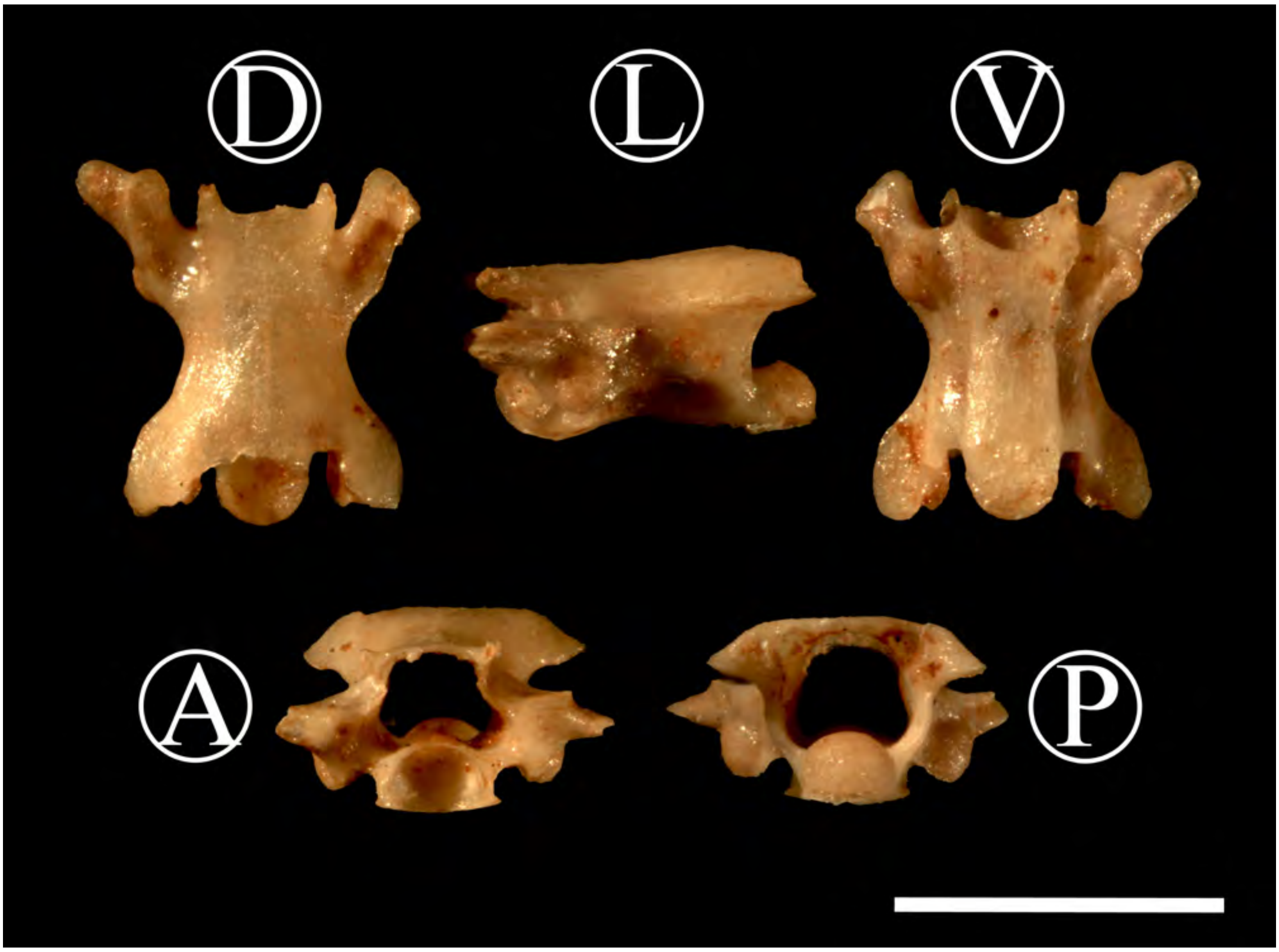


Figura 20: Vèrtebra dorsal (IMEDEA 103180) atribuïda a un **Scolecophidia** de NB-1. A, anterior; D, dorsal; L, lateral; P, posterior; V, ventral. Escala 2 mm.

Infraordre ALETHINOPHIDIA

Família COLUBRIDAE

S'han trobat més de 150 vèrtebres i un dentari d'aquest grup. Una part d'aquestes vèrtebres semblen correspondre a un colúbrid de petites dimensions semblant o pertanyent a *Hispanophis/Coluber planicarinatus* (Fig. 21) i unes altres corresponen a un morfotipus de mida similar a l'anterior però amb trets morfològics diferenciables. Aquestes darreres queden atribuïdes provisionalment a Colubrinae indet. (Fig. 22). El tercer grup de restes fòssils correspon a una espècie de major grandària que concorda amb el morfotipus d'*Elaphe/Coluber* (Fig. 23).

Les vèrtebres de cf. *Hispanophis/C. Planicarinatus* destaquen per la seva petita mida. Presenten un centrum relativament llarg i cilíndric. En les vèrtebres dorsals anteriors, la cresta hemal és pràcticament indistingible, ampla i molt aplanada (Fig. 21 a-e). Mentre que en les vèrtebres dorsals posteriors es troba ben delimitada per solcs profunds (Fig. 21 f-j). Foràmens subcentrals molt petits. Arc neural lleugerament arquejat. Espina neural llarga i molt baixa. Parapòfisis i diapòfisis ben diferenciades. Processos prezigapofisaris curts i amb una terminació arrodonida.

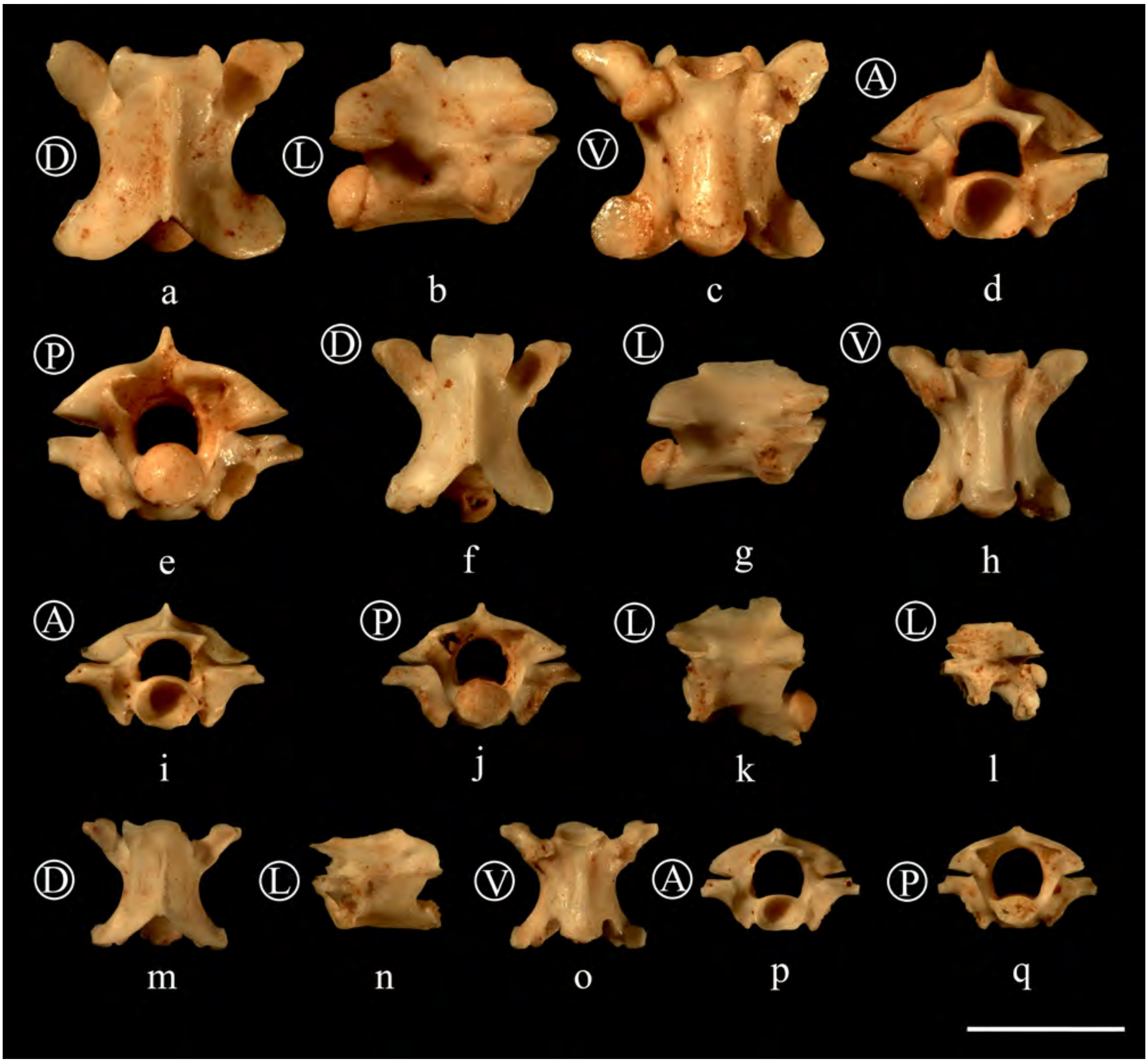


Figura 21: Restes fòssils atribuïdes a **cf. *Hispanophis/ C. Planicarinatus*** de NB-1: (**a-e**) vèrtebra dorsal anterior, IMEDEA 105397; (**f-j**) vèrtebra dorsal posterior, IMEDEA 105554; (**k i l**) vèrtebres caudals, IMEDEA 106450 i 105450; temptativament (**m-p**) vèrtebra dorsal d'individu juvenil, IMEDEA 105512. A, anterior; D, dorsal; L, lateral; P, posterior; V, ventral. Escala 3 mm.

Les altres vèrtebres determinades com Colubrinae indet. difereixen de les anteriors per unes vèrtebres dorsals, tant anteriors com posteriors, amb una cresta hemal més marcada i estreta (Fig. 22 d i e) i processos prezigapofisaris més allargats i amb una terminació lleugerament angulosa. També presenten un centrum relativament llarg i cilíndric. Foràmens subcentrals molt petits. Arc neural lleugerament arquejat. Espina neural llarga i molt baixa. I les parapòfisis i diapòfisis estan menys diferenciades que les de cf. *Hispanophis/C. planicarinatus*. La resta de materials (quadrat, os compost i dentari) queden agrupades en Colubrinae indet., ja que no es pot discernir a quina de les dues formes pertanyen (Fig. 22 a-c).

Figura 22: Restes fòssils atribuïdes a **Colubrinae indet** de NB-1: (**a**) quadrat, IMEDEA 105626; (**b**) os compost, IMEDEA 103309; (**c**) dentari, IMEDEA 105416; (**d**) vèrtebra dorsal anterior, IMEDEA 105563; (**e**) vèrtebra dorsal posterior, IMEDEA 103169. A, anterior; AM, anteromedial; D, dorsal; L, lateral; M, medial; P, posterior; PL, posterolateral; V, ventral. Escala 3 m.

D'altra banda, les vèrtebres dorsals d'*Elaphe*/*Coluber* tenen un centrum relativament curt. La cresta hemal està molt diferenciada. L'arc neural és alt i l'espina neural és més llarga que alta. Els foràmens laterals estan ben marcats. Les parapòfisis i les diapòfisis no estan molt diferenciades i el còtil i el còndil són lleugerament comprimits dorsoventralment. Els processos prezigapofisaris són molt allargats i angulosos.

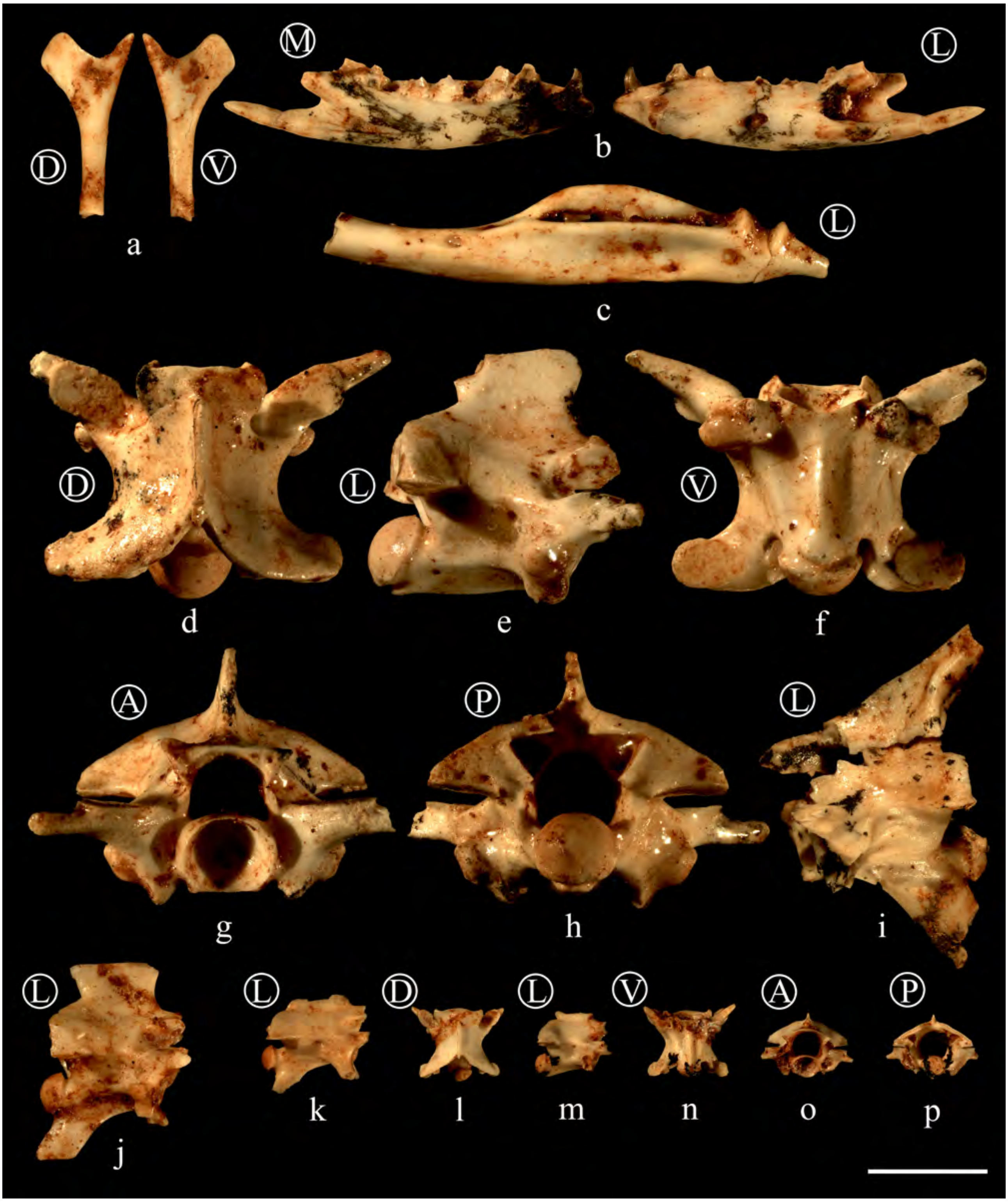


Figura 23: Restes fòssils atribuïdes a un morfotipus ***Elaphe/Coluber*** de NB-1: (**a**) ectopterigoide, IMEDEA 106398; (**b**) dentari, IMEDEA 105343; (**c**) os compost, IMEDEA 106375; (**d-h**) vèrtebra dorsal, IMEDEA 106198; (**i**) vèrtebra cervical anterior, IMEDEA 105413; (**j**) vèrtebra cervical posterior, IMEDEA 105402; (**k**) vèrtebra caudal, IMEDEA 105569; temptativament (**l-p**) vèrtebra dorsal d'individu juvenil, IMEDEA 103353. A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral. Escala 4 mm.

Família VIPERIDAE

En el cas dels escurçons s'han identificat 17 vèrtebres i 1 maxil·lar. La majoria de les vèrtebres són de grans dimensions i poden tenir una alta espina neural. Aquest trets corresponen als membres pertanyents al complex d'escurçons orientals. Inicialment eren atribuïdes a *Vipera* sp., però la recuperació de noves vèrtebres amb elevades espines neurals fa pensar que probablement corresponguin a *Daboia* (Fig. 24).

Les vèrtebres es caracteritzen per presentar una hipapòfisi recta, arcs neurals posteriorment deprimits, crestes neurals més altes que llargues, facetes articulars zigapofisàries inclinades dorsalment, processos parapofisaris direccionats anteroventralment, grans còtils i còndils i un centrum relativament curt. Els maxil·lars es reconeixen per presentar dues grans dents corbes inoculadores de verí amb uns canals ben tancats (condició solenoglifa), que eviten la pèrdua de verí durant la mossegada.

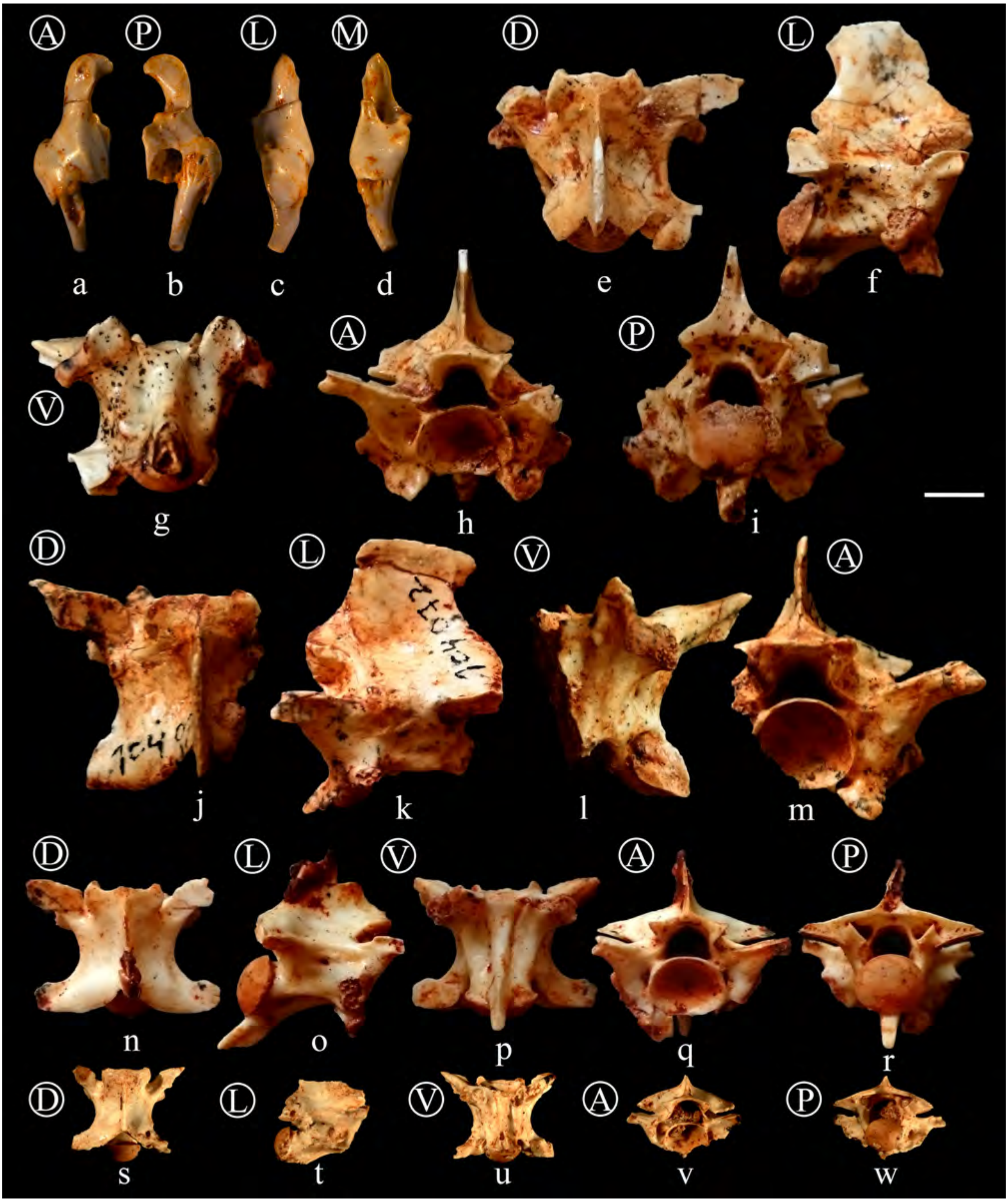


Figura 24: Restes fòssils atribuïdes a **cf. *Daboia* sp.** de NB-1: (**a-d**) maxil·lar, IMEDEA 105983; (**e-i**) vèrtebra dorsal, IMEDEA 103284; (**j-m**) vèrtebra dorsal, IMEDEA 104072; temptativament (**n-r**) vèrtebra dorsal, IMEDEA 105978; temptativament (**s-w**) vèrtebra dorsal d'individu juvenil, IMEDEA 105974. A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral. Escala 4 mm.

2. Els ocells

Les aus són el grup de vertebrats amb menor representació en el registre del jaciment de NB-1. Els resultats obtinguts de l'anàlisi del material paleornitològic s'ha extret (Torres-Roig et al., 2020: annex 1, 2) dels 583 ossos recuperats. Prop del 90% d'aquestes restes són falanges pedals de baix valor taxonòmic. A més, l'estat fragmentari d'una part important del material recuperat impedeix la seva identificació taxonòmica més enllà del nivell genèric. S'han diagnosticat fins a 321 elements per sota del nivell de classe, dels quals 200 han estat identificats a nivell d'ordre i 121 a nivell de gènere. Totes aquestes restes han estat agrupades en almenys deu tàxons diferents: dos Tytonidae, un corresponen a una olibassa gegant, *Tyto* sp. 1, de mida similar a *T. robusta*, i una segona olibassa, *Tyto* sp. 2, de mida similar a *T. sanctialbani*; un Strigidae de petita mida atribuït a *Otus* sp., encara que algunes de les falanges pedals obtingudes només s'inclouen provisionalment en aquest gènere; un Phasianidae atribuït a cf. *Coturnix*; un Charadriiforme indeterminat; i almenys cinc formes diferents de Passeriformes indeterminats. La importància en la recuperació de totes aquestes restes resideix principalment en presència d'aquest conjunt de rapinyares nocturns que ens permet realitzar inferències sobre la formació del dipòsit fossilífer de NB-1.

Fins ara, el registre fòssil de Strigiformes a Mallorca havia estat exclusivament emmarcat dintre del Quaternari i es reconeixien cinc espècies diferents. L'espècie de major mida és *Tyto balearica*, detectada a diferents dipòsits del Pleistocè inicial-mitjà (Mourer-Chauviré et al., 1980). Inicialment es pensava que era una espècie insular endèmica de les Balears, però el descobriment de restes fòssils més antigues en diferents localitats del continent (Península Ibèrica i S de França), han posat en dubte el seu origen insular (Mourer-Chauviré i Sanchez-Marco, 1988). També s'han trobat restes de *Tyto alba* en jaciments del Pleistocè tardà-Holocè (Mourer-Chauviré et al., 1977; McMinn i Alcover, 1992); Otus scops en el Pleistocè mitjà-tardà (Alcover et al., 1981); *Athene noctua* en el Pleistocè tardà (Seguí et al., 1998); i *Athene vallgornerensis*, presumiblement una espècie endèmica de Mallorca del Pleistocè inicial (Guerra et al., 2012).

Degut a l'absència de mamífers carnívors a les illes, les aus de presa solen ocupar el seu nínxol com a principals depredadors dels ecosistemes insulars (Alcover i McMinn, 1994), evolucionant per adaptar-se a les condicions especials que es donen en els medis insulars mitjançant canvis en la mida corporal i les proporcions. Nombrosos autors han destacat el paper dels rapinyaires nocturns com a bioacumuladors de restes de petits vertebrats (Andrews, 1990). Aquest fet les converteix en un dels agents de major potencial en la formació de dipòsits fossilífers, ja que normalment s'empassen la presa sencera i posteriorment regurgiten els ossos presentant pocs danys com a conseqüència del procés digestiu. Entre totes les estrigiformes, *Tyto* és la que produeix les menors modificacions en els ossos de les preses ingerides.

ORDRE STRIGIFORMES

El tret osteològic més característic dels membres d'aquest ordre és la presència d'un arc ossificat al radi, l'arcus origomusculi extensor longus digiti majoris (Bock i McEvery, 1969). El material que en aquest treball fa referència a Tytonidae, difereix de Strigidae en base a la combinació dels següents caràcters osteològics: el coracoide no es troba pneumatitzat; terminació escapular menys voluminosa; facies articularis scapularis, facies articularis sternalis i foramen nervi supracoracoidei proporcionalment més petit; facies articularis humeralis proporcionalment més gran; procés procoracoideu més ample i curt. El fèmur presenta una cresta trocantèrica més vertical; còndils medial i lateral més orientats cap endavant; còndil medial més gran en vista interna, amb el marge cranial que uneix de manera discontinua la diàfisi; epicòndil lateral ample en vista lateral; tubercle localitzat distalment per al M. gastrocnemialis lateralis. L'escàpula té la regió lateral de l'acròmion menys projectat lateralment, mentre que la regió costal de l'acròmion està més desenvolupada; la faceta articularis humeralis té morfologia oval, mentre en Strigidae és més arrodonida; l'acròmion no està pneumatitzat, usual en Strigidae (excepte en *Otus*). El radi presenta un cotyla humeralis més arrodonit; l'extrem distal presenta una concavitat millor definida en el tubercle medial. Les falanges basals del primer i segon dit presenten una longitud molt semblant, mentre que en

Strigidae la primera falange del segon dit té la meitat de la longitud de la falange basal del primer dit; el tarsometatars en Tytonidae no presenta un arcus extensorius (*bonyloop*).

Tytonidae

El material atribuït a *Tyto* sp. 1 (Taula 2) té una mida molt similar a la de *T. robusta* de Gargano, tot i que algunes mesures es troben dins del rang de mida de *T. mourerchauvirae* de Sicília. Alguns trets morfològics (com els caràcters femorals 3 i 9 de Ballmann, 1973) no s'ajusten amb la descripció de *T. robusta*, encara que es desconeix la variabilitat morfològica de *T. robusta* i *Tyto* sp. 1. A més, *Tyto* sp. 1 comparteix alguns caràcters diagnòstics de *T. mourerchauvirae*, però molt menys desenvolupats que en aquesta espècie (adquireix una prominència molt petita a la part tubercular de la línia intermuscularis cranialis i una epífisi distal del fèmur relativament ample). La massa corporal estimada de *Tyto* sp. 1 és d'aproximadament 1200 g en funció del seu diàmetre de diàfisi femoral (Campbell i Marcus, 1992) i, tot i que el trocànter de l'espècimen IMEDEA 106330 està un poc malmès, s'ha estimat una massa corporal d'uns 1360 g a partir de la seva longitud femoral (Olmos et al., 1996).

Material	Nº col·lecció	Nº espècimens	Tàxon
Fèmur	IMEDEA 106330	1	*Tyto* sp. 1
Coracoide	IMEDEA 106331	1	*Tyto* sp. 1
Fragment proximal de radi	IMEDEA 106332	1	*Tyto* sp. 1
Fragment humeral d'escàpula	IMEDEA 106333	1	*Tyto* sp. 1

Taula 2: Llistat de les restes fòssils estudiades que han estat atribuïdes a *Tyto* sp. 1 (Família Tytonidae) de NB-1.

El segon Tytonidae, denominat *Tyto* sp. 2, ha estat identificat per un únic fragment distal d'un radi dret (IMEDEA 107594). Es tracta d'una espècie lleugerament més gran que *Tyto alba* i considerablement més petit que *Tyto robusta*. Encara que no es coneix cap radi de *Tyto sanctialbani*, *Tyto* sp. 2 sembla una olibassa de mida equivalent. La diferència de mida amb *Tyto* sp. 1 podria interpretar-se com a resultat de dimorfisme sexual (així com suggereix Pavia, 2004), però la manca d'un dimorfisme sexual en la mida de *Tyto alba* porta a considerar que les olibasses fòssils de diferents mides poden representar espècies diferents. Les diferències de mida entre el diàmetre de la diàfisi del radi de *Tyto* sp. 1 i el de *Tyto* sp. 2 són considerables (un 26,5% més gran a *Tyto* sp. 1), i com succeeix a diverses illes (e.g., Cuba, Gargano), poden coexistir dues espècies diferents de *Tyto*. En base a això, es suggereix que el radi IMEDEA 107594 pertany a una espècie diferent de *Tyto* sp. 1.

Strigidae

Els fòssils atribuïts a *Otus* sp. constitueixen un total de 28 elements, 22 dels quals corresponen a falanges i la resta a un fragment d'ulna, un fragment d'estèrnum, tres fragments de fèmurs i un fragment de tibiotars (Taula 3). Les mides d'aquest ossos cauen dintre del rang de mides d'*Otus scops* i *Athene noctua*. La discriminació osteològica entre els dos gèneres, en base als elements ossis disponibles, es basa en el següent conjunt de trets morfològics: ulna, cotyla dorsalis no és prominent internament i la seva facies articularis radialis és més profunda i millor definida en *Athene* que en *Otus*; fèmur, la crista trochantericus està més desenvolupada en *Athene* que en *Otus*; tibiotars, la concavitat del tendó és més profunda en *Athene* que en *Otus*, còndils pràcticament paral·lels in *Athene* mentre que en *Otus* el còndil medial està medialment inclinat en el seu extrem distal. A més s'han utilitzat altres criteris morfològics utilitzant *Otus scops* i *Athene* noctua amb els següents elements: estèrnum, el labrum externum sternae té una major projecció en *Athene* que en *Otus*, mentre que *Athene* normalment presenta una petita concavitat en la part ascendent des del costat de la cresta pròxima al labrum en *Otus* és absent. Per tant, els elements llargs i l'estèrnum del petit estrígid de NB-1 s'ajusten més a *Otus* que a *Athene*.

Material	Nº col·lecció	Nº espècimens	Tàxon
Fragment distal de tibiotars	IMEDEA 106998	1	*Otus* sp.
Falange I dit 3	IMEDEA 106999	1	*Otus* sp.
Fragment proximal d'ulna	IMEDEA 107000	1	*Otus* sp.
Falange pedal	IMEDEA 107620	1	*Otus* sp.
Falanges pedals	IMEDEA 107625-107633	9	*Otus* sp.
Falange III dit 4	IMEDEA 107634	1	*Otus* sp.
Falange IV dit 3	IMEDEA 107635	1	*Otus* sp.
Falange I dit 1	IMEDEA 107636	1	*Otus* sp.
Falange III dit 3	IMEDEA 107637	1	*Otus* sp.
Falange VI dit 4	IMEDEA 107638	1	*Otus* sp.
Falange II dit 2	IMEDEA 107639	1	*Otus* sp.
Falanges pedals	IMEDEA 107640-107642	3	*Otus* sp.
Fragment d'estèrnum	IMEDEA 107643	1	*Otus* sp.
Falange I dit 2	IMEDEA 107644	1	*Otus* sp.
Fragment proximal de fèmur	IMEDEA 107645	1	*Otus* sp.
Fragment distal de fèmur	IMEDEA 107646	1	*Otus* sp.
Fragment proximal de fèmur	IMEDEA 107647	1	*Otus* sp.
Falange pedal	IMEDEA 107648	1	*Otus* sp.

Taula 3: Llistat de les restes fòssils estudiades que han estat atribuïdes a *Otus* sp. (Família Strigidae) de NB-1.

Pel que fa al conjunt de falanges totes presenten una robustesa intermèdia entre *Athene* i *Otus*. No obstant, presenten trets morfològics semblants als observats en *Otus* (falange I 1, I 3, terminal IV 3 i altres terminals), en *Athene* (falanges II 2, III 3, IV 4) o fins i tot una morfologia intermèdia (falange I 2, III 4). La falange I 1 presenta un tuberculum flexorum poc desenvolupat i un marge ventral continu entre el caput phalangis i el tuberculum flexorum. La falange I 2 no presenta un tuberculum extensorium medial i el tuberculum flexorum lateral és semblant al medial. La falange I 3 té un tuberculum ben desenvolupat al costat lateral del caput phalangis. La falange II 2, III 3 i IV 4 estan lleugerament arquejades i el caput phalangis es troba aixecat dorsalment. La falange IV 3 i la resta de terminals presenten un tuberculum extensorium orientat dorsocaudalment.

ORDRE GALLIFORMES, CHARADRIFORMES I PASSERIFORMES

Els restants espècimens obtinguts del jaciment de NB-1 pertanyen a almenys a dos individus d'un Galliformes de mida petita representats per 10 elements majoritàriament fragmentaris, un fragment proximal de carpometacarp d'un Charadriformes i uns 198 elements ossis que es poden atribuir a un màxim de cinc espècies diferents de Passeriformes (Taula 4). El Galliformes correspon a un Phasianidae que ha estat atribuït a cf. *Coturnix*. La seva condició fragmentària i la manca de revisió general de guàtleres del Mio-Pliocè dificulten qualsevol altra anàlisi. La premaxil·la és característicament curta i lleugerament corbada. L'extrem proximal de l'húmer presenta una fossa pneumotricipitalis secundària ben desenvolupada. El fèmur és allargat i característicament corbat. Pel que fa al Charadriformes, la morfologia general d'aquest únic fragment de carpometacarp permet registrar la presència d'una espècie de mida similar a la de *Philomachus pugnax*. I l'estat fragmentari de la majoria dels materials atribuïts a Passeriformes impedeix una identificació més enllà del nivell d'ordre.

Material	Nº col·lecció	Nº espècimens	Tàxon
Fèmur	IMEDEA 107595	1	cf. *Coturnix*
Fragment proximal d'húmer	IMEDEA 107596	1	cf. *Coturnix*
Fragment proximal de fèmur	IMEDEA 107596	1	cf. *Coturnix*
Fragment proximal de fèmur	IMEDEA 107597	1	cf. *Coturnix*
Fragment d'estèrnum	IMEDEA 107598	1	cf. *Coturnix*
Fragment distal de tarsometatars	IMEDEA 107610	1	cf. *Coturnix*
Fragment proximal de tarsometatars	IMEDEA 107611	1	cf. *Coturnix*
Premaxil·la	IMEDEA 107612	1	cf. *Coturnix*
Fragments de pelvis	IMEDEA 107621-107622	2	cf. *Coturnix*
Fragment proximal de carpometacarp	IMEDEA 107650	1	Charadriformes
Fragment distal de tarsometatars	IMEDEA 107601-107603	3	Passeriformes
Ulna	IMEDEA 107604	1	Passeriformes
Carpometacarp	IMEDEA 107605	1	Passeriformes
Fragment proximal de carpometacarp	IMEDEA 107606	1	Passeriformes
Fragment proximal d'húmer	IMEDEA 107607	1	Passeriformes
Fragments distals d'húmers	IMEDEA 107608-107609	2	Passeriformes
Fragments distals de tibiotarsos	IMEDEA 107613-107614	1	Passeriformes
Fragment proximal de carpometacarp	IMEDEA 107615	1	Passeriformes
Falanges pedals terminals	IMEDEA 107624	14	Passeriformes
Falanges pedals	IMEDEA 107649	173	Passeriformes

Taula 4: Llistat de les restes fòssils estudiades que han estat atribuïdes a cf. *Coturnix* (Ordre Galliformes, Família Phasianidae), Charadriformes i Passeriformes de NB-1.

3. Mamífers: els rosegadors

En aquest apartat s'aporten els resultats obtinguts de l'anàlisi dels rosegadors del jaciment de NB-1 que s'inclouen al present Programa de Doctorat (Torres-Roig et al., 2019 i Bover et al., 2020: annex 1, 1 i 4, respectivament) i que complementen les dades publicades anteriorment amb la descripció del cricètid *A. darderi* (Torres-Roig et al, 2019: annex 2, 10). Donat que els rosegadors són l'ordre faunístics més ben representats al jaciment i són els tàxons amb un major valor biostratigràfic i biogeogràfic, es va optar en centrar els estudis en aquest grup. Entre els mamífers queden pendents d'anàlisi el bòvid (molt mal representat al jaciment), el lepòrid (representat essencialment per elements d'exemplars juvenils) i el sorícid, pel que no quedaran inclosos en la present Tesi Doctoral.

Les espècies fòssils de rosegadors descrites al continent s'han definit predominantment en base a la morfologia dentaria. Tot i que es disposa d'una bona representació de material postcranial dels rosegadors de NB-1, tant sols s'ha utilitzat el material cranial en la seva descripció, ja que és el material més facilment comparable amb els tàxons continentals, tant fòssils com actuals, degut a la falta de material de comparació. Per tant, la descripció dels elements postcranials dels diferents tàxons resta pendent d'estudi. El material postcranial, inclòs el del lepòrid i del sorícid, únicament ha estat utilitzat per realitzar les estimes de la massa corporal.

3.1. Gliridae: dades preliminars

Actualment, els lirons (Gliridae) inclouen tres subfamílies (Graphiurinae, Glirinae i Leithiinae) que tant sols estan integrades per nou gèneres i aproximadament una trentena d'espècies (Holden et al., 2016). En el registre fòssil s'han reconegut fins a set subfamílies, prop de 40 gèneres i més de 170 espècies

(Daams i de Bruijn, 1995; Freudenthal i Martín-Suárez, 2007). La distribució geogràfica dels Gliridae (tant d'espècies actuals com fòssils) es troba limitada a Europa, Àsia i Àfrica. La diversificació d'aquesta família de rosegadors va començar a l'Eocè inicial i va culminar al Miocè mitjà d'Europa, assolint la diversitat màxima d'espècies al Miocè inicial (Freudenthal i Martín-Suárez, 2013). Posteriorment, des del Miocè tardà fins a l'actualitat, els glírids han estat representats per uns pocs gèneres, exceptuant les formes insulars (Rössner i Heissig, 1999).

La sistemàtica dels glírids fòssils es basa predominantment en la morfologia dels patrons dentals: nombre i posició de les crestes, connexions entre aquestes, forma de la superfície oclusal, posició i nombre d'arrels, etc (Daams i de Bruijn, 1995). La fórmula dental que presenten els glírids és 1013/1013, excepte *Selevinia* que no presenta premolars (Hennekam et al., 2020).

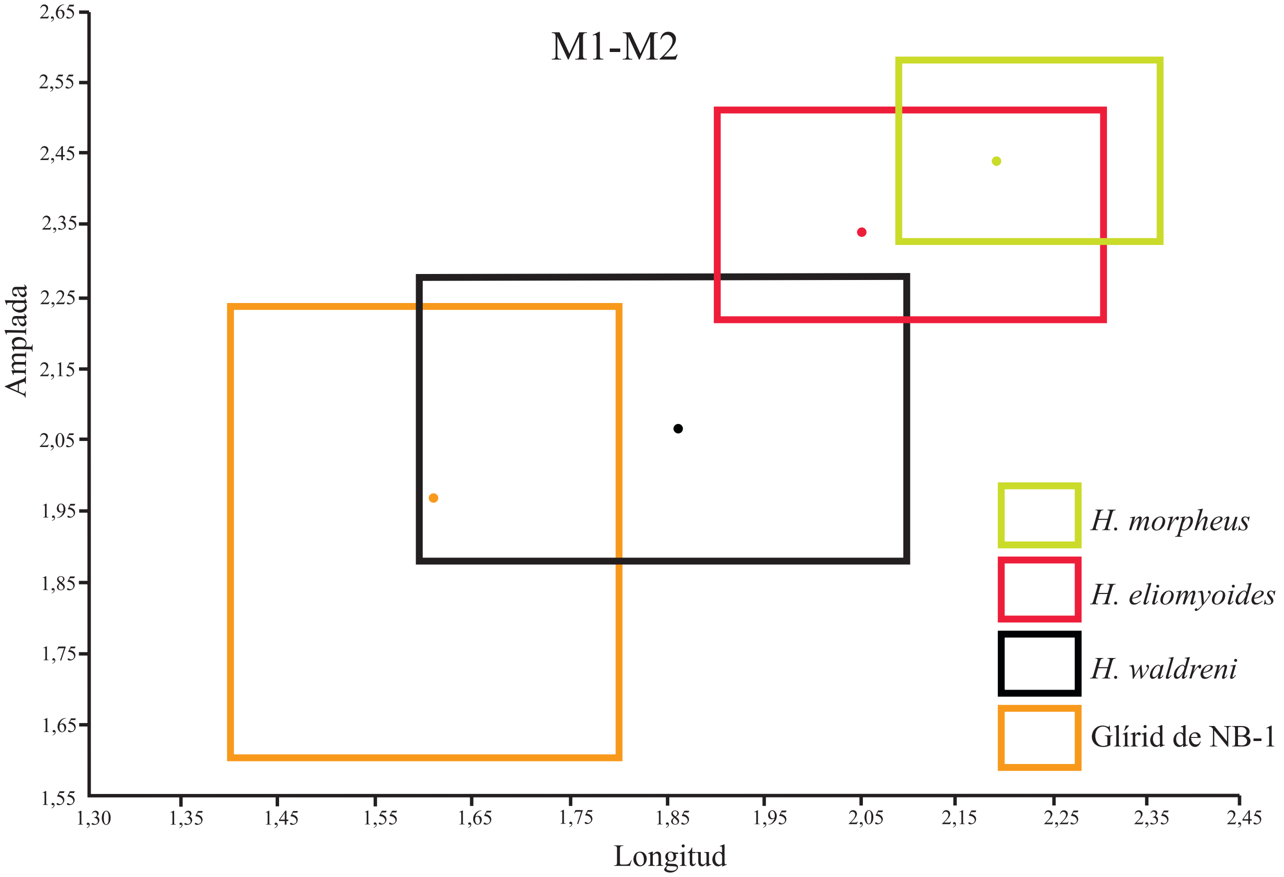
El gènere extingit *Hypnomys* és l'únic rosegador de la fauna de *Myotragus* que va viure a l'illa de Mallorca fins l'arribada dels humans. Es tracta d'un glírid que pertany a la subfamília Leithiinae, estretament relacionat amb el gènere *Eliomys*, que s'ha confirmat que és el gènere vivent més proper (Bover et al., 2020). Al jaciment de NB-1 s'han recuperat més de 2700 restes fòssils, aproximadament el 32% corresponen a materials cranials. Aquest tàxon és el representant més antic que es coneix a l'actualitat de la línia filètica d'*Hypnomys*, pendent d'un estudi més ampli. A aquesta Tesi Doctoral es presenten les següents dades preliminars.

El glírid de NB-1 és considerablement menor que totes les espècies descrites d'*Hypnomys* (Taules 5 i 6). El rang de les seves mides es veu solapat amb els valors inferiors del rang de variabilitat d'*H. waldreni*, però tot i així, és evident la diferència de mida entre ambdós tàxons (Taula 6). D'altra banda, s'observa que aquest nou glírid és clarament major que els glírids fòssils de l'Europa occidental *E. truci* i *E. yevesi* del Miocè tardà-Pliocè, i presenta un important solapament de mides amb *E. intermedius* del Pliocè-Pleistocè (veure Fig. 3 de Mansino et al., 2015).

	Longitud			n	**Amplada**		
	mín.	$\bar{x}$	màx.		mín.	$\bar{x}$	màx.
dp4	1,05	1,13	1,26	11	0,92	0,99	1,12
p4	1,23	1,44	1,58	63/62	1,15	1,33	1,47
m1	1,47	1,75	1,88	87/89	1,55	1,85	2,04
m2	1,57	1,69	1,79	75/79	1,75	1,92	2,13
m3	1,17	1,40	1,55	82/84	1,42	1,54	1,66
dP4	1,15	1,24	1,33	13	1,53	1,60	1,72
P4	1,13	1,25	1,40	59/58	1,43	1,62	1,78
M1	1,40	1,65	1,80	73/76	1,61	1,90	2,10
M2	1,46	1,60	1,73	71/70	1,85	2,04	2,24
M3	1,00	1,28	1,37	70	1,30	1,67	1,81

Taula 5: Mesures dentàries del glírid de NB-1.

M1-M2								
Tàxon	Longitud			n	Amplada			Ref.
	mín.	$\bar{X}$	màx.		mín.	$\bar{X}$	màx.	
H. morpheus	2,08	2,19	2,36	22	2,33	2,44	2,57	Bruijn (1966)
H. eliomyoides	1,89	2,05	2,31	15/13	2,22	2,34	2,51	Agustí (1980)
H. waldreni	1,60	1,86	2,10	19	1,87	2,06	2,27	Reumer (1979)
Glírid NB-1	1,40	1,62	1,80	144	1,61	1,97	2,24	



Taula 6: Comparativa de les mesures (en mm) de la longitud i de l'amplada dels M1-M2 del glírid de NB-1 amb *Hypnomys*. *Hypnomys morpheus* de localitat desconeguda de Mallorca (de Bruijn, 1966); *H. eliomyoides* del Barranc de Binigaus, Menorca (Agustí, 1980) i *H. waldreni* del Cap Farrutx, Mallorca (Reumer, 1979). Els punts corresponen a les mitjanes (×).

Morfològicament, el glírid de NB-1 mostra un patró dental inesperadament complex (Fig. 25). Fins ara, majoritàriament es proposava que *Hypnomys* descendia de les espècies fòssils d'*Eliomys* (per exemple, Agustí, 1980, 1986; Alcover i Agustí, 1985; Bate, 1918; Zammit-Maempel i de Bruijn, 1982) i es va suggerir que els membres del llinatge d'*Hypnomys* van evolucionar augmentant la complexitat del patró dental a través del temps a partir d'un ancestre amb un patró dental relativament senzill, com és el d'*Eliomys*. No obstant, Reumer (1982) va observar una tendència contrària cap a una simplificació del patró dental en el llinatge d'*Hypnomys* (des d'*H. waldreni* a *H. morpheus*). La morfologia dentària del glírid de NB-1 és congruent amb tendència observada per Reumer (1982) i posa de manifest que *Hypnomys* descendeix d'una forma amb un patró dental més complexe que el que presenta *Eliomys*.

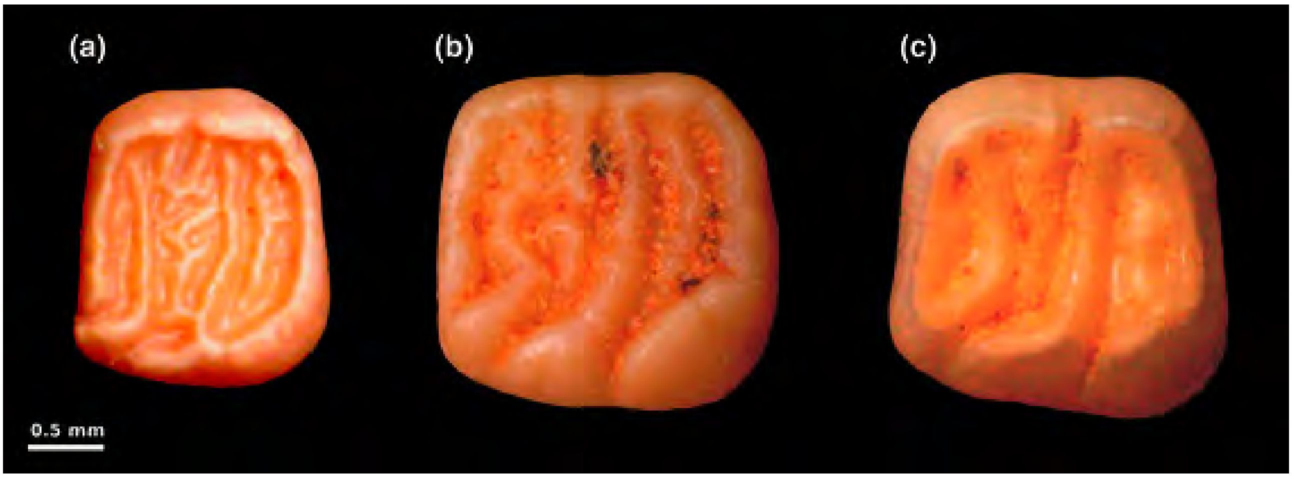


Figura 25: Disminució en el grau de complexitat del patró dental en el llinatge filètic d'*Hypnomys* des de l'element més antic fins al més modern utilitzant m1-m2. (a) glírid de NB-1, Zancleà (IMEDEA 107193); (b) *H. onicensis*, Pleistocè inicial; (c) *H. morpheus*, Pleistocè mitjà-Holocè.

3.2. Muridae

Actualment és una de les famílies de mamífers més diversificada i de major distribució geogràfica. Es tracta de rosegadors miomorf esciurognats amb una fórmula dentària 1003/1003. El molars superiors es caracteritzen per presentar una filera extra de cúspides linguals plenament funcionals; és a dir, els M1 contenen fins a nou cúspides principals distribuïdes en tres fileres. En el molars inferiors pot donar-se un tercera filera de cúspides labials, però són baixes pel que el seu ús es dona en estadis avançats de desgast de les cúspides principals.

Durant l'Oligocè i gran part del Miocè europeu les faunes de rosegadors eren dominades pels cricètids, però al Miocè tardà els múrids es convertiren en els rosegadors predominants dels ecosistemes terrestres. Per aquesta raó també són considerats un grup fonamental en la biostratigrafia del Miocè tardà i del Pliocè, oferint dades importants sobre els intercanvis faunístics entre Àsia, Europa i Àfrica (Rössner i Heissig, 1999).

Algunes de les característiques diagnostiques més importants en la determinació de les espècies a partir de la seva dentició són: la mida absoluta, ràtio longitud/amplada, presència/absència de crestes o cúspides addicionals, nombre d'arrels, grau d'hipsodòncia, grau d'estefanodòncia, presència absència de tma, nombre i morfologia de les cúspides labials accessòries dels molars inferiors, etc.

Al jaciment de NB-1 s'han recuperat unes 172 restes fòssils d'un múrid que no havia esta detectat a cap altre jaciment de les Balears. D'aquestes unes 85 són restes dentàries, mandibulars i maxil·lars. El seu estudi permet establir que es tracta d'una espècie insular endèmica de mida mitjana del gènere *Paraethomys*, que s'ha descrit com *P. balearicus*. La seva atribució a *Paraethomys* es basa en la següent combinació de caràcters: presència d'un illot d'esmalt (formant una fosseta) entre l'anterocònid i el segon parell de cúspides dels m1s, absència de la cúspide anterolabial als m3s, absència de t7 als molars superiors, reducció del t9 en els M2s, presència d'esperons posteriors als tubercles anteriors, i formació d'un illot d'esmalt mitjançant la unió dels tubercles als M3s.

L'arribada del gènere *Paraethomys* al continent europeu es va donar a través de la Península Ibèrica amb *P. meini* al Turolià superior, fa aproximadament 6,2 Ma, uns 0,25 Ma abans de l'inici de la Crisi de salinitat del Messinià. Aquest gènere és considerat un dels tàxons més representatius de l'intercanvi faunístic entre Europa i Àfrica (Agustí et al., 2006; Gibert et al., 2013; García-Alix et al., 2016). A Europa el gènere arriba fins al final del Ruscinià diversificant-se i amb una tendència a l'augment de la mida (*P. belzemensis*, *P. abaigari* i *P. jaegeri*). En alguns jaciments paleontològics del Pliocè de la Península Ibèrica s'han donat la coexistència de dues formes de *Paraethomys*: una de mida petita, corresponent a *P. meini* i una altra de mida més gran, pertanyent a *P. aff. abaigari* - *P. abaigari* - *P. aff. jaegeri* - *P. jaegeri* (Mein et al. 1990). Piñero i Agustí (2019) van proposar que el llinatge filètic *P. aff. abaigari* - *P. abaigari* - *P. jaegeri* va derivar d'un *P. meini* primitiu, marcat tant per un augment progressiu de la mida com del grau d'estefanodòncia al llarg del Pliocè, mentre que paral·lelament va evolucionar un llinatge més conservador de *P. meini*. *Paraethomys belmezensis* probablement també és una espècie derivada de *P. meini* (Castillo Ruiz, 1992), és lleugerament més gran que aquest i clarament més petit que *P. abaigari*. A més, sembla ser que antigues poblacions de *Paraethomys* de la Península Ibèrica varen donar lloc a una espècie africana al Miocè superior, *P. lissasfensis*, una espècie amb una mida lleugerament superior a la de *P. meini* (Geraads 1998).

Els molars de *P. balearicus* són relativament hipsodonts. Els molars inferiors es caracteritzen per la presència d'un cíngol labial ben desenvolupat. Els m1s i m2s tenen unes cúspides labials accessòries grans i altes, que recorden el patró d'*Apodemus*. A més, els m1s i alguns m2s presenten una fosseta entre l'hipocònid i el c1 com a resultat de la gran alçada del cíngol labial i de les cúspides labials accessòries. Els m1s presenten un cíngol anterior, inexistent o poc freqüent en el gènere, i en alguns casos un petit tma. Els M1s i M2s poden presentar un esperó posterior en el t1 i el t3 dirigits cap a les interseccions t4–t5 i t5–t6, respectivament. Les connexions entre el t1 i el t2, així com entre el t2 i el t3, estan ben desenvolupades als M1s, i el t4 contacta basalment amb el t8. En rares ocasions, aquest molar presenta una petita cúspide addicional entre el t1 i el t4. Els M2s tenen un esperó posterior sobre el t3 dirigit cap a la intersecció t5-t6 o cap al t6. Alguns exemplars tenen un t9 que tendeix a individualitzar-se i un t12 reduït. A més, alguns exemplars tenen una cresta anterior inusual formada per la connexió entre el t1 i el t3 (Fig. 26).

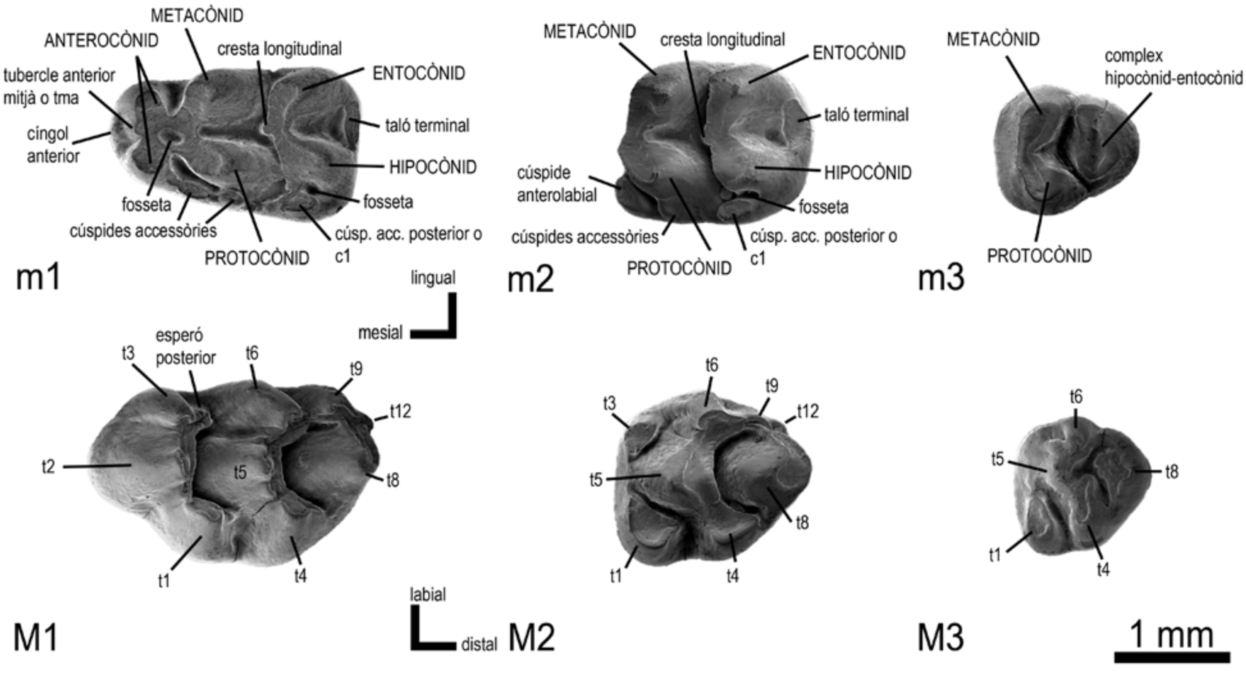


Figura 26: Elements anatòmics dels molars inferiors (m1, m2, m3) i superiors (M1, M2, M3) utilitzats en la descripció de *P. balearicus*.

Paraethomys balearicus presenta una mida mitjana superior a la de *P. meini*, *P. belmezensis* i *P. lissasfensis*, similar a la forma definida com *P. aff. abaigari*, i inferior a la de *P. abaigari* i *P. jaegeri*. Els molars de *P. balearicus* tenen un major grau d'hipsodòncia i presenten un major desenvolupament de les connexions entre les cúspides dels molars superiors que *P. meini* i presenta. *Paraethomys* aff. *abaigari* també presenta un menor grau en la hipsodòncia que *P. balearicus*, manca d'un cíngol anterior als m1s, manca d'una fosseta entre l'hipocònid i el c1, presenta una cresta longitudinal més desenvolupada i una connexió més ampla entre el t6 i el t9 en els M1s. *Paraethomys balearicus* es distingeix morfològicament de *P. abaigari* i *P. jaegeri* pel menor grau de desenvolupament de l'estefanodòncia, una estreta connexió entre el t6 i el t9 dels M1s, M2s que presenten un t3 amb un esperó posterior dirigit cap a la intersecció t5-t6, un t9 ocasionalment prominent i alguns espècimens presenten un t12 poc marcat. *Paraethomys belmezensis* presenta un tma ben desenvolupat connectat al lòbul lingual de l'anterocònid, els M1s tenen un t3 petit unit al t2 i un t6 separat del t9, el M2 no té t3 o t9 i presenta un t8 aïllat. En *P. lissasfensis* el t9 és absent als M2s i presenta una vall profunda entre el t2 i el t3 als M1s.

Algunes de les característiques morfològiques observades en *P. balearicus* són coincidents amb les poblacions antigues de *P. meini*. Així com *P. balearicus* presenta un esperó posterior sobre el t1 i un altre més marcat sobre el t3, en les poblacions de *P. meini* del Turolià tardà de la Conca de Granada és dona la mateixa morfologia. La connexió entre el t4 i el t8 dels M1s és baixa en *P. balearicus* i en *P. meini*, mentre en *P.* aff. *abaigari* i *P. abaigari* aquesta cresta és més alta. La connexió entre el t6 i el t9 dels M1s és estreta en *P. balearicus* i en les poblacions antigues de *P. meini*, mentre és més ample en *P.* aff. *abaigari* i *P. abaigari*. *Paraethomys balearicus* pot presentar un t9 prominent i ocasionalment un t12 reduït en els M2s, així com els espècimens de *P. meini* dels jaciments més antics de la Conca de Granada.

Per tant, d'acord amb les dades disponibles *P. balearicus* és una espècie relacionada amb les poblacions de *P. meini* del Turolià tardà ibèric. Aquesta espècie constitueix la segona evidència que permet relacionar l'origen de la fauna de *Myotragus* amb la MSC i representa el primer mamífer neogen registrat a les Gimnèsies d'origen africà dispersat a través del Sistema Bètic. En termes generals, el seu aïllament a Mallorca es va traduir en un lleuger augment de la mida i del grau d'hipsodòncia.

CAPÍTOL 6. Nou component de la paleofauna de vertebrats terrestres des Pouàs i Ca na Reia.

1. L'escurçó nan d'Eivissa

La subfamília Viperinae engloba els veritables escurçons actualment distribuïts per Àsia, Àfrica i Europa, i que comprèn fins a 102 espècies i 13 gèneres existents a l'actualitat (Phelps, 2010). El registre fòssil de viperins a Europa és extens i s'inicia a començaments del Miocè, aproximadament entre 23,8 i 22,8 Ma (Szyndlar i Rage, 2002). En canvi, els viperins són escassos al registre fòssil de les illes mediterrànies, on normalment han estat detectats a partir de vèrtebres aïllades, que sovint desafien una assignació taxonòmica precisa. En conseqüència, la diversitat i la història evolutiva dels escurçons insulars del mediterrani són poc coneguts. La identificació de llinatges d'escurçons autòctons respecte aquells que potencialment han estat translocats pels humans és fonamental per entendre el conjunt de la fauna d'escatosos de les illes mediterrànies i els orígens dels llinatges insulars.

Fins a la data, el registre fòssil balear d'ofidis es limitava al Pliocè/Pleistocè inicial de les Gimnèsies, amb l'aparent absència d'aquest grup a l'arxipèlag pitiús, una peculiaritat zoològica àmpliament acceptada (e.g., Boscá, 1883; Compte Sart, 1966; Hinckley et al., 2017). Les primeres restes d'escurçons fòssils de les Balears es varen detectar a Menorca amb la descripció de *V. natiensis* i *Vipera* sp. a uns de dipòsits del Pliocè, i d'un vipèrid indeterminat a un jaciment del Miocè mitjà (Bailon et al., 2002). A Mallorca, el jaciment de CdR proporcionà dues vèrtebres d'un gran vipèrid atribuït al Complexe Oriental d'Escurçons (OVC en les seves sigles angleses), altres vèrtebres petites atribuïdes a cf. *V. natiensis*, i possiblement un petit escurçó detectat al Crull de Cap Farrutx que estaria hipotèticament relacionat amb *V. natiensis* (Bailon et al., 2010; Bover et al., 2014). D'altra banda, a NB-1 sols s'han detectat restes d'un gran escurçó atribuïble l'OVC (Bover et al., 2014; Torres et al., 2014: annex 2, 5).

A la present Tesi s'inclou l'estudi de les restes d'un escurçó fòssil provinent dels nivells del Pleistocè superior–Holocè des Pouàs i del jaciment del Pleistocè inicial de la Cova de ca na Reia a l'illa d'Eivissa (Torres-Roig et al., 2020: annex 1, 3). Es presenta la descripció morfològica dels materials detectats i s'aporten dades genètiques mitocondrials obtingudes a partir de vèrtebres des Pouàs (quadrícula A2: nivell -110/-130) amb una edat radiocarbònica calibrada situada entre 17.620-17.320 anys BC. Aquestes dades han permès establir amb precisió la seva identitat taxonòmica, identificar la seva regió d'origen continental, així com el seu possible moment de colonització.

S'han recuperat al voltant de 6.000 vèrtebres procedents de diferents nivells estratigràfics des Pouàs, però per a la descripció s'han seleccionat fins a 45 exemplars, que inclouen 33 vèrtebres dorsals i 12 vèrtebres cervicals, seleccionades pels seu millor grau de conservació. També s'han obtingut i estudiat un fragment de pterigoide i 10 ossos compostos. A partir d'un conjunt de vèrtebres dorsals completes (incloses les vèrtebres més grans disponibles) s'ha estimat una longitud total mitjana de 36 cm (29-44 cm, N=18).

Les dades genètiques presentades suggereix que l'escurçó nan d'Eivissan va divergir de poblacions del llevant peninsular del clade CNS (Central-North-South clade, en el sentit de Martínez-Freiría et al., 2020) de *V. latastei* fa aproximadament 1 Ma (0,97 Ma; 95% HPD = 0,67-1,31 Ma). Aquestes dades ens permeten concloure que els avantpassats de l'escurçó nan d'Eivissa van arribar a la illa fa entre 1,31 Ma (límit superior de l'edat de separació amb el clade CNS) i c. 30.000 (primera aparició al registre fòssil a es Pouàs). Aquest rang de dates suggereix que la colonització de l'illa es va produir mitjançant un esdeveniment de dispersió ultramarina.

La combinació de caràcters morfològics ha permès caracteritzar l'escurçó nan d'Eivissa com una subespècie endèmica que ha estat denominada *V. l. ebusitana*. Els trets diagnòstics característics d'aquest escurçó inclouen: una mida més petita que la de les poblacions ibèriques de *V. latastei* i similar a la de les poblacions de *V. latastei*/*monticola* de l'Atles; el còtil i sobretot el còndil de les vèrtebres dorsals, són característicament arrodonits; el diàmetre del còndil és molt similar al del canal neural i proporcionalment més petit que el de les poblacions continentals de *V. latastei*; la diapòfisi és prominent i subesfèrica; la carena subcentral es troba poc desenvolupada; en vista dorsal, el zigosfè trilobular presenta un lòbul central amb la mateixa alçada (o lleugerament superior) que els laterals; els processos prezigapofisaris són aguts i predominantment curts; les facetes articulars del zigantre són parcialment visibles com dues petites puntes en vistes dorsal i ventral; el pterigoide (essencialment la branca anterior) és proporcionalment curta i ample i presenta una dentició compactada; l'os compost té una cresta prearticular vertical i rectilínia (Fig. 27 A-C).

La vèrtebra caudal posterior (Fig. 27 D, IMEDEA 106848) d'ofidi obtinguda a la Cova de ca na Reia no es troba en molt bon estat de conservació. Només es conserva una porció de la cresta neural, una part de la prezigapòfisi esquerra, una porció petita de les postzigapòfisis i la base de l'espina neural, mentre que el marge anterior del zigosfè es troba desgastat. El còtil, el còndil i les pleurapòfisis també estan totalment deteriorades. La longitud total d'aquesta vèrtebra fragmentada és d'1,92 mm. En vista anterior, la superfície dorsal del zigosfè és convexa. En vista posterior, l'arc neural està moderadament aplanat. L'espina neural és considerablement gruixuda i més llarga que alta. Les hemapòfisis estan clarament individualitzades a la meitat posterior del centrum i convergeixen anteriorment. Tot i que les hemapòfisis són incompletes, l'esquerra està clarament incurvada, és a dir, la concavitat es troba al costat interior.

El mal estat de conservació de la vèrtebra caudal del dipòsit Cova de ca na Reia impedeix determinar amb precisió la seva identitat taxonòmica. En conseqüència, la seva atribució a *Vipera* és només provisional i la designam com a cf. *Vipera* en base a la curvatura de les hemapòfisis. Si aquesta vèrtebra pertany en realitat a l'avantpassat de *V. l. ebusitana*, la seva presència en la Cova de Ca na Reia (en combinació amb la datació molecular de la separació l'escurçó nan d'Eivissa dels seus parents continentals) restringiria l'edat d'aquest dipòsit a el calabrià, mentre que anteriorment s'atribuïa provisionalment al Gelasià/Calabrià segons la fauna malacològica associada.

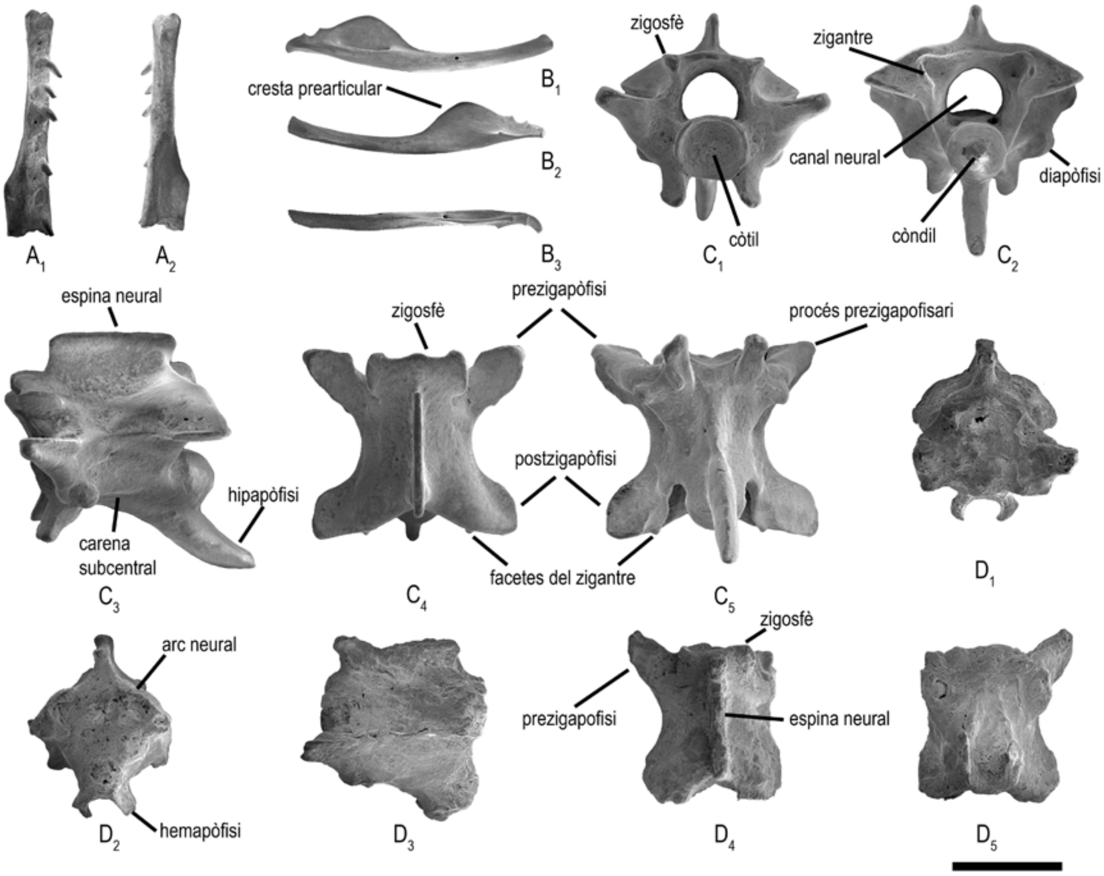


Figura 27: Elements ossis de *Vipera latastei ebusitana* (A: pterigoide, IMEDEA 106589; B: os compost, IMEDEA 106831; C: vèrtebra dorsal, IMEDEA 106587/holotipus) recuperats des Pouàs i vèrtebra caudal de cf. *Vipera* de la Cova de Ca na Reia (D, IMEDEA 106848). Vista anterior (C1 i D1), vista posterior (C2 i D2), vistal lateral (B1, C3 i D3), vista dorsal (A2, B3, C4 i D4), vista ventral (A1, C5 i D5) i vista medial (B2). Escala 2 mm.

El nanisme de *V. l. ebusitana* probablement està relacionat amb les condicions d'insularitat, com ara la mida de les preses disponibles. La dieta dels exemplars adults de *V. latastei* continentals es basa principalment en petits mamífers, mentre que els juvenils depreden sobre sargantanes (Martínez-Freiría et al., 2014). De manera similar, *V. l. monticola* (Saint-Girons, 1980; Freitas et al., 2018) i *V. aspis* de l'illa de Montecristo (Luiselli et al., 2015), pel seu aïllament geogràfic, els adults presenten una dieta restringida a sargantanes. La mida petita de l'escuró nan d'Eivissa pot estar relacionada amb una oferta alimentària basada essencialment en sargantanes i invertebrats.

L'evolució de la mida del cos de les serps insulars ha estat analitzada per molts autors. Case (1978) va trobar una tendència general - amb algunes excepcions - cap al nanisme de les serps a les illes, mentre que Boback (2003) i Boback i Guyer (2003) van descriure una tendència evolutiva cap al gigantisme en els colúbrids i cap al nanisme en els vipèrids. Aquest darrers documentats actualment per nou espècies de *Crotalus*, una espècie de *Bothrops* i dues espècies de *Vipera*. Fins ara no s'havien documentat exemples amb tendències d'evolució cap al nanisme entre els escurçons fòssils i, per tant, el cas presentat en aquest estudi és la primera evidència paleontològica que dóna suport a la tendència evolutiva cap al nanisme en els vipèrids insulars.

PART 3. DISCUSSIÓ GLOBAL

Discussió

1. Aspectes tafonòmics del jaciment de NB-1

La presència de tres estrigiformes en el conjunt d'ocells fòssils del jaciment de NB-1 contribueix a explicar l'origen del dipòsit (capítol 5, 2). Nombrosos autors han destacat el paper dels rapinyaires nocturns com a bioacumuladors de restes de microvertebrats. Les olibasses (*Tyto* sps.) es troben entre les rapinyaires que produeixen les menors modificacions sobre els ossos de les preses consumides (Andrews, 1990). La presència de dues olibasses gegants a NB-1, suggereix que almenys una part important d'aquest dipòsit hauria d'haver derivat de l'acumulació de les seves preses. Les anàlisis microscòpiques superficials de les dents i els ossos recuperats del jaciment revelen que la majoria no presenten alteracions per ingestió o digestió, cosa que és una signatura tafonòmica de les restes acumulades pels Tytonidae (Andrews, 1990). La recuperació de material associat a un mateix individu s'ha obtingut de forma repetida (com podrien ser mandíbules de rosegadors, vèrtebres de mamífers i d'escatosos), cosa que és habitual als depòsits procedents d'egagròpiles d'estrigiformes. Aquesta obtenció és encara més rellevant tenint en compte les dificultats inherents de l'extracció d'ossos d'una bretxa fossilífera dura amb àcid acètic. A més, la preservació d'aquesta gran quantitat d'ossos de micromamífers és notablement bona, inclou ossos complets o semi-complets tant d'elements robustos (e.g., ossos llargs d'*Apocricetus darderi*) com d'elements de petita mida altament fràgils (e.g., ossos llargs del sorícid), fet remarcable per un dipòsit fossilífer amb un elevat grau de cimentació.

Està ben establert que la mida de les preses està relacionada amb la mida dels depredadors (vegeu, per exemple, Comay i Dayan, 2018; Herrera i Hiraldo, 1976). La mida d'*A. darderi* (massa corporal estimada a l'edat adulta de 560–730 g), els exemplars juvenils del lepòrid (massa corporal estimada de 320–840 g), i el glírid no descrit (massa corporal estimada a l'edat adulta de 60–100 g) de NB-1 coincideix amb el rang de mida de les preses previstes per a *Tyto* sp. 1, amb una massa corporal estimada de 1190–1360 g (Fig. 28). Aquest rang de mida de preses (60–840 g) i la gran quantitat d'ossos d'aquests tàxons combinats amb el bon estat de preservació dels ossos suggereixen que *Tyto* sp. 1 va ser una espècie clau per a la formació del dipòsit. El paper que va jugar *Tyto* sp. 2 no està prou clar. Tot i que possiblement també va actuar com a agent bioacumulador, tal volta va ser introduït com a presa al dipòsit per *Tyto* sp. 1. Es coneix que grans estrigiformes tenen un ventall més ampli de preses que les estrigiformes de mida petita (e.g., Comay i Dayan, 2018) i, per tant, *Tyto* sp. 1 podria incloure espècies petites, com *Paraethomys balearicus* (massa corporal estimada a l'edat adulta, 42 g), alguns ocells, escatosos i amfibis en la seva dieta. Tot i així, alguns dels tàxons obtinguts del jaciment suggereixen que podrien haver estat introduïts per altres agents bioacumuladors al dipòsit. Restes de tàxons de mida molt petita (com, per exemple, un escolecofidi i un amfisbaènid), o tàxons de mida més gran, com ara individus adults/subadults del lepòrid, el bòvid, un testudínid, i un vipèrid, es trobarien fora del rang de preses previstes per *Tyto* sp. 1.

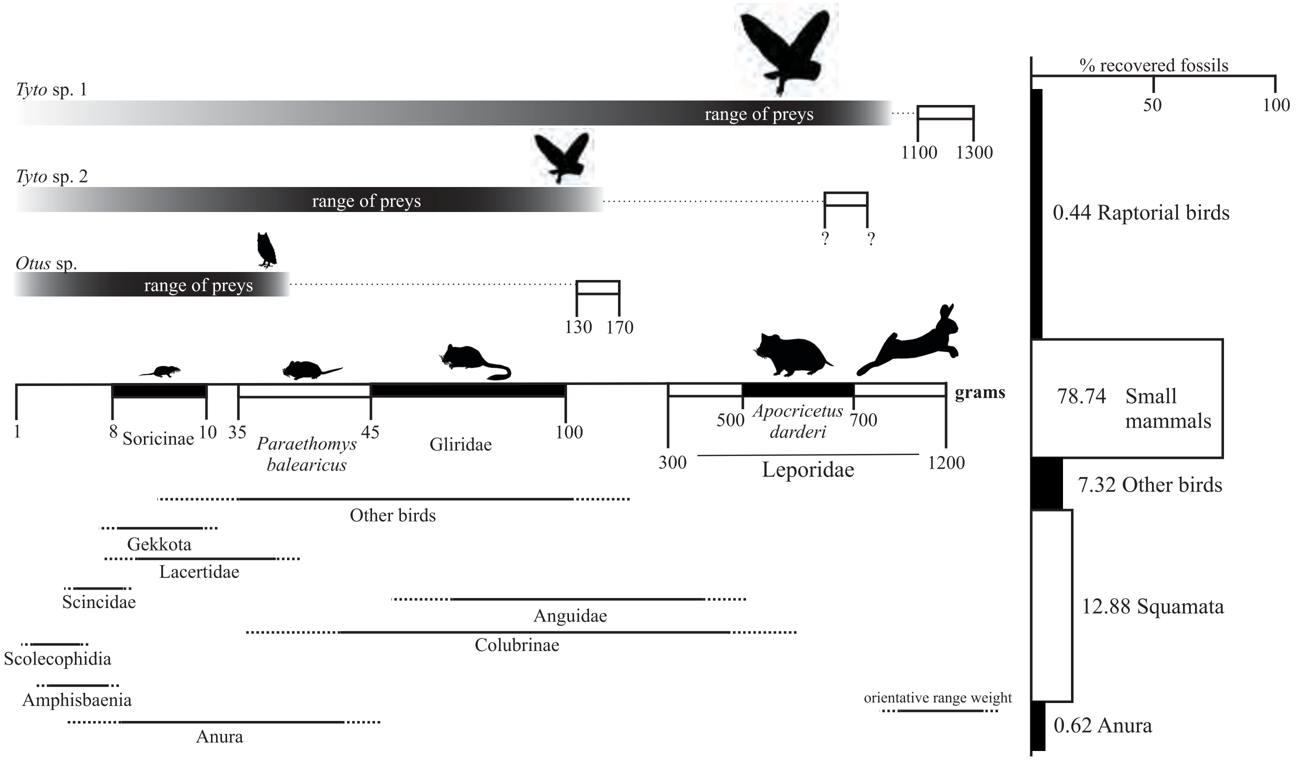


Figura 28: Diagrama esquemàtic que mostra les preses potencials dels estrigiformes en funció de l'estimació de la seva massa corporal (esquerra) i dels percentatges en la composició dels diferents vertebrats recuperats a NB-1 (dreta).

Tot i que s'han registrat casos de predació de titònids o grans estrígids sobre petits estrígids, com *Otus* (e.g. García et al., 2008), es tracta d'esdeveniments rars (e.g., Mikkola, 1976). És possible que *Otus* sp. s'incorporàs al dipòsit de NB-1 com a presa de *Tyto* sp. 1 (o fins i tot de *Tyto* sp. 2), però també pot ser que hi visqués a la mateixa cavitat on es va originar el depòsit. El paper d'*Otus* sp. com a agent bioacumulador potencial de petits vertebrats s'ha de considerar. Petits mamífers, com el sorícid (amb una massa corporal estimada de 8-10 g) i fins i tot el múrid, petits passeriformes, o petits escatosos (com els dragons Gekkonidae, les sargantanes, l'escolecofidi, els colubrins petits, i l'amfisbènid) i amfibis, cauen dins del rang de preses d'un mussol de mida petita, mentre que no semblen trobar-se al rang de preses de les olibasses gegants. L'abundància de vertebrats per sota del rang de mida estimada de les preses predilectes de les dues espècies de *Tyto* detectades, suggereix la possible existència d'un vincle entre aquestes petites preses i la presència d'*Otus*. Segons el material disponible, els ossos llargs de les extremitats posteriors del *Otus* sp. present a NB-1 són lleugerament més grans que els dels *Otus scops* actuals, mentre que les mesures dels ossos de les ales es troben dintre del rang de variabilitat d'*Otus scops*. Les falanges més grans i més estretes d'*Otus* sp. en comparació amb els d'*Otus scops* concorden amb els seus llargs ossos de les extremitats posteriors. Totes aquestes característiques suggereixen un elevat hàbit terrestre d'*Otus* sp., fet que afavoriria una predació sobre petits vertebrats terrestres (com l'escolecofidi, l'amfisbènid, etc.). L'adquisició d'hàbits terrestres és una tendència evolutiva que s'ha donat reiteradament entre els mussols insulars mancades de mamífers depredadors (e.g., Louchart, 2005). Al mateix gènere *Otus* trobam casos a Madeira i les Açores (Rando et al., 2012, 2013).

L'origen del depòsit de NB-1 sembla, per tant, estar relacionat amb la combinació d'actuacions de diversos agents bioacumuladors, cosa que ha permès la fossilització d'una fauna que inclou espècies que presenten un rang de mides molt més ampli que el que s'hagués pogut originar a partir d'un únic agent bioacumulador.

Cal dir que tot i que aquest origen per bioacumulació originada per diferents agents abasta un ampli espectre d'espècies, també continua presentant limitacions. Així, per exemple, el lepòrid de NB-1, pendent d'estudi, està representat bàsicament per ossos d'exemplars juvenils. Això es degut a que la mida dels adults d'aquesta espècie estava per damunt del rang de mides depredable per les olibasses gegants. Tot i que el depòsit permet constatar la presència d'un lepòrid, la seva descripció presenta dificultats, degut a la tafonomia del jaciment. Al depòsit de NB-1 s'han trobat molts pocs ossos fragmentats (8) d'un artiodàctil (presumible ancestre de *Myotragus*). La seva mida també l'excloïa de ser depredat per les olibasses. No es pot excloure que la fauna del Zancleà de Mallorca contengués altres espècies de mamífers de talla mitjana/gran que no hagin deixat rastre al registre fossilífer.

2. Origen i època de colonització de la fauna de *Myotragus* i de l'escurçó d'Eivissa

2.1. Origen de la fauna de *Myotragus*

L'estudi detallat del conjunt paleofaunístic del dipòsit de NB-1 aporta dades, tant filogenètiques com biogeogràfiques, sobre alguns dels seus components que ajuden a establir d'una manera força acurada l'edat i la regió d'origen més probable de tot el conjunt.

La regió d'origen i l'època de colonització de la fauna de *Myotragus* ha estat una qüestió àmpliament tractada. Colom (e.g., 1953, 1957, 1975) ja va establir que possiblement els vertebrats quaternaris de les Balears eren un conjunt faunístic relicte del Miocè superior en base a l'evolució geològica de la Mediterrània occidental. Aquesta proposta va estar ben recolzada per diversos autors i agafà més solidesa amb els estudis sobre el fons marí del Mediterrani realitzats durant els anys 70. Hsü, Ryan i Cita (1973) varen donar a conèixer l'existència d'uns dipòsits evaporítics molt potents que es formaren com a resultat d'un episodi d'evaporació de la Mediterrània fa uns 6-5 Ma i que es trobaven relacionats amb els dipòsits salins descrits a Messina (Sicília) per Selli (1960), i de la seva interpretació d'aquests depòsits sorgí el terme "Crisi de salinitat del Messinià". Actualment s'ha avançat considerablement en el coneixement sobre aquesta crisi que va afectar a tota la conca Mediterrània i a les condicions marines dels oceans (veure capítol 2.3). Aquest esdeveniment va tenir importants conseqüències climàtiques i biogeogràfiques, el que va permetre el darrer intercanvi de mamífers entre Europa i Àfrica pel corredor occidental del Mediterrani i la colonització d'illes com les Balears (Jaeger et al., 1975, Agustí et al., 2006; van der Made et al., 2006; Bover et al., 2008). Per tant, s'acceptà àmpliament que l'arribada del darrer conjunt faunístic insular de les Illes Balears es donà amb la MSC, a través d'un pont terrestre que connectava les Balears amb el continent, i el seu aïllament es donà amb la reinundació de la conca com a conseqüència de l'obertura de l'estret de Gibraltar.

Un dels majors inconvenients que ha arribat fins a l'actualitat és la falta de datacions absolutes dels diferents jaciments paleontològics antics de les Balears que permetin afinar la correlació faunística intra i inter-insular, i continental. L'establiment de l'edat i l'origen filogeogràfic de les especies insulars es fonamenta bàsicament en els episodis regressius que ha patit la Mediterrània, com és el cas de la MSC, i el grau de diferenciació evolutiu entre les espècies insulars respecte les continentals (Quintana, 2005). Aquesta darrera observació no s'ha pogut documentar d'una manera molt sòlida fins ara, donades les característiques extremadament derivades de les diferents especies insulars que es coneixien, amb l'excepció de *Debruijnimys* d'Eivissa que ja denotava un origen geogràfic i una època de colonització d'aquest conjunt faunístic congruent amb la MSC i, en menor grau, amb la relació entre *Muscardinus vireti* amb *Muscardinus cyclopeus* (Moyà-Solà et al., 1984; Agustí et al., 1982), que apuntava en la mateixa direcció.

Anurs: *Alytes* i *Discoglossus*

El conjunt d'anurs de NB-1 ha permès millorar el nostre coneixement sobre la colonització de les Balears i plantejar possibles vies de dispersió alternatives. Fins la publicació d'aquest conjunt d'anurs hi havia dos escenaris biogeogràfics plantejats per a la colonització de les Illes Balears en base als anàlisis moleculars dels Alytinae.

1. Martínez-Solano et al. (2004) varen estimar que la separació entre *A. muletensis* i *A. dickhilleni* es va produir fa aproximadament 3 Ma. Aquesta data suggeria que l'avantpassat d'*A. muletensis* va arribar a Mallorca per via ultramarina. Aquest tipus de dispersió es pot produir amb els anurs, tot i que els esdeveniments de vicariança s'han donat més àmpliament en la colonització d'illes pels anurs (Vences et al., 2003).
2. La segona alternativa, suggerida per Arntzen i García-París (1995), Fromhage et al. (2004) i Gonçalves (2007), plantejava que *Alytes* es va dispersar pel Mediterrani occidental parcialment dessecat durant la MSC, i que l'avantpassat d'*A. muletensis* va quedar aïllat a Mallorca a causa del reompliment de la conca mediterrània al final de la MSC, c. 5.33 Ma (Hsü et al., 1973; Krijgsman et al., 1999). Aquest fet també hauria provocat l'aïllament gairebé simultani dels llinatges que posteriorment donarien origen a *A. maurus* al nord d'Àfrica i *A. dickhilleni* a les serralades Bètiques.

La identificació de restes atribuïbles a *Alytes* a NB-1 (Torres-Roig et al., 2017; Annex 1.4) permet descartar la hipòtesi de la colonització ultramarina, recolzant de manera inequívoca la proposta d'Arntzen i García-Paris (1995) i d'altres autors (Gonçalves, 2007; Maia-Carvalho et al., 2014).

D'altra banda, diferents estudis genètics van suggerir que el clade de *Discoglossus* va aparèixer al Miocè tardà (Fromhage et al., 2004; Pabijan et al., 2012), tot i que hi ha fòssils assignats a *Discoglossus* que són coneguts a partir de l'Oligocè tardà d'Alemanya (Böhme 2008; Rage i Roček 2003) i del Miocè inicial de Sardenya (Venczel i Sanchiz, 2006). Els canvis ambientals associats a la MSC podrien haver influït en la dispersió i l'aïllament de l'últim avantpassat comú de les diferents espècies de *Discoglossus* existents (Zangari et al., 2006). Durant aquest esdeveniment de dispersió, *Discoglossus* va arribar a Mallorca, tal com es documenta amb les nombroses restes detectades a NB-1 (Torres-Roig et al., 2017; Annex 1.4).

Apocricetus

La presència a NB-1 d'un cricètid gegant, *Apocricetus darderi* (Torres-Roig et al., 2019: annex 2,10) (aporta també informacions sòlides sobre l'època de colonització de la fauna de *Myotragus*.

L'anàlisi morfològica suggereix que *A. darderi* està estretament relacionat amb una forma avançada d'*A. alberti* del Miocè tardà de la península Ibèrica (Turolià tardà, MN13). Les característiques dels molars superiors tenen un baix poder de resolució per establir les relacions entre les diferents espècies d' *Apocricetus*. En canvi, els molars inferiors semblen proporcionar una millor resolució per discriminar les espècies. L'estudi d'*A. darderi* demostra l'estret lligam d'aquest tàxon amb les poblacions continentals més avançades d'*A. alberti*, representant així la relació més estreta que s'hagi establert mai entre un taxó continental i el seu descendent insular a Mallorca. Aquest fet proporciona la millor correlació biostratigràfica disponible entre la fauna *Myotragus* amb una biozona continental de mamífers. Malgrat el seu gigantisme i els seus trets derivats associats a l'evolució insular, *A. darderi* conserva una sèrie de caràcters arcaics que el vinculen amb els membres del gènere *Apocricetus*. Tal com també s'observa també amb *T. macpheei* del CdR, la mida gegant d'*A. darderi* i la singularitat de la fauna de NB-1 (diversitat d'espècies relativament pobra i desequilibrada) indiquen que la fauna ja era insular (Torres-Roig et al., 2019; Annex 1.6). Així, malgrat que la morfologia dentària d'*A. darderi* el situaria al MN 13, la fauna NB-1 hauria de ser considerada com a coetània a les faunes de Pliocè inicial del continent assignades al MN 14. La relació proposada entre *A. alberti* i *A. darderi* situa el llevant de la península Ibèrica com la regió d'origen més probable del tàxon mallorquí.

Addicionalment, l'estudi de *T. macpheei* ens ha portat a considerar *A. darderi* com a l'avantpassat directe, o alternativament com a un tàxon germà que va evolucionar a partir d'un avantpassat comú. Es tracta de les úniques espècies de cricetins presents en el neogen de Mallorca i *T. macpheei* presenta els caràcters dentals més derivats. La presència de mesolòfids en el m1 i el m2, l'elevat desenvolupament de crestes com el protolòful anterior i el protolòful posterior del M1 o l'ectolòfol del M2 i del M3, fan que *T. macpheei* mostri una selenodòncia particular. Tanmateix, *T. macpheei* mostra un augment relatiu de la longitud molar i una reducció important del m3 respecte a el m2, així com un alt grau d'hipsodòncia.

A banda de l'adquisició d'un alt grau d'hipsodòncia i selenodòncia, la tendència més destacable del llinatge *A. darderi* (o de l'avantpassat comú) a *Tragomys macpheei* implica l'important desenvolupament que ha assolit el M1 pel que fa a la sèrie superior del molars i la reducció de la seva amplada, especialment els segons molars. Aquests trets no es donen a *Apocricetus*, tal com es troba definit per Freudenthal et al. (1998), cosa que deixa *Tragomys* com un gènere separat i presumiblement derivat d'*Apocricetus*. Segons la nostra interpretació, un estoc avançat d'*A. alberti* va colonitzar Mallorca durant el MSC. Després del reompliment de la conca mediterrània, aquest estoc va començar a evolucionar independentment en condicions d'insularitat fins donar origen a *A. darderi* i *a T. macpheei*. Si *A. darderi* fos l'avantpassat directe de *T. macpheei*, la fauna del CdR s'hauria de considerar com a descendent directe de la fauna NB-1. Aquest fet situaria el jaciment del CdR a la part superior del MN14 o, menys probablement, potser amb l'inici del MN15.

Paraethomys

En termes generals, el llinatge filogenètic del *Paraethomys* europeu es caracteritza per un augment de la mida amb el pas del temps. García-Alix et al. (2008) va registrar aquest augment de mida des de les poblacions més antigues (Turolià tardà) fins a la més recent (Ruscinià inicial) de *P. meini* a la conca de Granada. De la mateixa manera, Piñero i Agustí (2017) van reconèixer un augment de la mida des de les primeres poblacions de *P. meini* a *P.* aff. *abaigari* a la conca de Fortuna. Els jaciments paleontològics del Pliocè (MN14 i MN15) d'algunes conques de la península Ibèrica han donat dues formes coetànies de *Paraethomys*: una de mida petita, corresponent a *P. meini* i una altra de mida més gran, pertanyent al llinatge composat per *P.* aff. *abaigari* - *P. abaigari* - *P.* aff. *jaegeri* - *P. jaegeri* (Piñero. 1990). Mansino et al. (2017) va proposar que *P. meini* tendeix a augmentar la mida en les localitats que no tenen espècies del llinatge *P.* aff. *abaigari* - *P. jaegeri*, mentre que, després de l'aparició gradual de *P.* aff. *abaigari* en el Pliocè inicial (MN14), *P. meini* es va fer més petit en condicions simpàtriques. *Paraethomys belmezensis* és una espècie que probablement també ha derivat de *P. meini*, és lleugerament més gran que aquesta última i clarament més petita que *P. abaigari*. *Paraethomys lissasfensis* del Miocè superior del N d'Àfrica, aparentment es troba relacionat amb els *Paraethomys* ibèrics (Geraads 1998). Presenta una mida molar lleugerament més gran que els exemplars de *P. meini* de Venta del Moro, una de les poblacions de menor mida (Mansino et al., 2017a).

La mida dels molars de *P. balearicus* presenten una grandària significativament més gran que les de tot el llinatge evolutiu de *P. meini*, a excepció de les poblacions de *P. meini* del Turolià tardà i del Ruscinià tardà, amb les quals hi ha una certa superposició de mides. El m1 de *P. balearicus* és més gran que el de *P. belmezensis*, mentre que la mida del M1 es solapa considerablement. *Paraethomys balearicus* és una mica més gran que *P. lissasfensis*, tot i que hi ha alguna superposició en les longituds dels molars. Per contra, les mides dentàries de *P. balearicus* es solapen àmpliament amb les de *P.* aff. *abaigari* (Adrover et al., 1993; García-Alix et al., 2008; Piñero et al., 2017; Mansino et al., 2015b, 2016), però difereixen morfològicament de *P.* aff. *abaigari* per la presència d'un cíngol anterior al m1, una fosseta entre l'hipocònid i el tubercle c1 en el m1, i un esperó longitudinal més reduït i una estreta connexió entre t6-t9 al M1. En *P. balearicus* els molars són més petits que els de *P. abaigari* (Adrover et al., 1988) i són considerablement més petits que els de *P. jaegeri*

(Montenat i de Bruijn, 1976; Castillo i Agustí, 1996).

Diferents trets morfològics relacionen a *P. balearicus* amb les poblacions més antigues de *P. meini* (capítol 5, 3.2), ratificant de nou una relació molt propera temporalment entre la fauna insular mallorquina post-messiniana amb tàxons continentals. Aquest jaciment està proporcionant una fauna relativament diversa que conté algunes espècies que mostren clares relacions amb els seus avantpassats continentals del Turolià superior, com és el cas d'*A. darderi*, proper a *A. alberti* (Torres-Roig et al., 2019: annex 2, 10). La descripció de *P. balearicus* apunta, novament, l'origen del conjunt paleontològic registrat a NB-1 al final del Messinià. La hipòtesi més plausible de l'arribada d'aquesta fauna a les illes és dóna amb el pic de la dessecació del Mediterrani (5,60–5,54 Ma; Roveri et al., 2016), alguns tàxons de rosegadors d'origen africà varen arribar a les Illes Balears des del llevant de la península Ibèrica: segons el registre disponible *Paraethomys* va arribar a Mallorca i *Debruijnimys* a Eivissa (Agustí , 1989). En el mateix esdeveniment de colonització, altres tàxons d'origen ibèric també varen arribar a les Balears (per exemple, *Apocricetus*). *Paraethomys balearicus* junt amb *A. darderi* i *Alytes* aff. *muletensis* permeten suggerir que el Sistema Bètic era la principal regió font de la colonització de les Illes Balears durant la MSC. Aquest conjunt d'evidències apunta a que globalment el conjunt de la fauna de *Myotragus* prové d'aquesta regió, tot i que no es pot excloure que alguns elements tenguin un origen diferent.

Corredors riparians: una altra possible via de dispersió

Durant la MSC les Illes Balears es varen connectar amb la península Ibèrica a través del Promontori Balear. La dessecació messiniana hauria d'haver permès la dispersió d'una fauna continental cap a les illes (e.g., van der Made et al., 2006; Bover et al., 2008). No obstant, les condicions ambientals haurien actuat com a filtre i sols unes poques espècies de vertebrats terrestres haurien estat capaces d'arribar a unes illes envoltades d'un desert salí (Hsü 1983). Les seqüències de pol·len de la regió peri-mediterrània indiquen que existien entorns oberts i probablement secs a la regió sud del Mediterrani abans, durant i després de la crisi de salinitat (Fauquette et al., 2006). Els hàbitats amb corredors favorables que permetessin la dispersió d'animals terrestres a les Balears haurien d'haver estat presents (e.g., Blondel i Aronson, 1999). Tot i que el Promontori Balear podria haver estat un d'aquests ponts de connexió entre les Balears i el continent, una part important dels representants dels diferents grups de la fauna endèmica del Pliocè de Mallorca no ha estat registrada al jaciment de Ses Fontanelles d'Eivissa, fet que podria suggerir que probablement aquest pont de terra no era l'única via de dispersió. Tot i que no hi ha proves directes d'altres vies de dispersió, es reconeix una erosió massiva dels marges continentals exposats durant el gran esdeveniment de dessecació (Rizzini et al., 1978; Ryan i Cita 1978; Just et al., 2010). Els antics rius continentals van drenar sobre les noves terres emergides, tallant profunds canons que arribaven fins a les planes abissals. Si el cabal d'aigua d'aquests nous rius hagués estat prou gran, podrien haver representat corredors de dispersió favorables, especialment per als amfibis. En aquest sentit, els anurs trobats a la NB-1 proporcionen informació sobre aquests possibles corredors, coneguts com corredors riparians, en base a la inferència dels requeriments ecològics de les granotes i els gripaus actuals (Torres-Roig et al., 2017: annex 2, 8). La majoria dels anurs detectats al jaciment de NB-1, especialment els Alytinae i Bufonidae, tenen activitat crepuscular i nocturna i no depenen estrictament de l'aigua durant els estadis adults. En canvi, els Ranidae i les Discoglossinae estan més estrictament vinculats als ambients aquàtics, encara que amb un grau variable de tolerància a les aigües salobres. Els Ranidae inclouen espècies diürnes i nocturnes, que disminueixen la seva activitat durant les hores d'insolació més elevades. Dins dels Ranidae, algunes espècies són estrictament aquàtiques, com *Pelophylax*, que es poden trobar a tot tipus de cossos d'aigua dolça o ambients permanentment humits i tenen una alta tolerància a les aigües salobres. La disponibilitat i l'altitud d'aigua són factors limitatius en la seva distribució geogràfica. D'altra banda, la majoria d'espècies de *Rana* existents viuen en ambients humits, però passen la major part de la vida adulta a terra, només tornant a l'aigua per reproduir-se.

Alguns d'aquests trets, com ara l'activitat nocturna, el nivell baix de dependència de l'aigua, la tolerància a l'aigua salobre, etc., poden haver facilitat la dispersió terrestre d'algun dels representants d'aquest grup, com podria ser *Alytes* i el bufònid, afavorint la seva arribada a Mallorca. Mentre que la presència de corrents d'aigua que creuaven el desert messinià podrien haver estat clau per permetre la dispersió com a mínim del rànid i *Discoglossus*. Es considera que els hàbitats de ribera associats als rius són els ambients més productius de les regions desèrtiques o semi-desèrtiques (Free et al., 2013, 2015). Aquests hàbitats (paleo-rius i els seus hàbitats riparians associats) podrien haver actuat com a importants vies en la dispersió faunística durant el MSC quan els rius continentals drenaven cap a les planes abissals, com ho demostren les valls messinianes i les superfícies erosives al canal de València (Urgeles et al., 2010; García et al., 2011). Alguns torrents de la Serra de Tramuntana a Mallorca podrien haver estat afluents dels rius que fluïen de la part continental a la plana abissal, enllaçant corredors d'hàbitats lòtics i permetent la colonització de Mallorca per espècies relacionades amb medis aquàtics. L'ús d'aquest corredors riparians per anurs com a ruta per arribar a les Illes Balears es pot considerar com a una hipòtesi per explicar la dispersió dels anurs, assumint que cap d'aquest elements forma part d'algun tàxon relicte pre-messinià, en especial *Discoglossus* i el rànid. A més, aquesta hipòtesi també podria explicar aquesta diferenciació entre els representants dels diferents grups que composen les faunes vertebrades del Pliocè de Mallorca, Menorca i Eivissa, ja que podrien haver utilitzat diferents rutes que acabarien portant a una o altra illa.

2.2. Origen de l'escurçó d'Eivissa.

La descoberta inesperada de restes fòssils d'un escurçó a Eivissa (*Vipera latastei ebusitana*) ha permès realitzar el seu estudi morfològic i genètic. Malauradament només es disposa d'una diversitat limitada d'ossos fòssils d'aquest tàxon: vèrtebres (prop de 6000 fòssils), un os mandibular (10 fòssils) i un únic fragment de pterigoides. El seu estudi morfològic revela que l'escurçó d'Eivissa era un tàxon de mida relativament petita, i amb una morfologia vertebral peculiar. Es tracta d'un tàxon clarament endèmic de l'illa.

Les dades cronològiques i estratigràfiques des Pouàs confirmen la seva presència a Eivissa durant almenys c. 30.000 anys. Segons les dades genètiques, l'escurçó nan d'Eivissa va divergir de la població continental oriental de *V. latastei* fa entre 1,31 i 0,67 Ma (veure capítol 6). Per tant, els avantpassats de l'escurçó nan d'Eivissa van arribar a l'illa entre 1,31 Ma i un temps indeterminat (que abasta el temps que va necessitar per evolucionar cap a la seva peculiar morfologia) abans c. 30.000 (primera aparició segura d'aquest tàxon al registre fòssil). Aquesta data de separació té una clara implicació biogeogràfica, ja que només és compatible amb una colonització ultramarina de l'illa d'Eivissa per l'ancestre de l'escurçó estudiat, ja que l'última connexió terrestre entre península Ibèrica i les Illes Balears es va produir entre 5,6 i 5,33,3 Ma (e.g., Mas et al., 2018: annex 2,9). Aquest mecanisme de colonització ultramarina està àmpliament documentat en el cas de rèptils que arriben a illes, com ara les illes Canàries (e.g., *Gallotia*, Cox et al., 2010; o un boid a Lanzarote, Barahona et al., 1998) i les illes Galápagos (e.g., *Pseudalsophis*, Zaher et al., 2018). La distància actual entre Eivissa i la península Ibèrica és d'uns 90 km, que es va reduir a c. 70 quilòmetres durant els períodes glacials del Pleistocè i, per tant, es podrien haver superat plausiblement per ràfting sobre rais de vegetació a la deriva.

El mal estat de conservació de la vèrtebra caudal del dipòsit cova de ca na Reia impedeix la seva precisa identificació taxonòmica. En conseqüència, la seva atribució a *Vipera* és només provisional i la designem com a *cf. Vipera* en base a la curvatura de les hemapòfisis. Les diferencies observades amb les vèrtebres caudals de diferents colúbrids indiquen que la vèrtebra fòssil podria representar l'avantpassat de l'escurçó des Pouàs, tot i que caldria obtenir més material per confirmar-ho. Si la vèrtebra del jaciment de Cova de ca na Reia pertany realment a l'avantpassat de *V. l. ebusitana*, la seva presència en aquest jaciment (en combinació amb les dades moleculars disponibles) restringiria l'edat d'aquest dipòsit al Calabrià. Anteriorment el depòsit de la cova de ca na Reia s'atribuïa provisionalment al Gelasià/Calabrià, famentat sobre la fauna malacològica associada.

A hores d'ara *Vipera latastei ebusitana* és l´únic vertebrat endèmic de les Balears que s'ha demostrat que ha colonitzat una de les illes mitjançant colonització ultramarina. És notable la seva diferenciació morfològica, les implicacions de la qual encara estan pendents de ser resoltes. El coneixement d'aquest tàxon es troba a hores d'ara necessitat de l'obtenció de noves restes esquelètiques fossilitzades.

3. Evolució paleobiogeogràfica de les Illes Balears: implicacions en el procés de colonització dels vertebrats insulars

Els models paleobiogeogràfics utilitzats per explicar l'origen dels vertebrats terrestres post-messinians de les Illes Balears, des de fa temps s'han recolzat sobre el mateix esdeveniment, però amb diferents matisos. Tots els autors han considerat la MSC com la causa que va permetre la dispersió i colonització dels darrers conjunts de vertebrats terrestres a través de l'emersió de ponts de terra entre el continent i les Balears. Quintana (2005) va enfrontar els dos models establerts entre els anys 1980-2000. Aquest consistien en:

1. Model de colonització diacrònica (Pons-Moyà et al., 1981; Moyà-Solà et al., 1984; Agustí i Moyà-Solà, 1990). Basada en el fet de trobar dos grups faunístics diferenciats. Un primer grup trobat a Ses Fontanelles (Eivissa) situat entre el Miocè superior-Pliocè i als jaciments de Punta Nati-Cala's Pous (Menorca), que varen ser considerats com a intra-messinians (Agustí et al., 1982). I un segon grup que estaria representada per la fauna de *Myotragus* a Mallorca i Menorca, que quedarien definitivament aïllades durant la regressió pliocènica. Es va suposar que aquests dos grups faunístics representarien dos episodis colonitzadors. Per tant, s'establí que les Balears varen ser colonitzades durant dos episodis regressius que tingueren lloc durant la MSC. Actualment es reconeixen dues davallades del nivell del mar: la primera fa 5,97 Ma (Manzi et al., 2013), que va donar lloc a una caiguda màxima de 200 m (Clauzon et al., 1996) i la segona fa 5,60 Ma (CIESM, 2008), que correspondria a la gran davallada estimada entre uns 1500-2000 m (Clauzon et al., 1996). Quintana (2005) descartava aquest model donada la baixa magnitud de la primera caiguda del nivell de mar, insuficient per crear una connexió entre les illes i el continent. D'altra banda, el reajustament de les edats relatives dels jaciments mencionats (situats ara al Pliocè; Alcover et al,. 1999; Quintana, 1999; Quintana, 2005) i la millora sobre el coneixement dels vertebrats fòssils insulars de les Balears (on es descarta l'existència d'una relació de parentiu entre tàxons dels jaciments antics de les faunes d'Eivissa i Menorca; Quintana et al., 2010; Quintana et al., 2014), donen major suport al segon model de colonització.
2. Model de colonització sincrònica (Alcover et al., 1981; Alcover et al., 1999). Aquest model establia que els diferents conjunts faunístics de les Balears varen colonitzar les illes en un únic esdeveniment dispersiu afavorit per la gran davallada del nivell del mar durant la MSC, substituint presumiblement l'anterior fauna insular de Mallorca i Menorca (fauna de *Gymnesicolagus*). Alcover et al (1999) consideraven que el conjunt faunístic antic de Punta Nati-Cala's Pous tenia una edat post-messiniana i l'atribuïen temptativament al Pliocè. A més, els autors consideraren que aquesta fauna endèmica de Menorca va ser substituïda per la fauna de *Myotragus*, durant les glaciacions plio-pleistocenes, produint-se una homogeneïtzació faunística recurrent entre les Gimnèsies durant el Pleistocè fins l'últim màxim glacial.

Per tant, la millora sobre el coneixement dels diferents components faunístics de cada dipòsit fossilífer de les Balears i una definició més precisa de l'edat relativa dels dipòsits, han anat recolzant cada cop més el model paleobiogeogràfic que establia una dispersió dels conjunts faunístics post-messinians lligada al darrer episodi regressiu de la MSC. En els darrers 20 anys aquesta hipòtesi ha estat àmpliament acceptada i s'ha mantingut fins a l'actualitat amb un nombre creixent de dades que li donen suport (e.g., van der Made et al., 2006; Bover et al., 2008, 2010, 2014; Quintana et al., 2010; Agustí et al., 2012; Rofes et al., 2012).

La presencia de tàxons properament emparentats amb els seus ancestres continentals al jaciment de NB-1, com *A. darderi* amb *A. alberti* del Turolià tardà i *P. balearicus* amb *P. meini* del Turolià tardà (Torres-Roig et al., 2019: annex 2,10; veure capítol 5, 3.2), donen un important suport al model de la colonització sincrònica de les Balears. A Eivissa, *Debruijnimys* sp. de Ses Fontanelles és l'únic tàxon del jaciment que també reforça aquest model, ja que aquest gènere és un dels exemples que posa de manifest l'intercanvi faunístic entre el S d'Europa i el N d'Àfrica durant la MSC. D'altra banda, a Menorca, sembla que *M. cyclopeus* estaria emparentat amb *M. vireti* de Lissieu amb una edat compresa entre el Vallesià i el Turolià (Agustí et al., 1982), tot i que seria necessari comparar-lo amb *M. meridionalis* de la conca de Granada, d'edat compresa entre el final del Turolià i l'inici del Ruscinià. En definitiva, el fet de trobar tàxons properament emparentats amb tàxons continentals en els jaciments antics d'Eivissa i Mallorca (respectivament, Ses Fontanelles i NB-1), una diversitat de vertebrats terrestres superior a la de jaciments més recents i l'absència de nous llinatges filogenètics al llarg del temps, posa de manifest que el darrer episodi de colonització faunística continental es va donar amb una única onada de dispersió. Tot i així, sembla ser que almenys l'escurçó nan d'Eivissa va arribar a l'illa posteriorment i no es descarta que alguns elements siguin tàxons relictes de la fauna pre-messiniana. En particular, aquest pot ser el cas d'una part de l'herpetofauna de Mallorca i Menorca i, tal volta, del glírid de NB-1. Segons els resultats de les anàlisis moleculars *Eliomys* és el gènere vivent més proper d'*Hypnomys* (capítol 2.4), be que aquesta relació de parentiu no implica necessàriament l'origen del darrer a partir del primer. La dentició de les espècies arcaiques d'*Eliomys* és poc complexa, mentre que la del glírid de NB-1 ho és més. Un origen alternatiu i morfològicament més plausible per a *Hypnomys* és el seva derivació d'un glírid del Miocè mitjà-tardà amb una elevada complexitat dental, com, per exemple, *Vasseuromys*, o algun altre gènere estretament relacionat (capítol 2.4). *Vasseuromys* abasta des de l'Oligocè tardà fins al Miocè tardà (Sinitsa i Nesin, 2018), mentre que els *Microdyromys* més antics i *Bransatoglis*, que també tenen una elevada complexitat dental, abasten des de l'Oligocè inicial fins al Miocè mitjà i des de l'Oligocè tardà fins al Miocè mitjà, respectivament (Freudenthal i Martín-Suárez, 2013). Sota aquest escenari, el patró dental simplificat que mostren les espècies més recents d'*Hypnomys* seria un efecte de l'evolució insular (Reumer, 1982).

Una altra qüestió àmpliament tractada ha estat l'origen geogràfic de les faunes insulars de les Balears, principalment fonamentat sobre les relacions de parentiu amb els seus presumptes ancestres continentals. Un dels grans problemes al que s'han enfrontat els investigadors a l'hora de poder determinar aquestes relacions de parentiu es dona amb l'elevat grau de modificació morfològica que han patit els diferents tàxons al llarg de la seva evolució en condicions d'insularitat. Per aquesta raó ésde suma importància el descobriment de jaciments antics que conservin restes fòssils dels representats més basals dels llinatges filogenètics insulars.

Al llarg del temps les aproximacions històriques que s'han realitzat sobre la regió d'origen d'aquesta fauna han estat molt diverses. Les primeres aproximacions filogenètiques varen establir que els tres components clàssics de la fauna de *Myotragus* presentaven similituds morfològiques amb tàxons fòssils de Còrsega i Sardenya (e.g., Andrews, 1915; Dehaut, 1920; Gliozzi i Malatesta, 1980; Bate, 1945; Alcover et al., 1981), fet que feia plantejar l'existència d'una relació faunística entre Mallorca, Menorca i el massís corso-sard.

Dintre del context de la MSC i tenint en compte l'evolució tectònica de la mediterrània occidental, Azzaroli i Guazzone (1980) varen establir l'origen dels vertebrats post-messinians de les Balears al nord d'Àfrica amb una dispersió que transcorria a través de les Bètiques, les quals estarien connectades a les Balears pel Promontori Balear, mentre que aquests autors veien problemàtica una connexió entre les Gimnèsies i el massís corso-sard.

Alcover et al (1981) plantejaren que es podien diferenciar dos orígens diferents per al conjunt de les faunes post-messinianes de les Pitiüses i les de les Gimnèsies. Per una banda, la presència de *Debruijnimys* a

Eivissa establia la regió d'origen de la fauna de ses Fontanelles al sud de la península Ibèrica. Per una altre banda, la possible existència de relacions filogenètiques entre la fauna de *Myotragus* y les faunes de Còrsega i Sardenya (e.g., *Myotragus* amb *Nesogoral*) recolzaven que una amplia regió del sud d'Europa pogués ser l'àrea de dispersió dels ancestres d'aquestes faunes, sense que fos necessària una connexió directa entre les Gimnèsies i el massís corso-sard.

Moyà-Sola et al (1984) consideraven plausible que l'origen de les faunes post-messinianes de les Balears estigués a l'Europa occidental, a la península Ibèrica i el nord d'Àfrica. Tot i així, no es podia explicar l'origen de certs elements d'aquestes faunes aparentment relacionats entre diferents grups d'illes de la Mediterrània occidental (e.g., entre Mallorca i Sardenya o Menorca-Eivissa i Sicília), com a resultat de les relacions de parentiu establides entre alguns dels seus elements faunístics i de les descobertes iniciades a la Cova de Ca na Reia i als jaciments de Punta Nati-Cala's Pous. Utilitzant criteris paleobiogeogràfics, climàtics i ecològics varen establir que alguns d'aquest components faunístics (e.g., els lepòrids de Ses Fontanelles, Punta Nati-Cala's Pous i el de Sicília; *Myotragus* i *Nesogoral*), absents en el Turolià tardà continental, varen colonitzar la Mediterrània occidental a través de nous corredors emergits durant la MSC des de la Mediterrània oriental.

La millora en el coneixement sobre el registre fòssil del Neogen i la taxonomia d'aquest elements faunístics, tant a nivell insular com continental, proporcionen noves dades sobre les regions d'origen o han permès descartar algunes de les propostes anteriorment descrites.

Per una banda, van der Made (1999) va mantenir el gènere *Nesiotites* per la línia filogenètica de les Balears i els llinatges del bloc corso-sard els va situar al gènere *Asoriculus*. Molts autors estan d'acord que *Nesiotites* i *Asoriculus* tenen una forta relació de parentiu (e.g., Alcover et al., 1981; Reumer, 1984; Masini i Sara, 1998; van der Made, 1999; Rofes i Cuenca-Bescós, 2009; Bover et al., 2018). Aquest darrer gènere està present a la península Ibèrica des del trànsit Mio-Pliocè fins al Pleistocè inicial, sent *A. gibberodon* l'única espècie identificada en aquest territori amb registres que es remunten al Turolià tardà (e.g., Rofes i Cuenca-Bescós, 2006; Furió, 2007). Els llinatges insulars presumiblement varen derivar d'*A. gibberodon* (e.g., Kotsakis, 1980; Reumer, 1984; Pons-Monjo et al., 2010; Rofes et al., 2012), el qual es degué dispersar des del continent Europeu durant la MSC quedant aïllat en cadascuna de les illes després de la inundació pliocena del Mediterrani (e.g., Furió, 2007). El material del sorícid de NB-1, pendent d'estudi, permetrà aportar noves dades sobre la base del llinatge de *Nesiotites* i avaluar els canvis que ha patit al llarg de la seva evolució en condicions d'insularitat.

En el cas dels lepòrids balears, tant el tàxon d'Eivissa com el de Menorca inicialment varen ser relacionats amb *Hypolagus* sp. de Sicília, fet que permetia remarcar aquest possible origen oriental de les faunes insulars de la Mediterrània occidental (Moyà-Solà et al., 1984). Posteriorment, el lepòrid d'Eivissa i el de Menorca varen ser atribuïts a *Trischizolagus* (Agustí i Moyà-Solà, 1990), mentre que més endavant Moyà-Solà et al. (1999) els varen incloure a *Alilepus*. Finalment, Quintana (2005) a la seva tesi doctoral batià el lepòrid de Menorca com *Nuralagus rex*, un tàxon propi de la illa. Segons Quintana (2005) *N. rex* presenta una forta afinitat amb el gènere *Alilepus*, i en especial amb la forma d'Eivissa, concloent que aquesta darrera i *N. rex* possiblement serien descendents d'un ancestre comú. La definició d'*Hypolagus balearicus* al Pliocè de Mallorca posa de manifest l'existència d'una complexa distribució de lepòrids a les Illes Balears i possiblement va ser el desencadenant d'una revisió del material d'Eivissa, el qual va ser reasignat a *Hypolagus* sp. (Quintana et al., 2010). Posteriorment, Quintana i Moncunill-Solé (2014) conclouen que el tàxon d'Eivissa també pertany a *H. balearicus*. Aquest gènere va aparèixer a nord Amèrica al Miocè inicial-mitjà i es dispersà cap al continent euroasiàtic al Miocè tardà, perdurant fins al Pleistocè mitjà (Fladerer i Fiore, 2002; Fostowicz-Frelik, 2003). Es tracta d'un dels lepòrids més abundants del Pliocè del centre d'Europa i la seva presencia no ha estat detectada a l'extrem occidental d'Europa. Segons Quintana et al. (2010) hi deuria estar present durant la regressió messiniana, cosa que li hauria permès arribar a Eivissa i Mallorca.

Pel que fa a *Myotragus*, encara avui dia no es té la seguretat sobre les seves relacions de parentiu amb cap tàxon continental, i per tant, tampoc es té la certesa sobre el seu origen geogràfic. Les primeres aproximacions van plantejar la possible relació de parentiu de *Myotragus* amb *Nesogoral* de Sardenya (Andrew, 1915; Dehaut, 1920; Gliozzi i Malatesta, 1980), establint que probablement descendien d'un ancestre comú. Aquest fet senyalava cap a un origen oriental d'aquest tàxons, tal i com van suggerir Moyà-Solà et al. (1984). Alcover (1976) proposà que *Myotragus* estava estretament relacionat amb el gènere continental *Gallogoral* del Vil·lafranquià de l'Europa occidental, be que a hores d'ara està clar els trets comuns que comparteixen, igual que passa amb *Nesogoral*, poden ser conseqüència de la seva descendència d'un ancestre comú, tot i que són necessàries més dades que recolzin aquesta hipòtesi. Els darrers postulats suggereixen que *Aragoral* del Vallesià superior de la península Ibèrica i *Norbertia* del límit Turolià-Ruscinià de Grècia, podrien ser els avantpassats directes de *Myotragus* (Bover et al., 2010). I l'estudi de l'ADNa mitocondrial de *Myotragus balearicus* ha revelat que el seu parent més pròxim a l'actualitat és probablement *Budorcas taxicolor*, confirmant-se la seva inclusió en la tribu Caprini. A més, es suggereix per mitjà de l'anàlisi amb rellotges moleculars que la separació entre *Budorcas* i *Myotragus* va tenir lloc entorn als 7,1 Ma (Bover et al., 2019).

Tot aquests canvis en la determinació de les relacions filogenètiques dels diferents tàxons posen de manifest un cert grau d'incertesa en la seva autèntica identitat i es fa patent la necessària obtenció de més material fòssil per al seu aclariment, tant de les Balears com de les potencials regions continentals d'origen. L'amplia distribució geogràfica dels representants continentals mencionats (*Asoriculus*, *Alilepus*/*Hypolagus*) i/o la falta de registre fòssil a la península Ibèrica (com és el cas d'*Hypolagus*), no permeten precisar l'origen dels llinatges desenvolupats a les Balears, però les dades disponibles no contradiuen les hipòtesis paleogeogràfiques obtingudes sobre els tàxons insulars que sí presenten un clar origen geogràfic.

Les dades aportades durant l'estudi d'alguns dels components de la fauna del jaciment de NB-1 de la present Tesi Doctoral, com *Alytes* aff. *muletensis*, *A. darderi* i *P. balearicus*, junt amb *Debruijnimys* sp. del jaciment de ses Fontanelles d'Eivissa, proporcionen una major solidesa a la hipòtesi suggerida per Azzaroli i Guazzone (1980). Tots aquests tàxons posen de manifest l'existència d'una connexió de les Balears amb el llevant de la península Ibèrica com a principal via de colonització, que es donaria des de la serralada Bètica i a través del Promontori Balear amb la caiguda màxima del nivell del mar esdevinguda durant la MSC (veure capítol 2.3). Tot i així, queden components faunístics on les seves relacions de parentiu amb els ancestres continentals resten pendents de confirmació donat l'elevat grau de derivació morfològica que presenten (e.g., *Myotragus*, *Nuralagus*, *Muscardinus*), però que amb molta probabilitat provinguin de la mateixa regió geogràfica anteriorment esmentada o pròxima a aquesta.

En conseqüència, sembla que els diferents episodis de colonització de les Balears han estat lligats a l'evolució tectònica de la Mediterrània occidental. L'origen dels diferents conjunts faunístics insulars de les Balears solen estar situats al SE de la península Ibèrica, al N d'Àfrica i al centre d'Europa. La darrera colonització faunística a les Balears va tenir lloc durant la MSC. El mecanisme pel qual va tenir lloc aquest esdeveniment va ser pel despreniment d'un fragment de la litosfera en l'arc de Gibraltar, que s'hauria enfonsat en el mantell degut a la seva major densitat, afavorint l'aixecament tectònic dels relleus Bètic i Rifeny. En el moment en que l'aixecament va superar la capacitat erosiva d'entrada d'aigua des de l'Atlàntic, el Mediterrani quedà aïllat i es dessecà (Garcia-Castellanos i Villaseñor, 2011). Segons els models estructurals recents de la Mediterrània occidental, és plausible que els conjunts faunístics pre-messinians colonitzaren les Balears per mitjà d'unes connexions continentals que s'haurien establert per mecanismes tectònics semblants als citats anteriorment.

4. Extincions

El descobriment de la fauna NB-1 ha permès documentar una diversitat faunística molt més important del que es coneixia durant els primers estadis de la colonització de Mallorca. Aquesta fauna junt amb altres conjunts faunístics, com el de ses Fontanelles, posa de manifest l'existència d'un procés d'extinció complexa, que afecta de manera diferencial a cadascuna de les illes a llarg dels darrers cinc milions d'anys. Per establir les cronologies de les extincions es clau tenir dades de les darreres presències en el registres fòssils de les diferents especies detectades. Tot i així, manquen datacions absolutes que permetin situar amb major precisió els episodis d'extinció i el registre fòssil segueix sent incomplert. Per tant, segons les dades disponibles tant sols es pot oferir una idea aproximada dels esdeveniments que els varen poder afectar. Segons el registre fòssil actual s'han pogut diferenciar quatre episodis d'extinció que en alguns casos podrien haver afectat de manera global al conjunt de l'arxipèlag i de manera més local en altres (Fig. 29):

1. El primer episodi d'extinció es va donar entre el Zancleà i el Piasencià i va afectar de manera sincrònica o diacrònica a Mallorca i Eivissa. Es tracta del episodi més dràstic dels darrers cinc milions d'anys, que va afectar a 15 dels 23 tàxons detectats a NB-1 i a quatre dels set tàxons de ses Fontanelles. En el cas de Mallorca, el registre fòssil entre NB-1 i CdR documenta una disminució notable de tàxons, on dels 23 llinatges únicament queden registrats 11 al darrer jaciment. Es possible que aquesta discontinuïtat entre NB-1 i CdR sigui el resultat d'un biaix tafonòmic. Les causes d'aquestes extincions podrien estar relaciones amb un augment de la competitivitat interespecífica durant els primers estadis en condicions d'insularitat i/o amb els canvis climàtics i mediambientals que s'estaven produint a finals del Pliocè (reducció de les temperatures i augment de l'aridesa). No obstant, els dos herbívors més destacables de Mallorca i Eivissa, un testudínid de grans dimensions i un bòvid petit, presenten un èxit de supervivència invers. Es a dir, en el cas de Mallorca el bòvid documentat a NB-1, que presumiblement donaria lloc a *Myotragus*, arribaria fins a temps molt recents mentre que el testudínid acabaria per desaparèixer al Pliocè. A Eivissa es donà la situació contrària, el bòvid acabaria extingint-se mentre els testudínid es convertiria en el darrer llinatge de tortugues gegants en extingir-se a les Balears. Aquesta diferencia entre ambdues illes podria indicar que en el cas de Mallorca els factors de competitivitat interespecífica pogueren tenir una certa influència, mentre que a Eivissa els factors climàtics i mediambientals pogueren ser més durs (e.g., una major aridesa), afavorint la supervivència de rèptils i mamífers com els glírids, que es caracteritzen per una important capacitat de romandre en estat de letargia (hivernació i/o estivació) quan les condicions no els hi són favorables.
2. El segon episodi es troba únicament documentat a Menorca i possiblement a Mallorca. Tota la fauna endèmica de Menorca es va veure sobtadament interrompuda i s'inicià el registre de la fauna clàssica de *Myotragus*. Segons Quintana (2005), la desaparició de la fauna de *Nuralagus* estaria relaciona amb els canvis climàtics i mediambientals succeïts entre el Pliocè superior i el Pleistocè inferior. Però, la resta de les illes no mostra cap afectació i si es compara amb Eivissa, la seva tortuga gegant no es va veure afectada. Per tant, les dades disponibles recolzen la proposta d'Alcover et al. (1999), els quals postulen que la fauna de *Myotragus* substituí la fauna endèmica de *Nuralagus* amb l'inici de les connexions glacio-eustàtiques. La presumpta coexistència de *Nesiotites* i *Hypnomys* amb la tortuga gegant de Menorca en un dipòsit paleokàrstic del Cap d'Artrutx, també recolzaria aquest contacte entre la fauna de *Myotragus* i la fauna de *Nuralagus* (Quintana i Agustí, 2019). I no es descarta que alguns dels components de la fauna de *Nuralagus* (e.g., el Gekkota indeterminat, el *Blanus* sp. i/o les serps) sí que es pogueren veure afectades pel refredament del clima, així com la serp (?*Vipera* sp.) documentada en el jaciment des Crull de Cap Farrutx de Mallorca (Bover et al., 2014).

3. El tercer episodi d'extinció sembla ser de menor envergadura, encara que podria haver afectat a les tres illes entre el Pleistocè inferior i el superior. En aquest context es va extingir *Discoglossus* de Mallorca i Menorca, i els glírids i el testudínid d'Eivissa. Probablement l'extinció es va donar diacrònicament, sent el testudínid el darrer en ser afectat com testimonien les seves restes en els nivells inferiors des Pouàs. A més, durant aquest episodi si varen veure implicats tot un conjunt de gasteròpodes pulmonats, com *Rumina decollata* i *Tudorella ferruginea*, mentre que a les Gimnèsies no es varen veure afectats amb la mateixa intensitat. El constant refredament del clima i especialment l'augment de l'aridesa durant el Pleistocè, queda sobretot reflectida a les Pitiüses per un important desenvolupament d'encrostaments carbonatats propis d'ambients semiàrids. Aquestes formacions es troben molt menys representades a les Gimnèsies, pel que es podria pensar que les condicions climàtiques no serien tant rigoroses.

4. El quart i darrer episodi es troba relacionat amb l'arribada dels primers pobladors humans. A Mallorca la presència humana ja es patent abans del 2280 cal. BC (Bover et al., 2016), a Menorca abans de 2030 cal BC i a Eivissa abans del 2130 cal. BC (Alcover, 2008). En el cas de *Myotragus* a Mallorca, la darrera presència queda documentada per uns pocs centenars d'anys abans de l'arribada dels humans, mentre que la resta dels components faunístics endèmics de les Balears els superen per poc més. Aquesta proximitat temporal entre les darreres presències dels llinatges endèmics i les primeres presències humanes, descarten els factors climàtics i posen de relleu l'efecte que tingueren els humans sobre les illes produint l'extinció dels darrers mamífers endèmics de les Gimnèsies, així com ocells i l'escurçó nan d'Eivissa (McMinn et al., 2005; Bover et al., 2008; 2016; veure annex 1, 3 per l'extinció de l'escurçó nan d'Eivissa). Com a causes directes més probables per explicar les diferents extincions les dades disponibles apunten cap a la introducció de depredadors (cas de l'escurçó d'Eivissa -capítol 2.3- les sargantanes baleàriques de Mallorca i Menorca, i el ferreret a Menorca) i a la introducció de patògens (extinció de *Myotragus balearicus*, *Hypnomys morpheus* i *Nesiotites hidalgo*).

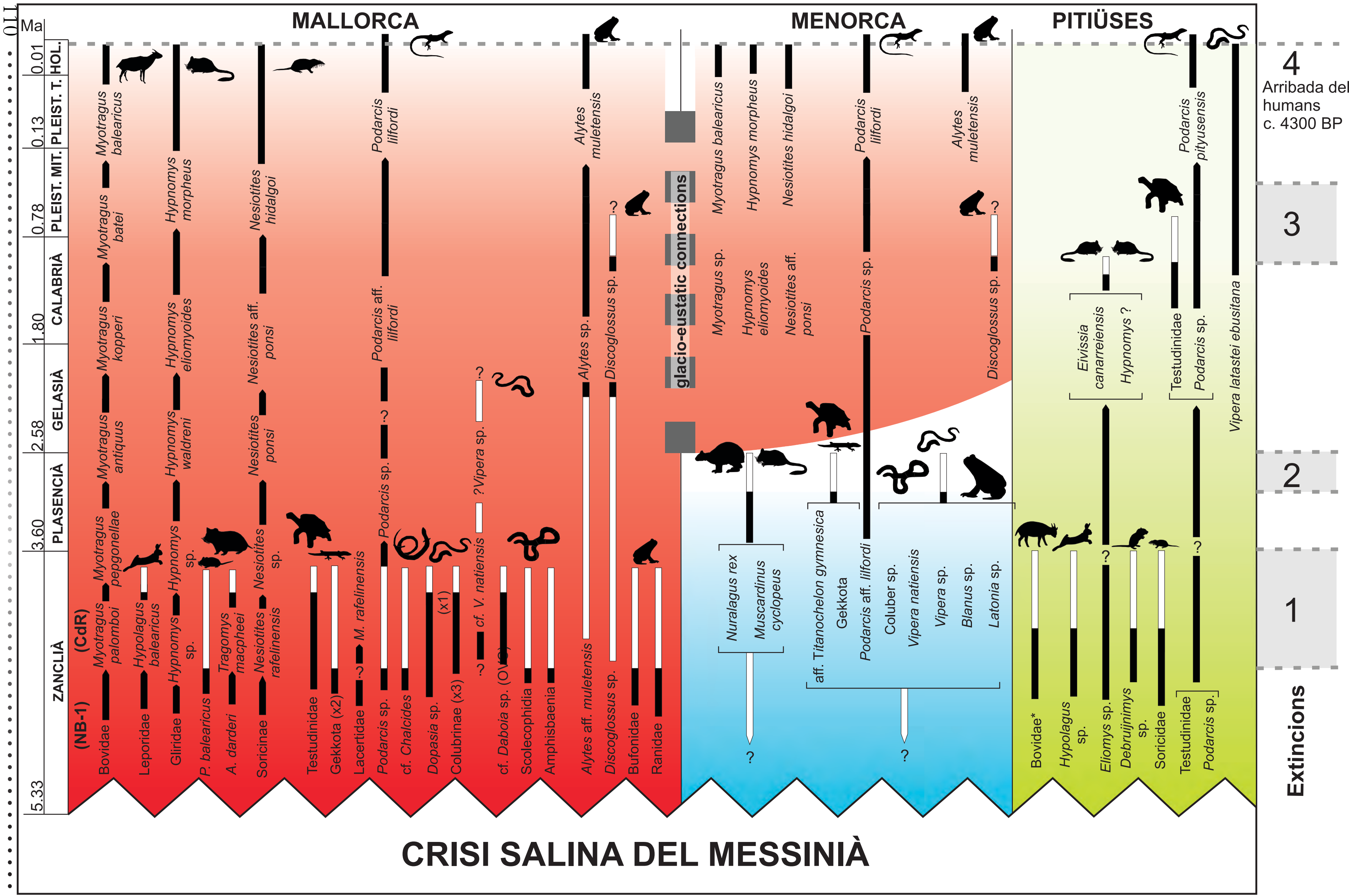


Figura 29: Síntesi actualitzada de les successions de vertebrats terrestres del Pliocè-Holocè de les Illes Balears d'acord amb els coneixements actuals.

PART 4. CONCLUSIONS GLOBALS

Conclusions Generals

1. S'ha millorat substancialment el coneixement sobre la composició de la fauna vertebrats del Pliocè basal de Mallorca i del Pleistocè-Holocè d'Eivissa. Aquesta millora s'ha realitzat principalment a partir de l'estudi de fòssils procedents dels jaciments de NB-1 a Mallorca i des Pouàs a Eivissa.

2. El registre de NB-1 ha aportat milers de restes fòssils de vertebrats. Aquesta Tesi ha permès descriure la fauna ornítica del jaciment, la qual inclou una desena d'ocells (*Tyto* sp.1, *Tyto* sp. 2, *Otus* sp., un Phasianidae, una espècie pertanyent a l'ordre Charadriformes i almenys cinc espècies de Passeriformes). Les dues espècies de Tytonidae són de gran mida, i el mussol presenta trets morfològics pròpies d'uns hàbits més terrestres que els dels mussols actuals.

3. S'ha pogut concloure que NB-1 és un dipòsit fossilífer originat predominantment per la bioacumulació de microvertebrats depredats per rapinyaires nocturns, tot i que, de manera ocasional, s'han incorporat algunes restes de vertebrats de mida major. Almenys dos estrigiformes, *Tyto* sp. 1 i *Otus* sp., han actuat com a agents bioacumuladors. El tercer rapinyaire, *Tyto* sp. 2, podria ser considerat com una presa de *Tyto* sp. 1 o com un altre agent bioacumulador. Les diferencies de mida entre *Tyto* sp. 1 i *Otus* sp. són suficientment importants com per a que hagin pogut actuat com agents bioacumuladors de preses de talles molt diferents. En conseqüència, es considera que la mostra obtinguda a NB-1 és molt representativa la fauna de vertebrats terrestres no voladors que van viure al Pliocè basal de Mallorca.

4. Les espècies trobades a NB-1 inclouen espècies i gèneres desconeguts als jaciments més moderns. S'inclouen tàxons que representen el registre més antic dels seus llinatges filogenètics a Mallorca. Gràcies a les característiques d'alguns dels seus components faunístics, s'ha pogut concloure que NB-1 esdevé el dipòsit conegut més antic de l'anomenada fauna de *Myotragus*, al mateix temps que és el jaciment més ric en diversitat d'espècies de les faunes post-messinianes de totes les illes Balears.

5. S'ha descrit *Paraethomys balearicus*, un múrid amb una dentició peculiar, hipsodonta, descendent de *Paraethomys meini* del Turolià tardà de la Península Ibèrica. La seva presència a NB-1 documenta una arribada durant la MSC. *Paratethomys* és l'únic gènere present a Mallorca d'origen africà. Aquest gènere, juntament amb *Apocricetus darderi* i *Alytes* aff. *muletensis* del mateix jaciment, i *Debruijnimys* sp. del jaciment grosserament coetani de ses Fontanelles a Eivissa, situen inequívocament la regió d'origen de les faunes del Pliocè i Pleistocè de les Balears principalment al SE de la península Ibèrica, a través d'una connexió que s'establiria des de la serralada Bètica per el Promontori Balear. L'estreta finestra temporal on s'agrupen tots els llinatges filogenètics proporciona un fort suport a la hipòtesi d'una única onada de colonització de Mallorca principalment per via terrestre i possiblement a través de corredors riparians.

6. S'ha document l'existència al Pleistocè superior d'Eivissa d'un escurçó nan, que s'ha descrit com a *Vipera latastei ebusitana*. Aquest tàxon es va separar de les poblacions orientals de *Vipera latastei* fa entre 1,3 i 0,67 Ma, i prové d'un estoc que va colonitzar Eivissa per via ultramarina a un moment indeterminat entre fa 1,3 Ma i c. 30.000 anys.

7. S'han pogut identificar quatre esdeveniments d'extincions que han tingut lloc a cadascuna de les illes estudiades al llarg dels darrers cinc milions d'anys. En alguns casos l'extinció ha afectat de manera global el conjunt de l'arxipèlag balear, mentre que en altres casos les extincions han estat més locals. Les causes de les extincions han estat diverses. Algunes es relacionen amb canvis en les condicions ecològiques (factors ambientals i competència interespecífica). El darrer esdeveniment d'extincions es relaciona amb l'arribada dels humans i la seva fauna acompanyant a les Balears. S'ha identificat la introducció de la rata de la cua blanca (*Eliomys quercinus*) com a agent causal més probable de l'extinció de l'escurçó nan d'Eivissa.
8. Finalment, no s'ha pogut descartar que algun de components faunístics de NB-1 procedeixi de nissagues pre-messinianes. Entre aquests destaca un nou glírid, l'espècie basal del gènere *Hypnomys*, que aparentment sembla derivar d'un glírid del Miocè mitjà/tardà amb una elevada complexitat dental. Aquest fet exclou la seva relació directa amb *Eliomys*, caracteritzat per un patró dental molt més simple, i se n'adiu amb la tendència evolutiva constatada de simplificació dels patrons dentaris d'*Hypnomys* al llarg de la seva evolució.

General conclusions

1. The level of knowledge of the vertebrate fauna of the basal Pliocene of Mallorca and the Pleistocene-Holocene of Eivissa has been substantially improved through the study of the fossil record present at the NB-1 site in Mallorca and at es Pouàs in Eivissa.

2. The NB-1 record has yielded thousands of vertebrate fossil items. In this report I describe the ornithic fauna of the site, which includes a dozen bird species (*Tyto* sp. 1, *Tyto* sp. 2, *Otus* sp., a Phasianidae, a species of Charadriiformes, and at least five species of Passeriformes). The two species of Tytonidae are large, whereas the owl displays morphological features indicative of more terrestrial habits than those of extant *Otus* owls.

3. It has been possible to elucidate that NB-1 is a fossil deposit originated predominantly by bioaccumulation of microvertebrates predated by nocturnal birds of prey, although occasionally remains of larger vertebrates were also incorporated in the deposit. At least two strigiforms, *Tyto* sp. 1 and *Otus* sp., acted as bioaccumulator agents. The third one, *Tyto* sp. 2, could be either as a prey of *Tyto* sp. 1 or as another bioaccumulator agent. The difference in size between *Tyto* sp. 1 and *Otus* sp. is enough as to enable covering a wide range of prey sizes. Consequently, the microvertebrate sample recovered at NB-1 is considered to be very representative of the fauna of non-flying terrestrial micro vertebrates present at the basal Pliocene of Mallorca.

4. The NB-1 site rendered several previously unknown species and genera. They represent the oldest records of their respective phylogenetic lineages known in Mallorca. Some of their features enable to conclude that NB-1 represents the oldest known deposit of the so-called *Myotragus* fauna, as well as the richest in species diversity of all post-Messinian sites of the Balearic Islands.

5. *Paraethomys balearicus* is a murid with a peculiar hypsodont dentition descendant of *Paraethomys meini* from the late Turolian of the Iberian Peninsula. Its discovery in NB-1 documents the occurrence of an episode of faunistic colonization of the archipelago during the MSC. *Paratethomys* is the only genus of African origin present on Mallorca. This genus, together with *Apocricetus darderi* and *Alytes* aff. *muletensis* from the same site, and *Debruijnimys* sp. from the roughly contemporary site of ses Fontanelles in Eivissa, allows to locate unequivocally the source region of the Pliocene and Pleistocene faunas of the Balearic Islands in the SE of the Iberian Peninsula. The colonization was most probably enabled by the establishment of a land connection between the Betic mountain range and the archipelago through the emerged Balearic Promontory. The narrow time frame where all these phylogenetic lineages appear grouped lends a strong support to the hypothesis that there was a single wave of colonization of Mallorca, either by land or via riparian routes.

6. The existence of a dwarf viper in the Upper Pleistocene of Eivissa, is recorded for the first time and described herein as *Vipera latastei ebusitana*. This taxon separated from the eastern Iberian populations of *Vipera latastei* between 1.3 and 0.67 Ma, and colonized the island by overseas dispersal sometime between 1.3 Ma and c. 30,000 years.

7. It has been possible to identify the occurrence of four different extinction events in the vertebrate fossil record of the archipelago of the last five million years. In some cases, extinction affected the entire archipelago, while in others its range was more local. Potential causes of these extinctions are diverse. Some might be related to the occurrence of changes in ecological conditions (such as environmental factors or interspecific competition). The last extinction event recorded is related to the first arrival of humans and their accompanying fauna to the archipelago. The introduction of the Garden Dormouse (*Eliomys quercinus*) has been identified as the most likely causal agent for the extinction of the Eivissan dwarf viper.

8. Finally, it has not been possible to discard that some of the faunal components of NB-1 represent pre-Messinian surviving lines. Among these, a new glirid stands out, the basal species of the genus *Hypnomys*, which apparently seems to derive from a mid/late Miocene glirid displaying a high dental complexity. This fact excludes its direct relationship with *Eliomys*, characterized by a much more simple dental pattern, and fits well with the documented evolutionary trend of simplification of dental pattern in *Hypnomys*.

Conclusiones Globales

1. Se ha mejorado substancialmente el conocimiento sobre la composición de fauna vertebrada del Plioceno basal de Mallorca y del Pleistoceno-Holoceno de Eivissa. Esta mejora se ha realizado principalmente a partir del estudio de fósiles procedentes de los yacimientos de NB-1 a Mallorca y des Pouàs a Eivissa.

2. El registro de NB-1 ha aportado miles de restos fósiles de vertebrados. Esta Tesis ha permitido describir la fauna ornítica del yacimento, la cual incluye una decena de aves (*Tyto* sp.1, *Tyto* sp. 2, *Otus* sp., un Phasianidae, una especie perteneciente al ordren Charadriformes y almenos cinco especies de Passeriformes). Las dos especies de Tytonidae son de gran tamaño, y el autillo presenta rasgos morfológicos propios de hábitos mas terrestres que los de autillos actuales.

3. Se ha podido concluir que NB-1 es un dipósito fosilífero originado predominantemente por la bioacumulación de microvertebrados depredados por rapaces nocturnas, aunque, de manera ocasional, se han incorporado algunos restos de vertebrados de tamaño mayor. Almenos dos estrigiformes, *Tyto* sp. 1 y *Otus* sp., han actuado como a agentes bioacumuladores. La tercera rapaz, *Tyto* sp. 2, podría ser considerada como una presa de *Tyto* sp. 1 o como otro agente bioacumulador. Las diferencias de tamaño entre *Tyto* sp. 1 y *Otus* sp. son suficientemente importantes como para que hayan podido actuar como agentes bioacumuladores de presas de tallas muy diferentes. En consecuencia, se considera que la muestra obtenida a NB-1 es muy representativa de la fauna de vertebrados terrestres no voladores que vivieron durante el Plioceno basal de Mallorca.

4. Las especies encontradas en NB-1 incluyen especies y géneros desconocidos un los yacimientos mas modernos. Se incluyen taxones que representan el registro más antiguo de sus linajes filogenéticos en Mallorca. Gracias a las características de algunos de sus componentes faunísticos, se ha podido concluir que NB-1 es el dipósito conocido más antiguo de la nombrada fauna de *Myotragus*, al mismo tiempo que es el yacimiento más rico en diversidad de especies de las faunas post-messinienses de todas las islas Baleares.

5. Se ha descrito *Paraethomys balearicus*, un múrido con una dentición peculiar, hipsodonta, descendiente de *Paraethomys meini* del Turoliense tardío de la península Ibérica. Su presència en NB-1 documenta una llegada durante la MSC. *Paraethomys* es el único genero presente en Mallorca de origen africano. Éste género, juntamente con *Apocricetus darderi* y *Alytes* aff. *muletensis* del mismo yacimiento, y *Debruijnimys* sp. del yacimiento coetáneo de ses Fontanelles en Eivissa, situa inequívocamente la región de origen de faunas del Plioceno y Pleistoceno de las Balears principalmente al SE de la península Ibérica, a través de una connexión que se establecería desde la cordillera Bética por el Promontorio Balear. La estrecha ventana temporal donde se agrupan todos los linajes filogenéticos proporciona un fuerte soporte a la hipótesis de una única oleada de colonización de Mallorca principalmente por via terrestre y possiblemente a través de corredores de ribera.

6. Se ha documentado la existencia al Pleistoceno superior de Eivissa de una víbora enana, que se ha descrito como *Vipera latastei ebusitana*. Éste taxón se separó de las poblaciones orientales de *Vipera latastei* entre 1,3 y 0,67 Ma, y proviene de un conjunto que colonizó Eivissa por via ultramarina en un

momento indeterminado entre 1,3 Ma y c. 30.000 años.

7. Se han podido identificar cuatro eventos de extinciones que ha tenido lugar en cada una de las islas estudiadas a lo largo de los últimos cinco millones de años. En algunos casos la extinción ha afectado de manera global el conjunto del archipiélago balear, mientras que en otros casos las extinciones han sido mas locales. Las causas de las extinciones han sido diversas. Algunas se relacionan con cambios en las condiciones ecológicas (factores ambientales y competencia interespecífica). El último evento de extinciones se relaciona con la llegada de los humanos y su fauna acompañante en Baleares. Se ha identificado la introducción del lirón careto (*Eliomys quercinus*) como agente causal más probable de la extinción de la víbora enana de Eivissa.

8. Finalmente, no se ha podido descartar que alguno de los componentes faunístics de NB-1 proceda de linajes pre-messinienses. Entre estos destaca un nuevo glírido, la especie basal del género *Hypnomys*, que aparentmente parece derivar de un glírido del Mioceno medio/tardío con una elevada complejidad dental. Este hecho excluye su relación directa con *Eliomys*, caracteritzada por un patrón dental mucho más simple, y congruente con la tendencia evolutiva constatada de simplificación de los patrones dentales de *Hypnomys* a lo largo de su evolución.

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ANNEXOS

Annex 1. Articles elaborats dintre del Programa de Doctorat de Ciències de la Terra de la UB per a la realització de la present Tesi Doctoral

1. Torres-Roig E., Piñero P., Agustí J., Bover P. i Alcover J.A. 2019. First evidence of endemic Murinae (Rodentia, Mammalia) in the early Pliocene of the Balearic Islands (western Mediterranean). *Geological Magazine*, 156: 1742–1750.

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First evidence of endemic Murinae (Rodentia, Mammalia) in the early Pliocene of the Balearic Islands (western Mediterranean)

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Abstract

A new insular species of *Paraethomys* (Muridae, Rodentia) with medium-sized hypsodont teeth is described from the Zanclean of Mallorca (Balearic Islands, western Mediterranean). The m1 displays the most distinctive traits: hypsodonty, a high occurrence of an unusual anterior cingulum, a well-developed labial cingulum, high accessory labial cuspids resembling the *Apodemus* pattern and a funnel between c1 and the hypoconid. *Paraethomys balearicus* sp. nov. preserves traits close to those present in the earliest populations of *Paraethomys meini* from the upper Turolian, such as a developed posterior spur on t3 in the M1, a connection between t4 and t8 in the M1, a narrow connection between t6 and t9 in the M1 and the occasional presence of an individualized t9 and a t12 in some M2s. The relationship between the new taxon and its direct mainland ancestor gives additional support to a Messinian origin for the so-called *Myotragus* fauna, which became isolated after the refilling of the Mediterranean Sea 5.33 Ma ago. The absence of *Paraethomys* in other known younger Mallorcan sites suggests that its extinction most probably occurred at an indeterminate time during the Pliocene Epoch.

1. Introduction

Scientific research on the fossil vertebrates of the Balearic Islands started with Bate (1909), who published the description of the first endemic fossil mammal from the Pleistocene of Mallorca and Menorca, *Myotragus balearicus* Bate, 1909. Later, she described *Hypnomys morpheus* Bate, 1918 and *Nesiotites hidalgo* Bate, 1944 from fossils found on both islands (Bate, 1918, 1944). All these taxa exhibit traits linked to their long insular evolution. Until the end of the 1990s, several late Pliocene and Pleistocene species were described belonging to the same phyletic lineages as these three mammals. These lineages, together with those of the endemic midwife toad *Alytes muletensis* (Sanchiz & Adrover, 1979) and the endemic lizard *Podarcis lilfordi* (Günther, 1874), form the so-called *Myotragus* fauna (Bover *et al.* 2008) that presumably colonized Mallorca during the Messinian Salinity Crisis (MSC). It was widely accepted that the *Myotragus* fauna evolved gradually and without undergoing any change in its composition, which allowed the establishment of local biozones.

The discovery in 2005 of the Caló den Rafelino site (CdR, Mallorca) improved the knowledge on the composition of the *Myotragus* fauna during Pliocene time (Bover *et al.* 2007). At this locality, five different mammals were described, representing a new genus, four new species and one taxon identified only at generic level: *Nesiotites rafelinensis* Rofes, Bover, Cuenca-Bescós & Alcover, 2012 (with a controversial status: see Furió & Pons-Monjo, 2013 and Rofes *et al.* 2013), *Tragomys macpheei* Agustí, Bover & Alcover, 2012; *Hypnomys* sp., *Hypolagus balearicus* Quintana, Bover, Alcover, Agustí & Bailon, 2010 and *Myotragus palomboi* Bover, Quintana & Alcover, 2010. The archaic traits of *M. palomboi* and the derived features of the cricetid *Tragomys macpheei* in comparison with their assumed continental relatives suggested an early Pliocene age for the CdR fauna (Bover *et al.* 2010; Agustí *et al.* 2012).

More recently, a new early Pliocene site in Mallorca, Na Burguesa-1 (NB-1), was discovered in 2012 (Bover *et al.* 2014). Six species of mammals were obtained at this site, five of them belonging to the already known Soricidae, Cricetidae, Gliridae, Leporidae and Bovidae lineages (Bover *et al.* 2014). The final one is the first fossil record of the family Muridae in Mallorca. Analysis of the Anura and Cricetidae specimens (Torres-Roig *et al.* 2017*a*,*b*) indicated that

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Fig. 1. Geological and geographic location of the early Pliocene palaeontological deposit of Na Burguesa-1.

NB-1 can be considered older than CdR. It was assigned a Zanclean age, on the basis of the close relationship between *Apocricetus darderi* and its ancestor *A. alberti*.

In view of this age, the presence of Muridae, a family not yet known from the fossil record of the Balearics, is intriguing. In this paper, we describe a new species of *Paraethomys* based on the murid fossils from NB-1, and we discuss its biogeographic and stratigraphic significance based on its phylogenetic relationships with its mainland relatives.

2. Location, material and methods

The material here studied was recovered from the karstic deposit of NB-1, located at the southwest end of the Serra de Tramuntana, near to Palma, Mallorca, Balearic Islands (Fig. 1). This deposit and the methodology of the extraction of bones from the hard matrix have been described in Torres-Roig *et al.* (2017*a*,*b*). The material was individually catalogued and is curated at the Institut Mediterrani d'Estudis Avançats, Esporles, Mallorca (collection acronym: IMEDEA). It has been compared directly with the largest *P.* aff. *abaigari* population so far recorded (Baza-1 from the Guadix-Baza Basin) and with several *P. meini* populations (Sifón de Librilla section in the Fortuna Basin, Murcia; Puerto de la Cadena, Murcia; and the Botardo section in the Guadix-Baza Basin).

Scanning electron microscope (Hitachi S-3400N) photographs of teeth were taken at the Scientific and Technical Services of the Universitat de les Illes Balears (UIB). The measurements of teeth were obtained using an Edge AM7915MZT Dino-Lite digital microscope, following the method of Martín Suárez & Freudenthal (1993), and the values are expressed in millimetres. The nomenclature used in the description of the molars follows van de Weerd (1976) and Miller (1912). Lower molars are referred to as m1–3 and upper molars as M1–3. Only the best-preserved specimens are included in the descriptive morphological analysis, whereas all the obtained specimens, including those partially eroded or with a high degree of occlusal wear, have been measured.

3. Systematic palaeontology

Order RODENTIA Bowdich, 1821
Family MURIDAE Illiger, 1811
Subfamily MURINAE Illiger, 1811
Genus *Paraethomys* Petter, 1968

The adscription of the NB-1 murid remains to the genus *Paraethomys* is based on the presence of an enamel islet between the anteroconid and the second pair of tubercles in m1, the absence of the anterolabial cuspid in m3, the absence of t7 in the upper molars, the reduction of the t9 in M2, the presence of posterior spurs on the anterior tubercles and an enamel islet formed by the union of the tubercles in M3. This combination of characters allows it to be differentiated from other Miocene–Pliocene murine genera, such as *Apodemus*, *Parapodemus*, *Rhagapodemus*, *Castillomys*, *Micromys*, *Occitanomys* or *Stephanomys*.

Type species. *Paraethomys filfilae* Petter, 1968 from the upper Pleistocene of Algeria.

Paraethomys balearicus sp. nov.
Figure 2

Derivation of name. The specific name refers to the Balearic Islands.

Holotype. IMEDEA **94869**, right mandible with m1, m2 and m3 (Fig. 2a).

Paratypes. Four mandibles with m1–3 (IMEDEA **94870**, 104312, 104313, 105048); one mandible with m1–2 (IMEDEA 104314); one mandible with m2–3 (IMEDEA 106284); 10 isolated m1 (IMEDEA **104337**, 104345, 104350, 104355, **104357**, **104366**, 105150, 106275, **106276**, 106281); 13 isolated m2 (IMEDEA **103954**, 103955, **104343**, 104349, 104356, 104359, 104363, 105154, 105157, 105159, 105160, **106278**, **106279**); six isolated m3 (IMEDEA 103956, **103957**, 103958, **104367**, **105153**, 105158). Four maxillas with M1–M2 (IMEDEA 94871, 104320, 105046, 105047); one maxilla with M3 (IMEDEA 104321); 17 isolated M1 (IMEDEA 94874, 94875, 94876, 104338, **104339**, 104341, 104342, 104344, 104346, 104351, 104358, **104360**, **105148**, 105149, 105155, 106277, **106280**); 13 isolated M2 (IMEDEA 94877, 94880, 94882, 104347, 104348, **104352**, **104353**, 104362, 104364, **105152**, **105156**, 105161, 105163); 12 isolated M3 (IMEDEA 94878, **94879**, 94881, 103959, **104335**, 104336, **104340**, 104354, **104361**, 104365, 105151, 105162). Bold numbers refer to specimens presented in Figure 2.

Locality and horizon. Na Burguesa-1 (Palma, Mallorca); lower Pliocene (MN14).

Diagnosis. Medium-sized and relatively hypsodont *Paraethomys* species. Lower molars characterized by the presence of a well-developed labial cingulum. m1 and m2 with large and high accessory labial cuspids, resembling the *Apodemus* pattern. In addition, the m1 and some m2 present a funnel between the hypoconid and the c1 as a result of the great height of the labial cingulum and the accessory labial cuspids. The m1 presents an anterior cingulum, unusual in the genus, and in some cases a tiny tma lingually located. The M1 and M2 may present a posterior spur on t1 and t3 directed towards the t4–t5 and t5–t6 intersections, respectively. The connections between t1 and t2, as well as between t2 and t3, are well developed in the M1, and t4 contacts basally with t8. Rarely, this molar has a small extra cusp between t1 and t4. The M2 has a posterior spur on t3 directed towards the

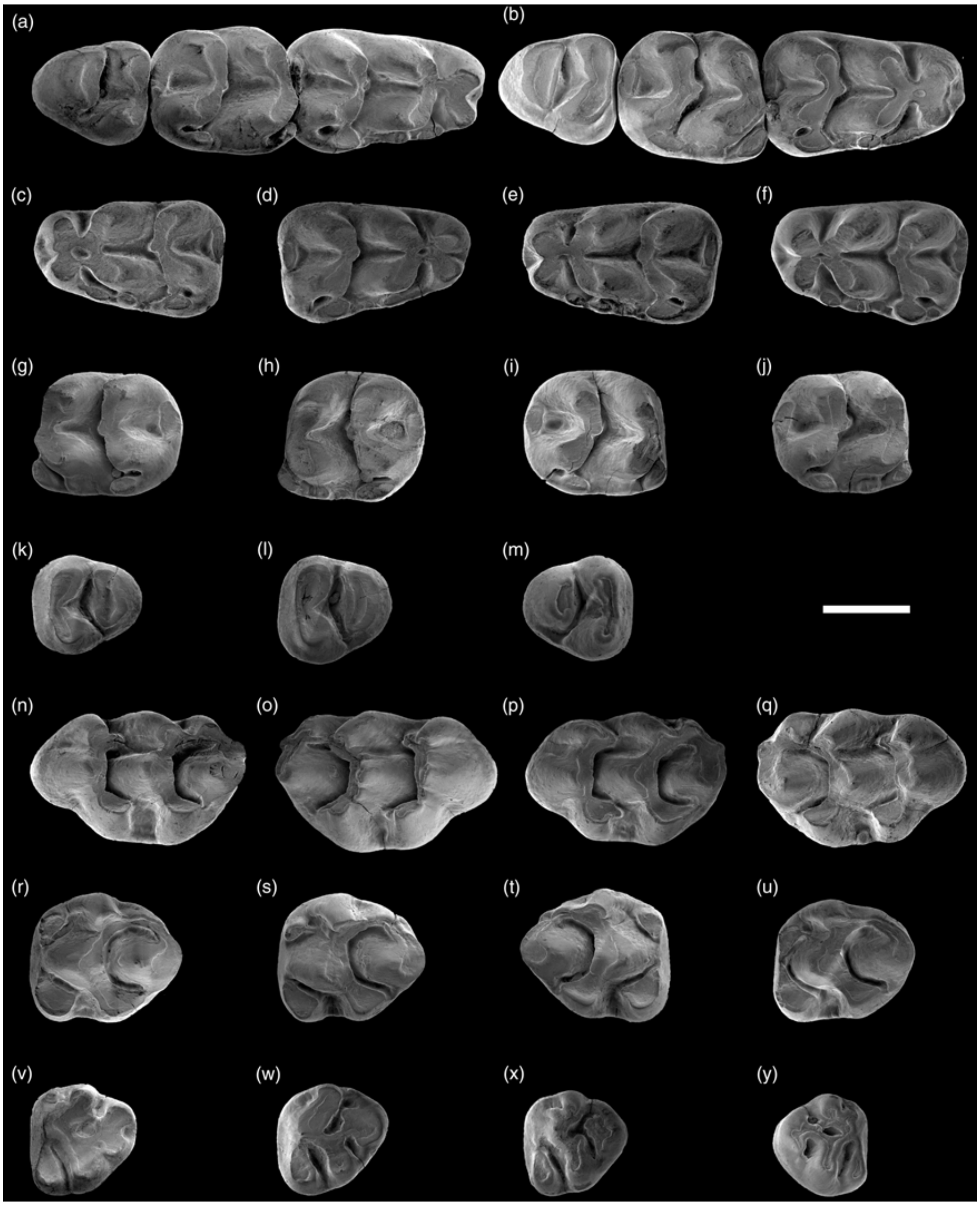

Fig. 2. *Paraethomys balearicus* sp. nov. from Na Burguesa-1, Mallorca: (a) right lower tooth row, mandible IMEDEA 94869 (holotype); (b) right lower tooth row, mandible IMEDEA 94870; (c) left m1, IMEDEA 104337; (d) right m1, IMEDEA 104357; (e) left m1, 104366; (f) left m1, IMEDEA 106276; (g) left m2, IMEDEA 103954; (h) left m2, IMEDEA 104343; (i) right m2, IMEDEA 106278; (j) right m2, IMEDEA 106279; (k) left m3, IMEDEA 103957; (l) left m3, IMEDEA 104367; (m) left m3, IMEDEA 105153; (n) left M1, 104339; (o) right M1, IMEDEA 104360; (p) left M1, IMEDEA 105148; (q) right M1, IMEDEA 106280; (r) left M2, IMEDEA 104352; (s) left M2, IMEDEA 104353; (t) right M2, IMEDEA 105152; (u) left M2, IMEDEA 105156; (v) left M3, IMEDEA 94879; (w) left M3, IMEDEA 104335; (x) left M3, IMEDEA 104340; (y) right M3, IMEDEA 104361.

t5–t6 intersection or t6, and some specimens have a t9 that tends to be individualized and a small t12. Additionally, some specimens have an unusual anterior crest formed by the connection between t1 and t3.

Differential diagnosis. Paraethomys balearicus sp. nov. is on average larger and more hypsodont than *Paraethomys meini* Michaux, 1969 and the connections among cusps in the upper molars are better developed. By contrast, the teeth of *P. balearicus* sp. nov. are smaller than in *Paraethomys abaigari* Adrover, Mein & Moissenet, 1988, and are markedly smaller than in *Paraethomys jaegeri* Montenat & de Bruijn, 1976. Additionally, *P. balearicus* sp. nov. is distinguished from the latter two by its lesser degree of stephanodonty, a narrow connection between t6 and t9 in the M1, the presence in the M2 of a t3 with a posterior spur directed towards the t5–t6 intersection, generally isolated in the other species, an individualized t9 and an occasional t12. The molars of *P. balearicus* sp. nov. are slightly larger than those of *Paraethomys belmezensis* Castillo

Table 1. Measurements of the teeth and the lower tooth row of *P. balearicus* sp. nov. from NB-1

	Length (mm)				Width (mm)			
Element	N	Min.	Mean	Max.	N	Min.	Mean	Max.
m1	16	2.16	2.33	2.44	16	1.33	1.45	1.52
m2	20	1.56	1.72	1.84	19	1.37	1.50	1.58
m3	11	1.27	1.37	1.46	11	1.13	1.22	1.32
M1	18	2.39	2.53	2.67	19	1.54	1.65	1.77
M2	15	1.68	1.77	1.93	15	1.43	1.55	1.66
M3	11	1.12	1.29	1.40	13	1.11	1.21	1.29
Lower tooth row	4	5.01	5.30	5.46				

Ruiz, 1992. However, *P. belmezensis* displays a well-developed tma connected to the lingual lobe of the anteroconid; a small t3 attached to t2, and t6 separated from t9 in the M1; and an M2 without t3 or t9 and an isolated t8. *Paraethomys lissasfensis* Geraads, 1998 is slightly smaller than *P. balearicus* sp. nov., the t9 is absent in the M2, and it has a deep valley between the t2 and t3 in the M1.

Measurements. See Table 1.

4. Description

m1: Generally the tma is absent, but 3 out of 16 specimens have a small tma located labially (Fig. 2b, c). In addition, 12 out of 16 specimens present an anterior cingulum (Fig. 2a–c, e. f). The anteroconid is slightly asymmetrical in 12 out of 16 specimens, the labial side being narrower than the lingual one, and it is symmetrical in the rest of the specimens (4 out of 16). There is a small and round enamel islet between the anteroconid complex and the protoconid–metaconid pair in 7 out of 16 specimens (Fig. 2b–d, f). Usually, the connection of the labial lobule of the anteroconid is narrower than the lingual lobule, and it is absent in 3 out of 16 m1s (Fig. 2a, e). The labial cingulum is well developed. There are two or three large and high accessory labial cuspids, occasionally merged, located on the mesio-labial side of the protoconid. The c1 is high, large and subtriangular. It is attached anteriorly to the hypoconid. Additionally, in 13 out of 16 specimens the c1 has a posterior spur connected to the posterolabial side of the hypoconid, forming a funnel between both cuspids. Only one specimen has a small extra tubercle on the posterior side of the c1 (Fig. 2f). The hypoconid–entoconid pair is isolated from the anterior cuspids. There is a reduced longitudinal spur in 15 out of 16 specimens. The terminal heel can be compressed or elongated and is posterolingually located. There are two roots.

m2: The anterolabial cuspid is oval or oval-compressed and isolated from the protoconid. The labial cingulum is well to moderately developed, reaching the protoconid in some individuals. There is a small accessory labial cuspid in contact with the protoconid in 9 out of 16 specimens (Fig. 2b, g, h. j). The c1 is oval and similar in size to the anterolabial cuspid. Generally, the c1 posteriorly contacts the base of the hypoconid, and 4 out of 17 specimens have a funnel between the c1 and the hypoconid as a result of a spur connection on the posterolabial side of the hypoconid (Fig. 2g, i). The hypoconid–entoconid pair is isolated from the anterior pair. There is a small longitudinal spur in 15 out of 18 specimens. The terminal heel is oval-compressed or semilunar. There are two roots.

m3: The pattern is very simple and globose (Fig. 2k–m). The protoconid–metaconid complex is slightly asymmetrical, the protoconid being narrower than the metaconid in 8 out of 12 specimens. The labial cingulum is well developed and interrupted at the protoconid. The labial accessory cuspids are absent. There is neither an anterolabial cuspid nor a c1. As in m2, the hypoconid–entoconid complex is isolated from the anterior pair. There are two roots.

M1: The t1 is much larger than the t3 and it is displaced backwards with respect to the latter. Both the t1 and the t3 have a posterior spur directed towards the t4–t5 and t5–t6 intersections, respectively (Fig. 2n–q). They can contact them basally (Fig. 2o, q). The posterior spur of the t3 is better developed than that of the t1. Only in 2 out of 16 specimens is the posterior spur on t1 absent. The t1–t2 contact is narrower than that of the t2–t3 contact. There is neither a t1bis nor t2bis. The t4 contacts the t8 very basally through a low spur. There is a round and low extra cusp between the t1 and t4 (Fig. 2q) in 4 out of 19 individuals. A narrow t6–t9 connection is present in 8 out of 11 M1 specimens (Fig. 2n, o, q). A small t12 is present in 13 out of 16 specimens. There are three roots. Occasionally, there is a fourth reduced root on the labial central side.

M2: The t1 is much larger than the t3. In 11 out of 13 specimens, the t1 possesses a posterior basal spur directed towards the t4–t5 intersection (Fig. 2r, s), and 11 out of 15 specimens have an anterior spur directed towards the anterolingual side of the t5. In 9 out of 14 specimens, the t3 has a small posterior spur directed towards the t5–t6 intersection or the t6 (Fig. 2s, u), and 10 out of 16 have an anterior spur directed towards the anterolabial side of the t5. There is an anterior crest formed by the connection between the anterior spurs of the t1 and the t3 in 3 out of 15 individuals (Fig. 2t–u). This crest is separated from the anterior side of the t5 by a valley (Fig. 2u). An individualized t9 is present in 8 out of 17 specimens, a character that is more evident as wear advances (Fig. 2t). In 4 out of 12 specimens there is a small t12 (Fig. 2s, t). There are three roots.

M3: Hypsodont molar with highly variable morphology (Fig. 2v–y). Usually, the t1 is oval and it has a spur directed towards the t5, contacting it basally in 11 out of 12 specimens. A tiny t3 is present in 4 out of 10 specimens (Fig. 2v, x, y). The t4, t5, t6 and t8 are united, forming a central closed depression in 7 out of 11 M3s (Fig. 2v, y). The valley between the t4 and t8 can be developed into a funnel owing to the presence of enamel in the lingual space between the t4 and t8 in 9 out of 12 specimens (Fig. 2v, y). Similarly, there is a third funnel between the t8 and t6 in 10 out of 11 specimens in which they are joined by the presence of lingual enamel (Fig. 2v, y). Just 1 out of 10 specimens displays a bilobular t8 with a small posterior cingulum (Fig. 2v). There are three roots.

5. Discussion

In general terms, the European *Paraethomys* lineages increased in size over time. García-Alix *et al.* (2008) recorded this size increase from the earliest (late Turolian) to the latest (early Ruscinian) populations of *P. meini* in the Granada Basin, Spain. Similarly, Piñero & Agustí (2017) recognized an increase in size from the first populations of *P. meini* to *P.* aff. *abaigari* in the Fortuna Basin, Spain. Pliocene palaeontological sites (MN14 and MN15) in some basins on the Iberian Peninsula have yielded two coeval *Paraethomys* forms: one of small size, corresponding to *P. meini*, and another of larger size, belonging to the lineage composed by *P.* aff. *abaigari* – *P. abaigari* – *P.* aff. *jaegeri* – *P. jaegeri* (Mein *et al.* 1990). Among these basins are the Granada (García-Alix *et al.* 2008), Fortuna (Piñero & Agustí, 2017), Guadix-Baza (Piñero *et al.* 2017, 2018), Cabriel (Mansino *et al.* 2015*b*), Alcoi (Mansino *et al.* 2013, 2015*a*, 2016) and Teruel (Adrover *et al.* 1993). Piñero & Agustí (2017) proposed that the phyletic lineage *P.* aff. *abaigari* – *P. abaigari* – *P. jaegeri* was derived from a primitive *P. meini*, marked by both a progressive size and stephanodonty increase through early Pliocene time, which evolved in parallel with a conservative *P. meini* lineage. A. García-Alix (unpub. Ph.D. thesis, Univ. Granada, 2006) observed that the size of *P. meini* from the Granada Basin decreased when a new lineage containing a larger species (*P.* aff. *abaigari* or *P. abaigari*) appeared. This trend seems to change in the last populations of *P. meini* from the Granada Basin (early Pliocene, late MN14), in which its size increases again. Mansino *et al.* (2017*b*) proposed that *P. meini* tends to increase in size in localities that lack species of the lineage *P.* aff. *abaigari* – *P. jaegeri*, while, after the gradual appearance of *P.* aff. *abaigari* in early Pliocene time (MN14), *P. meini* became smaller in sympatric conditions. *Paraethomys belmezensis* from the Belmez-1 locality (southern Iberian Peninsula; Castillo Ruiz, 1992), a species probably also derived from *P. meini*, is slightly larger than the latter and clearly smaller than *P. abaigari*. The African *P. lissasfensis* from the upper Miocene, apparently related to the Iberian *Paraethomys* (Geraads 1998), has a molar size slightly larger than the specimens of *P. meini* from Venta del Moro (Mansino *et al.* 2017*a*). This locality contains one of the smallest sized populations of *P. meini*. *Paraethomys balearicus* sp. nov. presents a significantly larger size than *P. meini* across practically all its evolutionary lineage, with the exception of the late Turolian and the late Ruscinian *P. meini* populations, with which there is some size overlap (fig. 5 in Mansino *et al.* 2017*a*). The size of the m1 of *P. balearicus* sp. nov. is larger than *P. belmezensis*, whereas the M1 size overlaps considerably. *Paraethomys balearicus* sp. nov. is only slightly larger than *P. lissasfensis*, although there is some overlap in the range of tooth lengths. By contrast, the tooth sizes of *P.balearicus* sp. nov. overlap widely with those of *P.* aff. *abaigari* (Adrover *et al.* 1993; García-Alix *et al.* 2008; Piñero *et al.* 2017; Mansino *et al.* 2015*b*, 2016), but they differ morphologically from *P.* aff. *abaigari* by the presence of an anterior cingulum on the m1, a funnel between the hypoconid and c1 in m1, and a more reduced longitudinal spur and a narrow connection between t6–t9 in M1. The *P. balearicus* sp. nov. molars are smaller than those of *P. abaigari* (Adrover *et al.* 1988), and they are considerably smaller than the teeth of *P. jaegeri* (Fig. 3; Montenat & de Bruijn, 1976; Castillo & Agustí, 1996).

Paraethomys balearicus sp. nov. shows some morphological traits that are close to the earliest populations of *P. meini*:

(1) *Paraethomys balearicus* sp. nov. presents a posterior spur both on t1 and on t3 in M1, markedly more developed on t3. In *P. meini* the posterior spur is also more developed on the t3, although it is variable across time. In the late Turolian *P. meini* specimens from Venta del Moro and SIF-61, it is not markedly developed (Mansino *et al.* 2017*a*; Piñero & Agustí, 2017). On the other hand, this spur is more developed in the latest Turolian specimens from the Granada Basin, whereas the earliest Ruscinian *P. meini* presents a more reduced t3 (García-Alix *et al.* 2008). Finally, in the Pliocene populations of the Teruel and Alcoi basins, there are specimens that have lost the spur completely (Adrover *et al.* 1988; Mansino *et al.* 2013, 2016).

(2) Generally, the connection between t4 and t8 in the M1 is low in *P. balearicus* sp. nov., as in *P. meini*, whereas in *P.* aff. *abaigari*/*P. abaigari* this crest is quite high.

(3) The connection between t6 and t9 in the M1 is narrow in *P. balearicus* sp. nov., as in the oldest populations of *P. meini*, whereas in *P.* aff. *abaigari*/*P. abaigari* it is wide.

(4) *Paraethomys balearicus* sp. nov. frequently presents an individualized t9 and occasionally a reduced t12 in the M2. In the earliest sites in the Granada basin, *P. meini* may present a reduced t12 in the M2, usually when the t9 is slightly inflated (A. García-Alix, unpub. Ph.D. thesis, Univ. Granada, 2006; R. Minwer-Barakat, unpub. Ph.D. thesis, Univ. Granada, 2005).

5.a. Palaeogeography

Paraethomys was first recorded on the Iberian Peninsula as *P. meini* at Sifón de Librilla (Fortuna Basin, southeastern Spain; level SIF-61) and at Venta del Moro (Cabriel Basin, eastern Spain), both roughly dated to *c.* 6.2 Ma (Garcés *et al.* 1998; Agustí *et al.* 2006; Gibert *et al.* 2013; Piñero & Agustí, 2017; Mansino *et al.* 2017*b*).

Paraethomys reached the Iberian Peninsula slightly prior to the MSC, and it has been considered as one of the representative taxa of the African–Iberian faunal exchange (Garcés *et al.* 1998; van Dam *et al.* 2001; Agustí *et al.* 2006). *Paraethomys meini* (= *P. miocaenicus* Jaeger, Michaux & Thaler, 1975) was initially described from the site of Khendek-el-Ouaich (Morocco; Jaeger *et al.* 1975). From there, it arrived on the Iberian Peninsula at the same time as the camelid *Paracamelus*, present at Venta del Moro and Librilla (Garcés *et al.* 1998; Agustí *et al.* 2006). Thus, the arrival of these genera probably took place *c.* 0.25 Ma before the onset of the MSC, through a faunal exchange across an ephemeral land bridge in a restricted Rifian corridor (Agustí *et al.* 2006; Gibert *et al.* 2013; García-Alix *et al.* 2016) or by crossing a narrow sea channel. An alternative scenario, although currently questioned (e.g. R. Minwer-Barakat, unpub. Ph.D. thesis, Univ. Granada, 2005), assumed that a similar population of *P. meini* (= *P. anomalous* de Bruijn, Dawson & Mein, 1970; described from the uppermost Miocene or lower Pliocene of Maritsa, Rhodes) colonized the two shores of the Mediterranean from the east at the same time (e.g. Jaeger *et al.* 1975).

The MSC represents one of the most important events in the Neogene period of the Mediterranean area. The closing of the connection with the Atlantic Ocean involved the isolation and partial desiccation of the Mediterranean Sea (Hsü *et al.* 1973, 1977). This event had major climatic and biogeographic consequences, allowing the last mammalian exchange between Europe and Africa over the western Mediterranean corridor (Jaeger *et al.* 1975, Agustí *et al.* 2006; van der Made *et al.* 2006). New species of African affinities, such as *Myocricetodon jaegeri* Benammi, 2001 and *Debruijnimys almenarensis* (Agustí 1990), reached the Iberian Peninsula (Minwer-Barakat *et al.* 2009), and simultaneously mammals of European origin spread into Africa (e.g. the pika *Prolagus* Pomel, 1853 and the murid *Occitanomys* Michaux, 1969).

It is widely accepted that the arrival of the Plio-Pleistocene fauna on the Balearic Islands is related to the MSC, crossing via a land bridge that connected the Balearics with the mainland (van der Made *et al.* 2006; Bover *et al.* 2008). The arrival of the NB-1 fauna to Mallorca (including at least 6 mammals, 12 reptiles, and 4 amphibians) is unequivocally related to their dispersal during Messinian time (late Miocene) via a terrestrial route. The narrow window of time in which the group appears supports a terrestrial connection, and cannot be explained by the random drift of animals over time one-by-one from the mainland to far-away islands on flotsam (Mas *et al.* 2018). The whole fauna recorded at NB-1 together with the evidence of a very fast and short episode of refilling of the

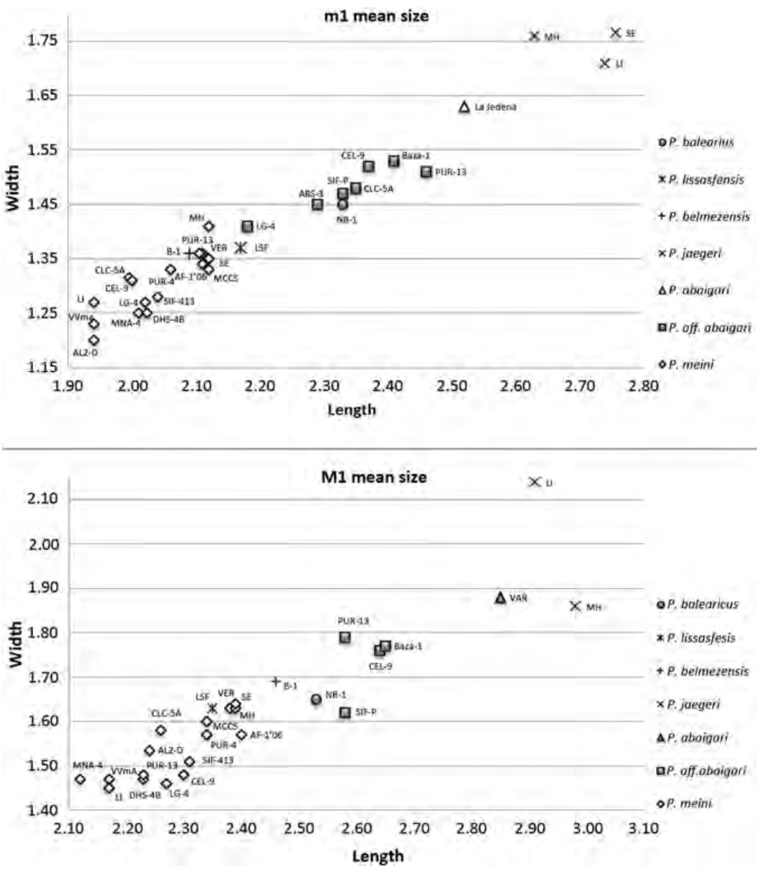

Fig. 3. (Colour online) Scatter diagram showing m1 and M1 mean size of several late Miocene and Pliocene populations of *P. meini*, *P.* aff. *abaigari*, *P. abaigari*, *P. jaegeri*, *P. belmezensis*, *P. lissasfensis* and *P. balearicus* sp. nov. Abbreviations: VVmA – Venta del Moro A (late Miocene, Mansino *et al.* 2017*a*); MNA-4 – Mina-4 (late Miocene, A. García-Alix, unpub. Ph.D. thesis, Univ. Granada, 2006); DHS-4B – La Dehesa-4B (late Miocene, A. García-Alix, unpub. Ph.D. thesis, Univ. Granada, 2006); VER – Verduno Level 1 (late Miocene, Colombero *et al.* 2013); MCC5 – Moncucco Torinese (late Miocene, Colombero *et al.* 2014); PUR-4 – Purcal-4 (early Pliocene, A. García-Alix, unpub. Ph.D. thesis, Univ. Granada, 2006); SIF-413 – Sifón de Librilla-413 (early Pliocene, Piñero & Agustí, 2017); NB-1 – Na Burguesa-1 (this work); LSF – Lissasfa (early Pliocene, Geraads, 1998); AF-1'06 – Alcoi Forn (early Pliocene, Mansino *et al.* 2016); ABS-3 – Alcoi Barranc Sud (early Pliocene, Mansino *et al.* 2015*a*); CLC-5A – Calicasas-5A (early Pliocene, A. García-Alix, unpub. Ph.D. thesis, Univ. Granada, 2006); PUR-13 – Purcal-13 (early Pliocene, A. García-Alix, unpub. Ph.D. thesis, Univ. Granada, 2006); LG-4 – La Gloria-4 (early Pliocene, Adrover *et al.* 1993); CEL-9 – Celadas-9 (early Pliocene, Adrover *et al.* 1993); SIF-P – Sifón de Librilla-P (early Pliocene, Piñero & Agustí, 2017); Baza-1 (early Pliocene, Piñero *et al.* 2017); AL2-D – Alcoi 2D (early Pliocene; Mansino *et al.* 2013); VAR – Villalba Alta Río (middle Pliocene, Adrover *et al.* 1988); LJ – La Juliana (middle Pliocene, Montenat & de Bruijn, 1976); B-1 – Belmez-1 (middle Pliocene, Castillo Ruiz, 1992); MH – Mont-Hélène (middle Pliocene, Aguilar *et al.* 1986); SE – Sète (middle Pliocene, Adrover, 1986).

western Mediterranean Basin (Garcia-Castellanos *et al.* 2009) after the opening of Gibraltar (that quickly provided a high degree of isolation to Mallorca), and the total absence of new terrestrial vertebrate immigrants arriving onto the island over the last 5 Ma, strongly supports a terrestrial pathway for the fauna's appearance.

Although affinities between some of the endemic mammals from the Balearic Islands and mainland European-related species have been suggested (e.g. Reumer, 1980; Bover *et al.* 2010), direct evidence for the origin of this fauna was elusive until the discovery of the NB-1 site. The Pliocene fauna from CdR (Bover *et al.* 2014) improved knowledge on the fauna that arrived on the islands, increasing the number of taxa, but the high degree of endemicity displayed by the components of this fauna already obscures any kind of unquestionable relationship with their continental ancestors. NB-1 is the key site linking the Plio-Pleistocene Mallorcan fauna with its mainland source stocks. This site yielded a relatively diverse fauna containing some species that show clear relationships with their continental ancestors from the upper Turolian. This is the case for *Apocricetus darderi*, a giant species with a dental morphology very close to *Apocricetus alberti* (Torres-Roig *et al.* 2017*b*). *Apocricetus darderi* is the first endemic Mallorcan mammal that was confidently related to a direct mainland ancestor, providing the first solid palaeontological evidence of a Messinian origin for the Plio-Pleistocene fauna of Mallorca. The description of *P. balearicus* sp. nov. points again – in an even more solid way – to the Messinian origin of the palaeontological assemblage recorded in NB-1, and of its derived Plio-Pleistocene Mallorcan fauna. The most plausible hypothesis is that at the peak of the Mediterranean desiccation (5.60–5.54 Ma; Roveri *et al.* 2016), some rodent taxa of African origin reached the Balearic Islands from eastern Iberia: *Paraethomys* arrived on Mallorca and *Debruijnimys* reached Eivissa (Agustí, 1989). In the same colonization event, other taxa of Iberian origin also reached the Balearics (e.g. *Apocricetus*). *Paraethomys balearicus* sp. nov. together with *A. darderi* and the anuran *Alytes* aff. *muletensis* allow us to suggest that the Baetic System was the main source region for the MSC colonization of the Balearic Islands, based on the distribution of fossils of their ancestors.

5.b. Island evolution

Several murines evolved under insular conditions in the western Mediterranean region. Endemic species have been described from the upper Miocene of Tuscany (Bacinello; Engesser, 1989), Fiume Santo (Sardinia; Casanovas-Vilar *et al.* 2011) and the Gargano promontory (Freudenthal, 1976; Abbazzi *et al.* 1993; Savorelli *et al.* 2016). Other species have been described from the Plio-Pleistocene of Corsica, Sardinia (Hensel, 1856; Major, 1905; Brandy, 1978) and Sicily (Thaler, 1972). In Bacinello, a lineage starting with *Huerzelerimys vireti* from level V0 gave rise to the larger *Huerzelerimys oreopitheci* (level V1) and the endemic genus *Anthracomys* (*A. majori* from level V2 and *A. lorenzi* from level V3; Engesser, 1989). The main evolutionary trends observed in this lineage are size and hypsodonty increases. In Gargano, a number of lineages have been recognized within the endemic genus *Mikrotia*, in which the major evolutionary trends are the proliferation of lobes in the m1 and M3, in a similar way to arvicolids, and size and hypsodonty increases (Freudenthal, 1976; Abbazzi *et al.* 1993; Maul *et al.* 2014). Although a relationship with the late Miocene continental genus *Stephanomys* has been suggested (Freudenthal, 1985), the origin of *Mikrotia* should most probably be considered to be the late Miocene genus *Parapodemus* (Agustí, 1986). A second endemic genus, *Apatodemus*, is present in the fissure infillings from Gargano (Savorelli *et al.* 2016). Two taxa have been accepted for this lineage: *A. degiulii* (type species) and an unnamed and larger *Apatodemus* sp. A moderate increase in size is observed as an evolutionary pattern in this endemic lineage, although always within the range of the continental species of *Apodemus*, such as *Apodemus gudrunae* (from which they most probably derive).

In Corsica and Sardinia, a lineage has been recorded starting with the species *Rhagapodemus azzarolii* (present at the site of Mandriola, Sardinia; Angelone & Kotsakis, 2001), which derives from the continental species *Rhagapodemus ballesioi*. *Rhagapodemus azzarolii* gave rise to an endemic Sardinian genus *Rhagamys* (*R. minor* Brandy, 1978, from Capo Figari, Sardinia, and *R. orthodon*, from Corsica and Sardinia). A trend towards size and hypsodonty increase is also observed in this lineage. Other endemic murids are the large-sized *Apodemus mannu* from the Pliocene site of Mandriola (Sardinia; Pecorini *et al.* 1974), and another large representative of *Apodemus*, *A. maximus*, at Monte Pellegrino (Sicily; Thaler, 1972). The presence at this latter site of an African ctenodactylid (*Pellegrinia panormensis*) strongly suggests a Messinian origin for the fauna from Monte Pellegrino (Moyà-Solà *et al.* 1984).

Therefore, according to the available data, most cases of insular endemism in murids in the western and central Mediterranean derive from an *Apodemus*-related stock (*Parapodemus, Rhagapodemus, Apodemus*), with an exception in the Tusco-Sardinian province (where some endemic island species were originated from *Huerzelerimys*). In contrast, *P. balearicus* sp. nov. represents the first case of insular evolution described for *Paraethomys*. The derived features recorded in *P. balearicus* sp. nov. with respect to its presumed continental precursor (*P. meini*) are in full agreement with those observed in other insular murids (*Anthracomys, Rhagamys, Apodemus*): an increase in size and hypsodonty (Fig. 4), a general trend for insular Muridae (e.g. Locatelli *et al.* 2012). However, *P. balearicus* sp. nov. does not reach the gigantic size attained by the late representatives of *Mikrotia*, as was also the case for *Anthracomys* and *Rhagamys*. The early insular evolutionary stage of *P. balearicus* sp. nov. contrasts with that of *Apocricetus darderi*, also present at NB-1. Probably, the ecological insular conditions of Mallorca, with its limited area and resources, prevented the presence of a second large rodent species on the island.

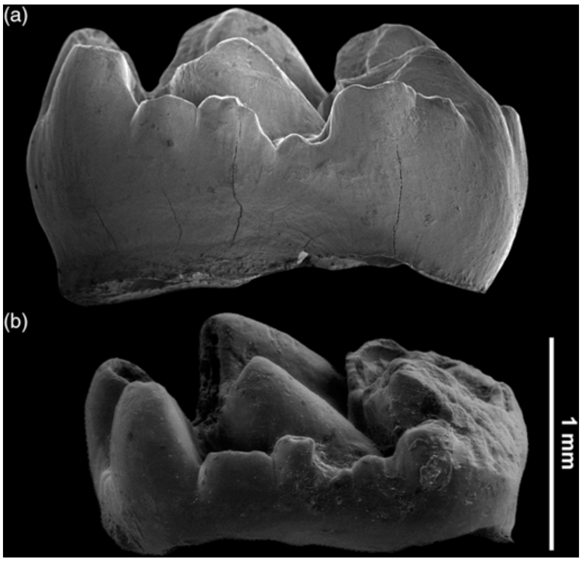

Fig. 4. Comparison of the hypsodonty between the m1s of (a) *P. balearicus* sp. nov., MEDEA 106276, and (b) *P. meini*, BO-D-2-14; Botardo-1D, Guadix-Baza basin, in labial view.

5.c. Extinction

Paraethomys has not been recorded in the other Pliocene sites of Mallorca so far. Although this lack of records could suggest that the species probably vanished soon after its arrival on Mallorca, the scarce and partially eroded remains of micromammals retrieved from deposits such as CdR precludes establishing any accurate chronology for the extinction of *Paraethomys*. Nevertheless, other species recorded in the early Pliocene sites of NB-1 and CdR (e.g. *Maioricalacerta*, *Hypolagus*, *Apocricetus*/*Tragomys*) are not recorded in deposits with a more recent chronology, suggesting an extinction event slightly before or during Piazencian time.

6. Conclusions

A new species of *Paraethomys* from the lower Pliocene of Mallorca is described as *P. balearicus* sp. nov. based on the following dental traits: lower molars with well-developed labial cingulum; m1 and m2 with large and high accessory labial cuspids and a funnel between the hypoconid and the c1; m1 with an anterior cingulum, unusual in the genus; M1 and M2 with a posterior spur on the t1 and the t3; M1 with well-developed connections between t1–t2 and t2–3, and with a t4 that reaches the t8; M2 with an individualized t9 and a small t12; and an M3 with three funnels. The greatest development of the posterior spur on t3 in the M1, the connection between t4 and t8 in the M1, and the presence of an individualized t9 and a reduced t12 in the M2 allows us to relate *P. balearicus* sp. nov. to the late Turolian populations of the Iberian *P. meini*. Its arrival to the island occurred during the MSC, and after the refilling of the Mediterranean Sea it started to evolve under insular conditions, increasing slightly in size and degree of tooth hypsodonty, originating *P. balearicus*. This species represents the first Neogene mammal recorded in the Gymnesic Islands that could have had an African origin, although it likely arrived in Mallorca through the Baetic System. The accurate timing and causes of its extinction are unknown.

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Un assemblage paléornithologique du début du Pliocène de l'île méditerranéenne de Majorque : oiseaux rapaces comme bioaccumulateurs à Na Burguesa-1

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ABSTRACT

A palaeornithological assemblage from the early Pliocene of Mallorca (Balearic Islands) is documented on 583 fossil bones from Na Burguesa-1 site. Ten different taxa have been identified: two Tytonidae, one small-sized Strigidae, one Phasianidae, one Charadriiform, and at least five Passeriformes. The specimens included in the Tytonidae correspond to a giant Barn Owl, *Tyto* sp. 1, with size similar to *Tyto robusta*, and a second Barn Owl, *Tyto* sp. 2, similar in size to *Tyto sanctialbani*. The small-sized Strigidae is attributed to *Otus* sp., although some of the pedal phalanges obtained are included only tentatively in this genus. The presence of these nocturnal raptorial birds combined with the prevalence of small vertebrates (mainly ranging from *ca.* 8 g to almost 1 kg) with practically unaltered bones suggests that this deposit was originated by the accumulation of prey remains of these owls.

RÉSUMÉ

Un assemblage paléo-ornithologique du début du Pliocène de Majorque (îles Baléares) est documenté à partir de 583 os fossiles obtenus dans le gisement de Na Burguesa-1. Dix taxons différents ont été identifiés dans cet assemblage : deux Tytonidae, un Strigidae de petite taille, un Phasianidae, un Charadriiforme et au moins cinq Passeriformes. Les fossiles inclus dans les Tytonidae correspondent à une chouette effraie géante, *Tyto* sp. 1, de taille similaire à *Tyto robusta*, et à une deuxième chouette effraie, *Tyto* sp. 2, de taille similaire à celle de *Tyto sanctialbani*. Les Strigidae de petite taille sont attribuées à *Otus* sp., bien que certaines

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des phalanges pédales obtenues ne soient attribuées à ce genre que de manière provisoire. La présence de ces rapaces nocturnes et celle, prédominante, de restes de petits vertébrés (dont la taille varie entre environ *ca.* 8 g et presque 1 kg), avec leurs ossements pratiquement inaltérés, permet d'interpréter l'origine du gisement comme une accumulation dérivée de la prédation par ces strigiformes.

1. Introduction

The Balearic Islands form the most isolated archipelago in the Mediterranean Sea. They consist of two groups of islands: the Gymnesic Islands (Mallorca, Menorca and surrounding islets) and the Pityusic Islands (Eivissa, Formentera and surrounding islets). Before the arrival of the first humans in these islands, about 4300 years ago (Bover et al., 2016), the fauna and ecosystems present on both groups of islands were highly peculiar (Palmer et al., 1999). At that time, the community of terrestrial vertebrates in the Pityusics did not have terrestrial mammals and consisted only of birds, bats, the endemic Pityusic lizard *Podarcis pityusensis*, and an extinct endemic snake recently discovered (Torres-Roig et al., in press). In contrast, on the Gymnesics lived an endemic terrestrial vertebrate fauna consisting of three non-flying endemic mammals (a dwarf and highly modified bovid, *Myotragus balearicus*; a large-sized dormouse, *Hypnomys morpheus*, and a shrew, *Nesiotites hidalgo*), the endemic Balearic lizard *Podarcis lilfordi*, the endemic Mallorcan midwife toad *Alytes muletensis*, plus birds and bats (Bover, 2011). All these faunas were the result of a complex palaeogeographic and evolutionary history that started 5.3 million years ago (Mya), at the end of the Messinian Salinity Crisis (MSC), when the Balearic Islands arose as separated entities isolated from their neighbouring continental landmasses.

Bover et al. (2008) established that three different faunistic assemblages lived in Mallorca, Menorca, and Eivissa during the Pliocene. While the foregoing *Myotragus* fauna lived in Mallorca, Menorca was inhabited by a peculiar fauna characterized by the presence of the giant leporid *Nuralagus rex*, the giant glirid *Muscardinus cyclopeus* and a giant tortoise, aff. *Titanochelon gymnesica* (Bate, 1914; Luján et al., 2017; Quintana et al., 2011). In Eivissa, the early Pliocene was characterised by the presence of a giant and not yet formally described gerbillid, *Debruijnimys* sp. (Moyà-Solà et al., 1984, 1999). On Menorca, the *Nuralagus* fauna was later replaced by the *Myotragus* fauna of Mallorca, since both islands merged for the first time during the first glaciation event, roughly 2.58 Mya ago (Bover et al., 2008). The geographic isolation between the Pityusics and the Gymnesics has remained unchanged and as it currently stands since 5.3 Mya until the present.

The recent discovery of two early Pliocene paleontological sites in Mallorca has enabled one to shed light on the oldest faunistic assemblage present on the Balearics. First, the discovery of the Caló den Rafelino deposit, which yielded the ancestors of the classic triad of mammals of the *Myotragus* fauna together with the giant and highly modified cricetid *Tragomys macpheei*, the leporid *Hypolagus balearicus*, and several reptiles (a large-sized tortoise, a giant viper, a large-sized lizard, and others; see Bover et al., 2014, for a review of this deposit). Later on, the fossiliferous karstic deposit of Na Burguesa-1 (hereafter, NB-1) was discovered and it has become a key site to understand the origin of the endemic *Myotragus fauna* from Mallorca (e.g., Bover et al., 2014; Mas et al., 2017; Torres-Roig et al., 2017, 2019a, and in press). The aim of the present paper is to describe the bird assemblage recovered at NB-1 and analyse the key role that nocturnal birds of prey have played in the formation of this vertebrate deposit. This sample represents the best available window to know the peculiar vertebrate faunal assemblage that lived in Mallorca *ca.* 5 million years ago.

2. The NB-1 deposit

The NB-1 deposit is located in the Na Burguesa mountains, on the southwestern part of the Serra de Tramuntana range of Mallorca (Balearic Islands, western Mediterranean; Fig. 1). It consists of a fossil-rich breccia infilling a palaeocave or fissure excavated in lower Lias grey limestone, situated at 160 m asl, close to the road from Génova to Mirador de Na Burguesa (Palma). Nowadays, this ancient cavity is completely eroded and only the infilling sediments are preserved as isolated blocks. The breccia consists of sharp pebbles of limestone embedded in a matrix of red–brown silts strongly cemented by calcite. The recovered blocks contain layers with abundant remains of small vertebrates (Bover et al., 2014).

3. Material and methods

The palaeornithological material obtained at NB-1 consists of 583 fossil bird bones curated at the "Institut Mediterrani d'Estudis Avançats" (acronym: IMEDEA; see Supplementary Table 1) of which *ca.* 90% are pedal phalanges of low taxonomic value. Furthermore, the fragmentary condition of an important part of the rest of the material recovered precludes its taxonomic identification beyond the genus level. Up to 321 bones have been diagnosed below the class level, of which 200 have been identified at order level and 121 at the genus level.

The fossils were recovered using a chemical treatment to dissolve the breccia blocks. The preparation task, which lasted up to two years, consisted of cyclic immersions of these blocks in acetic acid (10–15%) for 48 h, then in water for 48 h, air-drying, and consolidation of bones with a thermoplastic acrylic resin (Paraloid B-72). Once extracted, the bones were manually cleaned to eliminate the remains of the adhesive matrix.

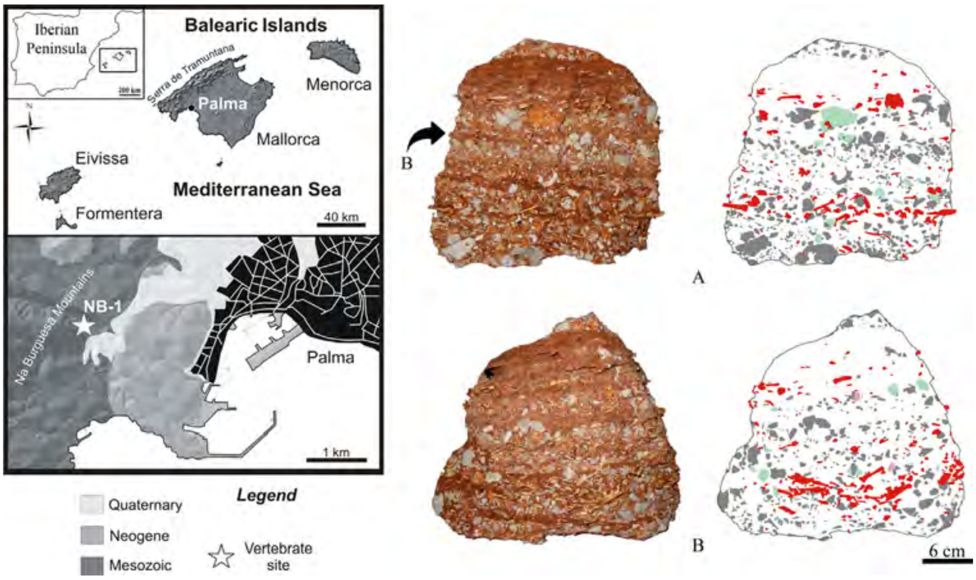

Fig. 1. Geological and geographical location of the early Pliocene palaeontological site of Na Burguesa-1 (NB-1) with details and schematic illustration of a fossiliferous breccia block from the deposit here studied from two different views (**A** and **B**). The different bone elements are highlighted in red, clasts of limestone in grey, clasts of sterile breccia resedimented in green, and speleothem clasts in pink.

Fig. 1. Localisation géologique et géographique du site paléontologique du Pliocène inférieur de Na Burguesa-1 (NB-1) avec le détail et l'illustration schématique d'un bloc de brèche fossilifère en provenance du dépôt ici étudié, selon deux vues différentes (**A** et **B**). Les différents éléments osseux figurent en rouge, les clastes de calcaire en gris, les clastes de brèche stérile resédimentés en vert et les clastes de spéléothème en rose.

The NB-1 bird bones were identified by direct comparison with material curated at the osteological bird collection of the "Institut Mediterrani d'Estudis Avançats" (Esporles, Mallorca; acronym of the collection: IMEDEA; see Supplementary Table 2), and using the available bibliography for each identified taxon (e.g., Bock and McEvery, 1969; Dyke et al., 2003; Fitzgerald, 1969; Ford, 1967; Holman, 1964; Langer, 1980; Louchart, 2002; Lydekker, 1893; Milne-Edwards, 1869–1871; Olson, 1976).

Measurements of bird long bones were taken when possible following the criteria of von den Driesch (1976) or Mourer-Chauviré (1975). Body mass for the different bird taxa, when possible, was estimated using two approaches: (a) the equation for the femur $Y = –0.069X^{2.414}$; where Y = body mass and X = perimeter of the femur diaphysis (Campbell & Marcus, 1992), estimating the diameter as the average of the depth and width of the diaphysis, and (b) $Y = 0.56X^{0.342}$ (Olmos et al., 1996), where Y = femur length and X = body mass. We estimated the body mass of the potential prey of the recorded raptorial birds (i.e. small mammal bones from NB-1) using the allometric equations to predicting body mass (Y) of Moncunill-Solé et al., 2014; Moncunill-Solé et al., 2015; Moncunill-Solé et al. (2014, 2015, 2016): $Y = 0.323X^{0.960}$, where X = distal humeral antero-posterior diameter, for murids and glirids; $Y = 0.009X^{0.935}$, where X = distal femoral transverse diameter, for the cricetid and for one adult glirid; $Y = 0.498X^{2.217}$, where X = proximal transversal diameter, for a femur of an adult leporid; $Y = 1.13X^{2.553}$, where X = distal antero-posterior diameter, for a humerus of an adult leporid; and $Y = 0.219X^{2.577}$, where X = proximal tibia transversal diameter, for young leporids (see Supplementary Table 3).

The micro-specimens were examined under a Leica S8 APO stereomicroscope and images were obtained with a digital camera Leica DFC420 digital camera. Macro-specimens images were obtained with a Cannon EOS 1200D. The nomenclature used in the description follows Livezey and Zusi (2006). The specific identity of all specimens remains unsolved, and for this reason we applied to them an open nomenclature following Bengtson (1988).

4. Systematic palaeontology

4.1. *Order Strigiformes (Wagler 1830)*

Extant species used for comparison: Tytonidae: *Tyto alba*. Strigidae: *Strix aluco*, *S. uralensis*, *S. nebulosa*, *Asio otus*, *A. flammeus*, *Athene noctua*, *Aegolius funereus, Bubo, Otus scops, Glaucidium passerinum, Surnia ulula*. Extinct species used for comparison: Tytonidae: *Tyto balearica* (type series), *Tyto ostologa*. Strigidae: *Athene cretensis, Athene vallgornerensis, Otus frutuosoi* (See Supplementary Table 2).

The members of this order present a skeleton with numerous diagnostic features (e.g., Milne-Edwards, 1869–1871). The most characteristic osteological trait is the presence of an ossified arch in the radius, the arcus origo musculi extensor longus digiti majoris (Bock and McEvery, 1969). The osteological differences between Tytonidae and Strigidae have been described by many authors (e.g., Arredondo and Olson, 1994; Ballmann, 1973, 1976; Ford, 1967; Louchart, 2002; Lydekker, 1893; Mourer-Chauviré, 1987; Pavia, 2004; Steadman and Hilgartner, 1999; Suárez and Olson, 2015, among others). Unlike the Strigidae, in Tytonidae the first and second toes present the same

Table 1
Measurements (mm) of *Tyto* sp. 1, *Tyto* sp. 2 from Na Burguesa-1 and different extinct and extant *Tyto* species.
Tableau 1
Mesures (en mm) de *Tyto* sp. 1 et *Tyto* sp. 2 de Na Burguesa-1 et de différentes espèces de *Tyto* éteintes et actuelles.

		Tyto sp. 1	*Tyto* sp. 2	*Tyto balearica*	*Tyto balearica* cyrneichnusae	*Tyto robusta*	*Tyto mourerchauvirae*	*Tyto sanctialbani*	*Tyto alba*
Radius	Bp	6.1		5.7[b]	5.25–5.45[b] *n* = 3	–	–	–	3.68–4.28[g] *n* = 11
	SC	3.4	2.5	3.5[b]	2.75–3.05[b]	–	–	–	1.8–2.2e *n* = 26
	Bd		7.2		7.1–7.9[b] *n* = 4	–	–	–	5.5–6.6e *n* = 25
Coracoid	Lm	43.5		42.1[b]	38.0–40.5[b] *n* = 5	–	–	34.9–35.7[a] *n* = 3	30.4–37.0[c] *n* = 26 31.6–35.9e *n* = 33
	SC	6.4		5.4–5.9[b] *n* = 3	4.7–5.6[b] *n* = 10	–	–	4.1–4.8[b] *n* = 4	3.4–4.6[c] *n* = 26 3.3–4.3e *n* = 33
Scapula	Dic	11.8		–	–	–	–	–	7.7–9.5e *n* = 32
	LAF	8.3		–	–	–	–	5.2[a]	4.74–5.97 *n* = 11
	WAF	4.8		–	–	–	–	3.7[a]	2.98–4.15 *n* = 11
Femur	GL	68.8		–	62.9–67.2[b] *n* = 4	–	74.3–85.5[f] *n* = 4	51.5–55.8[a] *n* = 2	46.4–53.7e *n* = 34
	Lm	65.9		–	59.8–65.1[b] *n* = 5		–		44–51.2e *n* = 34
	Bp	15.2		–	12.0–13.1[b] *n* = 16	16[d]	15.2–17.5[f] *n* = 6	9.5–11.4[a] *n* = 3	8.5–10.1e *n* = 34
	SC	6.5		6–(5.6)[b] *n* = 2	5.3–6.3[b] *n* = 25	–	6.4–7.7[f] *n* = 6	4.3–5.0[a] *n* = 12	3.8–4.4e *n* = 34
	Bd	15.3		12.6–12.7[b] *n* = 2	11.9–13.5[b] *n* = 11	15[d]	16.0–18.9[f] *n* = 5	8.9–11.8[a] *n* = 13	8.9–10.5e *n* = 34

Bd: breadth of the distal end; Bp: breadth of the proximal end; Dic: greatest cranial diagonal diameter; GL: greatest length; LAF: length of the articular facet; Lm: medial length; SC: smallest breadth of the corpus; WAF: width of the articular facet. [e]*Tyto alba/guttata*, in Louchart, 2002.

[a] Pavia and Mourer-Chauviré (2011).

[b] Louchart (2002).

[c] Pavia et al. (2015).

[d] Ballmann (1973).

[f] Pavia, 2004. Measurements of *Tyto* spp. bones, in mm.

[g] See Supplementary Table 4.

Table 2
Measurements (mm) of *Otus* sp. from Na Burguesa-1, *Otus scops* and *Athene noctua*.
Tableau 2
Mesures (mm) d'*Otus* sp. de Na Burguesa-1, *Otus scops* et *Athene noctua*.

		Otus sp.	*Otus scops*	*Athene noctua*
Ulna	Bp	5.0	4.7–5.1*n* = 11	4.9–6 *n* = 9
	SC	2.4	1.9–2.3n = 11	2.3–2.7 *n* = 9
Femur	Bp	6.1	5.4–6.1*n* = 11	5.9–7.3 *n* = 9
	Bd	6.5	5.1–5.9*n* = 11	6.4–7.4 *n* = 9
	SC	2.8	2.3–2.5*n* = 11	2.9–3.3 *n* = 9
Tibiotarsus	Bd	6.2	4.9–5.5n = 11	6.5–7.2 *n* = 9
	SC	2.6	2.1–2.4*n* = 11	2.6–3.2 *n* = 9

Bd: breadth of the distal end; Bp: breadth of the proximal end; SC: smallest breadth of the corpus.

length. Both basal phalanges of the second toe in Tytonidae are very similar, while in Strigidae the first phalanx of the second toe is only half as long as the second phalanx; Ford, 1967. The tarsometatarsus of the Tytonidae lacks a retinaculum extensorium osseum or arcus extensorius (bony loop), whereas the premaxilla is more elongated than in the Strigidae.

4.2. Family Tytonidae Ridgway 1914

The material included herein is referred to Tytonidae and differs from the Strigidae from the western Palaearctic by the following combination of osteological features: coracoid with scapular end less voluminous and not pneumatized; facies articularis scapularis, facies articularis sternalis and foramen nervi supracoracoidei proportionally smaller; facies articularis humeralis proportionally larger; procoracoideus process wide and shorter. Femur with a trochanterian edge more vertical; medial and lateral condyles more forwardly oriented; medial condyle larger in internal view, with a cranial margin that joins the diaphysis stepwise; a wide lateral epicondyle in lateral view; tubercle for the M. gastrocnemialis lateralis located distally. The scapula has the lateral region of the acromion less laterally projected than in the Strigidae, while the costal side of the acromion is more developed; the articularis humeralis facet is more elongated (oval) than in the Strigidae; the acromion is not pneumatized, contrary to the usual condition in the Strigidae (except *Otus*). In Tytonidae, the radius presents a cotyla humeralis more rounded than in the Strigidae, where it is narrower dorso-ventrally; finally, the distal end of the radius presents a concavity better marked in its medial tubercle in the Tytonidae.

The genus *Tyto* is known at least from the Middle Miocene (MN7 to MN10), with *Tyto sanctialbani* (Ballmann, 1969; Lydekker, 1893; Pavia and Mourer-Chauviré, 2011). The taxonomy of the Miocene and Pliocene species of *Tyto* is controversial. In the Late Miocene of eastern Europe is known *Tyto campiterrae*, which is larger and slenderer than *Tyto sanctialbani* (Jánossy, 1991). However, there are other Miocene taxa without resolved identity (Pavia & Mourer-Chauviré, 2011). Two Mediterranean giant insular barn owls, *Tyto robusta* and *Tyto gigantea*, both described from Gargano, lived during the Late Miocene/Early Pliocene, while during the Early/Middle Pleistocene appears *Tyto balearica* in the fossil record, also a giant species, but smaller than the Gargano taxa. The description of *Tyto balearica* was based on bones from the Gymnesic Islands (Mallorca and Menorca; Mourer-Chauviré et al., 1980), and the species was later identified in many localities on the mainland (e.g., Mourer-Chauviré & Sánchez-Marco, 1988), although the attribution of all this continental material should be re-evaluated (e.g., Louchart, 2002). Remains from Pleistocene sites in Corsica and Sardinia were described as a subspecies, *Tyto balearica cyrneichnusae*, which could be potentially raised to species status (Pavia et al., 2012). *Tyto mourerchauvirae* was described from the Middle Pleistocene of Sicily, displaying a size similar to *Tyto robusta*. Some other large continental Barn Owls probably represent species pending description (Louchart, 2002).

4.3. Genus Tyto Billberg 1828

4.3.1. Tyto sp. 1 (size similar to Tyto robusta Ballmann, 1973)

Material: IMEDEA 106330, near complete left femur. IMEDEA 106331, near complete right coracoid. IMEDEA 106332, proximal fragment of right radius. IMEDEA 106333, humeral fragment of right scapula (Fig. 2A–D).

The material included under *Tyto* sp. 1 has a size very similar to *Tyto robusta* from Gargano. The minimum number of individuals (MNI) in the deposit is one. Some of their measurements (see Table 1) fall also within the range of measurements of *Tyto mourerchauvirae* from Sicily, while others are slightly smaller (see Table 1). Some morphological traits (e.g., femoral characters 3 and 9 of Ballmann, 1973) are not in full agreement with the description of *Tyto robusta*, although the actual range of variability of *Tyto robusta* and *Tyto* sp. 1 remains unknown. Additionally, *Tyto* sp. 1 shares some diagnostic characters of *Tyto mourerchauvirae*, but much less developed than in this species (such as a very small tubercular prominence in the tubercular part of the linea intermuscularis cranialis and a relatively wide distal epiphysis of the femur). The body mass of *Tyto* sp.1 has been estimated at *ca.* 1200 g on the basis to its femoral diaphysis diameter (Campbell and Marcus, 1992) and, although the trochanter of IMEDEA 106330 is slightly damaged, a body mass about 1360 g has been estimated on the basis of its femoral length (Olmos et al., 1996).

4.3.2. Tyto sp. 2 (size similar to Tyto sanctialbani [Lydekker, 1893])

Material: IMEDEA 107594, distal fragment of right radius (Fig. 2E).

This distal fragment of radius is slightly larger than in *Tyto alba*, and considerably smaller than in *Tyto robusta*. (see Table 1). It corresponds to a Barn Owl of similar size to *Tyto sanctialbani* (Lydekker, 1893), but no radii of this species have ever been found. Differences in size have been eventually interpreted as a result of sexual dimorphism (e.g., Pavia, 2004), but the lack of such sexual dimorphism in bones of extant *Tyto alba* do not show such sexual dimorphism in bones (see measurements in Langer, 1980) leads us to consider that fossil Barn Owls of different sizes actually represent different species. As the differences in size between the radii IMEDEA 106332 from *Tyto* sp. 1 (see above) and IMEDEA 107594 are considerable (diaphysis diameter 26.5% larger in the former), and as on various islands (e.g., Cuba, Gargano), two different species of *Tyto* coexisted, we can suggest that the radius IMEDEA 107594 actually belongs to a species different to *Tyto* sp. 1.

4.4. Family Strigidae (Vigors 1825)

4.4.1. Genus Otus Pennant 1769

4.4.1.1. Otus sp.. Material: IMEDEA 106998, distal fragment of right tibiotarsus (Figs. 3–5

). IMEDEA 106999, left pedal phalanx I of toe 3. IMEDEA 107000, proximal fragment of right ulna. IMEDEA 107620, pedal phalanx. IMEDEA 107625, pedal phalanx. IMEDEA 107626, pedal phalanx. IMEDEA 107627, pedal phalanx. IMEDEA 107628, pedal phalanx. IMEDEA 107629, pedal phalanx. IMEDEA 107630, pedal phalanx. IMEDEA 107631, pedal phalanx. IMEDEA 107632, pedal phalanx. IMEDEA 107633, pedal phalanx. IMEDEA 107634, right pedal phalanx III of toe 4. IMEDEA 107635, left pedal phalanx IV of toe 3. IMEDEA 107636, left pedal phalanx I of toe 1. IMEDEA 107637, left pedal phalanx III of toe 3. IMEDEA 107638, left pedal phalanx IV of toe 4. IMEDEA 107639, left pedal phalanx II of toe 2. IMEDEA 107640, pedal phalanx. IMEDEA 107641, pedal phalanx. IMEDEA 107642, pedal phalanx. IMEDEA 107643, sternum fragment. IMEDEA 107644, right pedal phalanx I of toe 2. IMEDEA 107645, proximal fragment of left femur. IMEDEA 107646, distal fragment of right femur. IMEDEA 107647, proximal fragment of right femur. IMEDEA 107648, pedal phalanx.

Fig. 2. Comparison of *Tyto* sp. 1 (specimens **A**–**D**) and *Tyto* sp. 2 (specimen **E**) from NB-1, with *Tyto alba* (specimens **F**–**I**) and *Tyto balearica* (specimens **J**–**L**). Specimen **A** (IMEDEA 1063316), right coracoid in dorsal (left) and ventral (right) views; specimen **B** (IMEDEA 106333), proximal fragment of right scapula in costal (left) and lateral (right) views; specimen **C** (IMEDEA 106332), proximal fragment of right radius in dorsal, medial and ventral views (from left to right); specimen **D** (IMEDEA 106330), left femur in cranial, caudal and medial views (from left to right); specimen **E** (IMEDEA 107594), distal fragments of right radius in dorsal (top), lateral (bottom left) and ventral (bottom right) views; specimen **F** (IMEDEA 106870), right coracoid in dorsal (left) and ventral (right) views; specimen **G** (IMEDEA 21884), right scapula in costal (left) and lateral (right) views; specimen **H** (IMEDEA 21884), right radius in dorsal, lateral and ventral views (from left to right); specimen **I** (IMEDEA 106870), left femur in cranial, caudal and medial views (from left to right); specimen **J** (IMEDEA 473), left coracoid in dorsal (left) and ventral (right) views; specimen **K** (IMEDEA 481), proximal fragment of right scapula in costal (left) and lateral (right) views; specimen **L** (IMEDEA 477), distal fragment of right femur in cranial, caudal and medial views (from left to right).

Fig. 2. Comparaison de *Tyto* sp. 1 (spécimens **A**–**D**) et *Tyto* Sp. 2 (spécimen **E**), en provenance de NB-1, avec *Tyto alba* (spécimens **F**–**I**) et *Tyto balearica* (spécimen **J**–**L**). Spécimen **A** (IMEDEA 1063316), coracoïde droit en vues dorsale (gauche) et ventrale (droite) ; spécimen **B** (IMEDEA 106333), fragment proximal de scapula droite en vues costale (gauche) et latérale (droite) ; spécimen **C** (IMEDEA 106332), fragment proximal de radius droit en vues dorsale, médiale et ventrale (de gauche à droite) ; spécimen **D** (IMEDEA 106330), fémur gauche, en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **E** (IMEDEA 107594), fragments distaux de radius droit en vues dorsale (en haut), latérale (en bas à gauche) et ventrale (en bas à droite) ; spécimen **F** (IMEDEA 106870), coracoïde droit en vues dorsale (gauche) et ventrale (droite) ; spécimen **G** (IMEDEA 21884), scapula droite en vues costale (gauche) et latérale (droite) ; spécimen **H** (IMEDEA 21884), radius droit en vues dorsale, latérale et ventrale (de gauche à droite) ; spécimen **I** (IMEDEA106870), fémur gauche en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **J** (IMEDEA 473), coracoïde gauche en vues dorsale (gauche) et ventrale (droite) ; spécimen **K** (IMEDEA 481), fragment proximal de scapula droite en vues costale (gauche) et latérale (droite) ; spécimen **L** (IMEDEA 477), fragment distal de fémur droit en vues crânienne, caudale et médiale (de gauche à droite).

The material listed above belongs to a small Strigidae that falls in the size range of *Otus scops* and *Athene noctua* (see Table 2 and Supplementary Tables 4 and 5). The obtained fossils are slender than those of *Aegolius*, *Glaucidium* and *Surnia*. Thus *Otus* and *Athene* are the best candidates, amongst European owls, to explore the taxonomical affinities of the fossil strigid present at NB-1. The osteological discrimination between *Athene* and *Otus* was initially approached by Olson and Hilgartner (1983). Ulna: the cotyla dorsalis, in proximal view, is not internally pointed and its facies articularis radialis is deeper and better defined in *Athene* than in *Otus*. Femur: the trochanterian edge is more developed in *Athene* than in *Otus*. Tibiotarsus: the tendon concavity is deeper in *Athene* than in *Otus*; in cranial view, the condyles are practically parallel in *Athene*, while in *Otus* the medial condyle is medially inclined to its distal end. In addition to these characteristics, we used *Otus scops* and *Athene noctua* as representatives of both genera to establish new discrimination criteria. Sternum: the labrum externum sterni is more projected in *Athene* than in *Otus*, whereas *Athene* usually displays a small concavity in the ascendant part from the side of the ridge closest to the labrum, while it is absent in *Otus*. The long bones and sternum of the NB-1 strigid fit better to *Otus* than to *Athene*. Regarding pedal phalanges, phalanx I 1: the tuberculum flexorum is poorly developed as in *Otus*, whereas it is larger in *Athene*; the ventral margin of the phalanx has a continuous profile between the caput phalangis and the tuberculum flexorum as in *Otus*, while in *Athene* it is interrupted by a pointed prominence. Phalanx I 2: it lacks a small

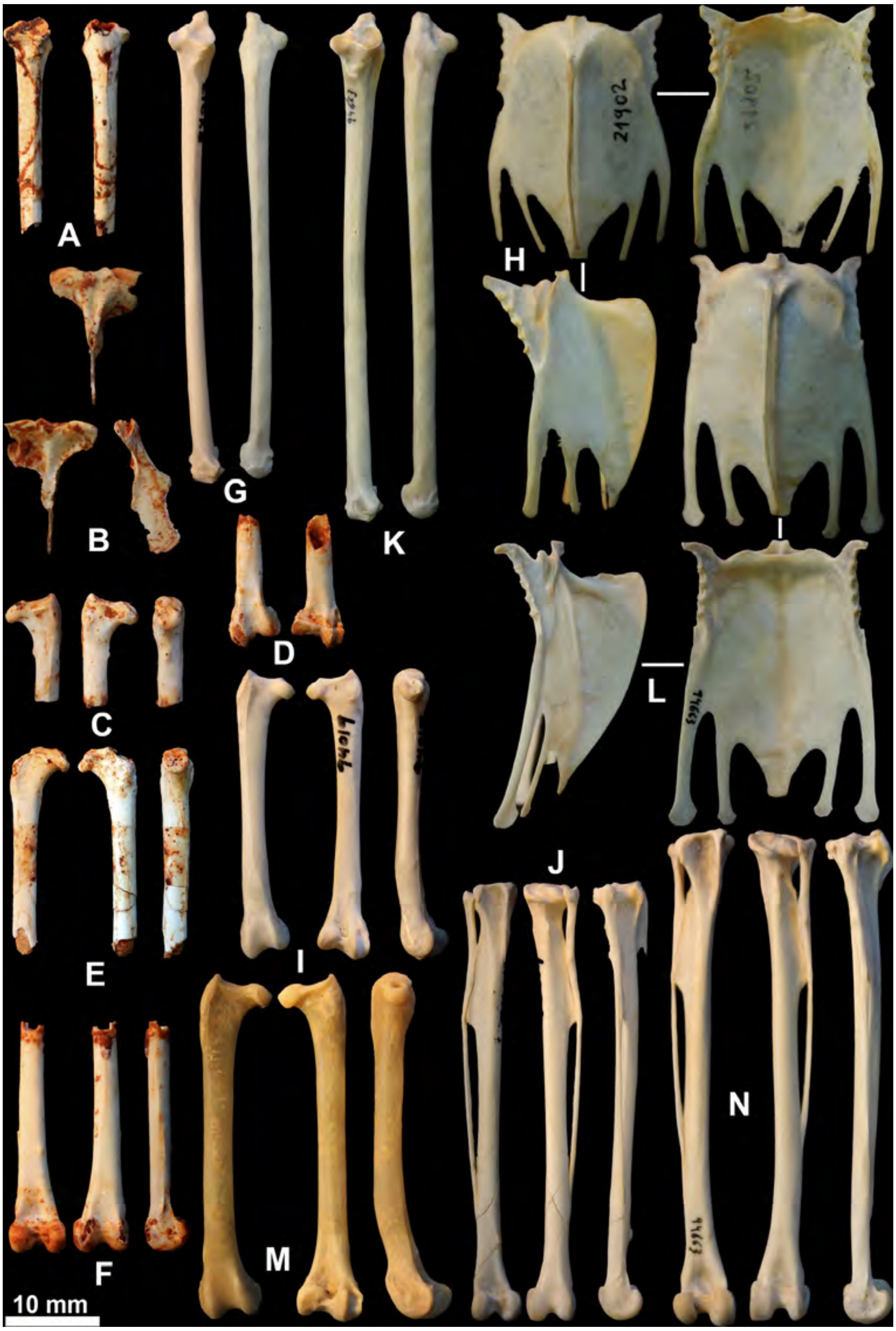

Fig. 3. Comparison of *Otus* sp. (specimens **A**–**F**) from NB-1 with *O. scops* (specimens **G**–**J**) and *Athene noctua* (specimens K-N). Specimen **A** (IMEDEA 107000), proximal fragment of right ulna in palmar (left) and anconal (right) views; specimen **B** (IMEDEA 107643), sternum fragment in ventral (top), dorsal (bottom left) and lateral (bottom right) views; specimen **C** (IMEDEA 107645), proximal fragment of left femur in cranial, caudal and medial views (from left to right); specimen **D** (IMEDEA 107646), distal fragment of right femur in cranial, caudal and medial views (from left to right); specimen **E** (IMEDEA 107647), proximal fragment of right femur in cranial (left) and caudal (right) views; specimen **F** (IMEDEA 106998), distal fragment of right tibiotarsus in cranial, caudal, and lateral views (from left to right); specimen **G** (IMEDEA 94019), right ulna in palmar (left) and anconal (right) views; specimen **H** (IMEDEA 21902), sternum in ventral (top left), dorsal (top right) and lateral (bottom) views; specimen **I** (IMEDEA 94019), right femur in cranial, caudal and medial views (from left to right); specimen **J** (IMEDEA 94019), right tibiotarsus in cranial, caudal, and lateral views (from left to right); specimen **K** (IMEDEA 94663), right ulna in palmar (left) and anconal (right) views; specimen **L** (IMEDEA 94663), sternum in ventral (top), dorsal (bottom right) and lateral (bottom left) views; specimen **M** (IMEDEA 21717), right femur in cranial, caudal and medial views (from left to right); specimen **N** (IMEDEA 94663), right tibiotarsus in cranial, caudal, and lateral views (from left to right).

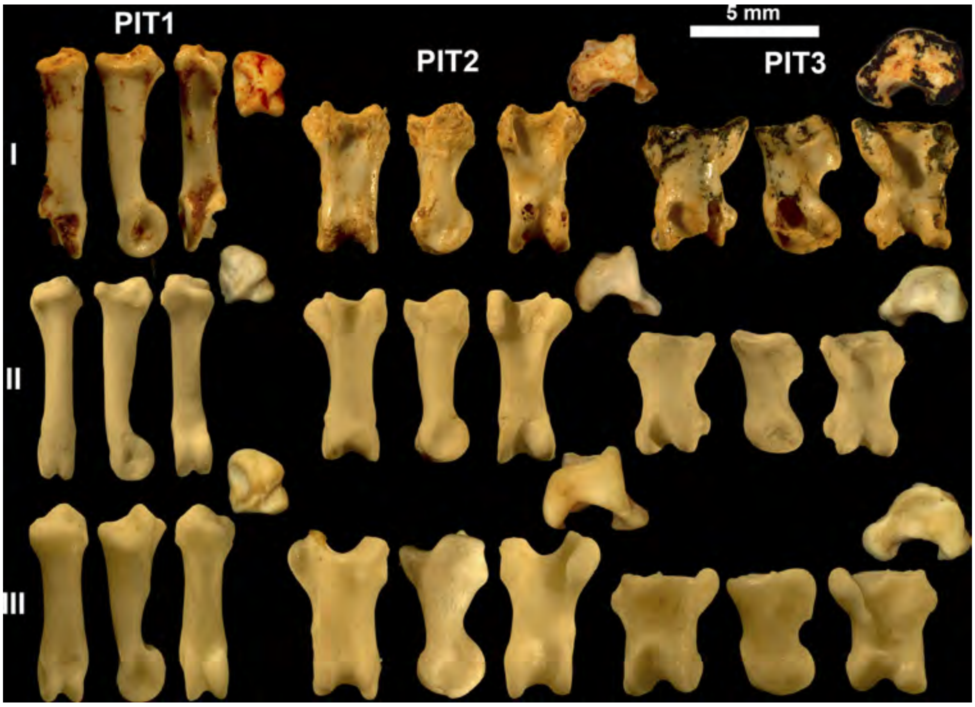

Fig. 4. Comparison of proximal pedal phalanges. PIT1, phalanx I toe 1; PIT2, phalanx I toe 2; PIT3, phalanx I toe 3. Row I: *Otus* sp. from NB-1 (left PIT1 IMEDEA 107636, right PIT2 IMEDEA 107644 and left PIT3 IMEDEA 106999). Row II: *O. scops* (IMEDEA 94019). Row III: *Athene* noctua (IMEDEA 21717). Views in dorsal, lateral, ventral, and proximal (from left to right).

Fig. 4. Comparaison des phalanges à pédales proximales. PIT1, phalange 1 doigt 1 ; PIT2, phalange 1, doigt 2 ; PIT3, phalange 1, doigt 3. Rangée I : *Otus* sp. de NB-1 (PIT 1 gauche IMEDEA 107636, right IMEDEA 107644 et PIT3 IMEDEA 106999). Rangée II : *O. scops* (IMEDEA 94019). Rangée III : *A. noctua* (IMEDEA 21717). Vues dorsale, latérale, ventrale et proximale (de gauche à droite).

medial tuberculum extensorium as in *Athene*, while in *Otus* it is present. Phalanx I 3: it has a well-developed tuberculum in the lateral site of the caput phalangis, as in *Otus*, whereas it is very reduced or absent in *Athene*. Phalanx II 2: it is slightly arched, as in *Otus*, while in *Athene* is more rectilinear. In contrast, the orientation of the caput phalangis of the fossil specimen is more similar to *Athene*. Phalanx III 3 and phalanx IV 4: both display a well delimited caput phalangis with respect to the dorsal wall as in *Athene*, while in *Otus* it is practically not interrupted. The terminal phalanx IV 3 (and all other terminal phalanges of unidentified): present tuberculum extensorium dorso-caudally oriented as in *Otus*, while in *Athene* it is oriented caudally. Finally, with regard to phalanx III 4, the main differences between these two genera rely on size and proportions. The fossil specimen is robust as in *Athene*, while in *Otus* is more gracile.

These remains could represent a single individual. Based on the characters listed above, we consider that the small-sized Strigidae fossils of NB-1 should be included in the genus *Otus*. However, the pedal phalanges obtained at NB-1 display characters similar to those observed in *Otus*, in *Athene*, or even display an intermediate morphology between the latter two genera. The size and proportions of the proximal and medial phalanges are more similar to those encountered in *Athene*, in which they are generally more robust than those of *Otus*. The morphology of the distal phalanges studied herein is better fitted to *Otus*.

So far, the whole known record of the genus *Otus* is mainly limited to the Quaternary (Kessler, 2017; Tyrberg,

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Fig. 3. Comparaison d'*Otus* sp. (spécimens **A**–**F**) en provenance de NB-1 avec *O. scops* (spécimens **G**–**J**) et *Athene noctua* (spécimens **K**–**L**). Spécimen **A** (IMEDEA 107000), fragment proximal d'ulna droite en vues palmaire (gauche) et anconale (droite) ; spécimen **B** (IMEDEA 107643), fragment de sternum en vues ventrale (en haut), dorsale (en bas à gauche) et latérale (en bas à droite) ; spécimen **C** (IMEDEA 107645), fragment proximal de fémur gauche en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **D** (IMEDEA 107646), fragment proximal de fémur droit, en vues crânienne (gauche) et caudale (droite) ; spécimen **E** (IMEDEA 107647), fragment proximal de fémur droit en vues crânienne (gauche) et caudale (droite) ; spécimen **F** (IMEDEA 106998), fragment distal de tibiotarse droit, en vues crânienne, caudale et latérale (de gauche à droite) ; spécimen **G** (IMEDEA 94019), ulna droite en vue palmaire (gauche) et anconale (droite) ; spécimen **H** (IMEDEA 21092), sternum en vues ventrale (en haut à gauche), dorsale (en haut à droite) et latérale (en bas) ; spécimen **I** (IMEDEA 94019), fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **J** (IMEDEA 94019), tibiotarsus droit en vues crânienne, caudale et latérale (de gauche à droite) ; spécimen **K** (IMEDEA 94663), ulna droite en vues palmaire (gauche) et anconale (droite) ; spécimen **L** (IMEDEA 94663), sternum en vues ventrale (en haut), dorsale (en bas à droite) et latérale (en bas à gauche) ; spécimen **M** (IMEDEA 21717) fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **N** (IMEDEA 94663), tibiotarsus droit en vues crânienne, caudale et latérale (de gauche à droite).

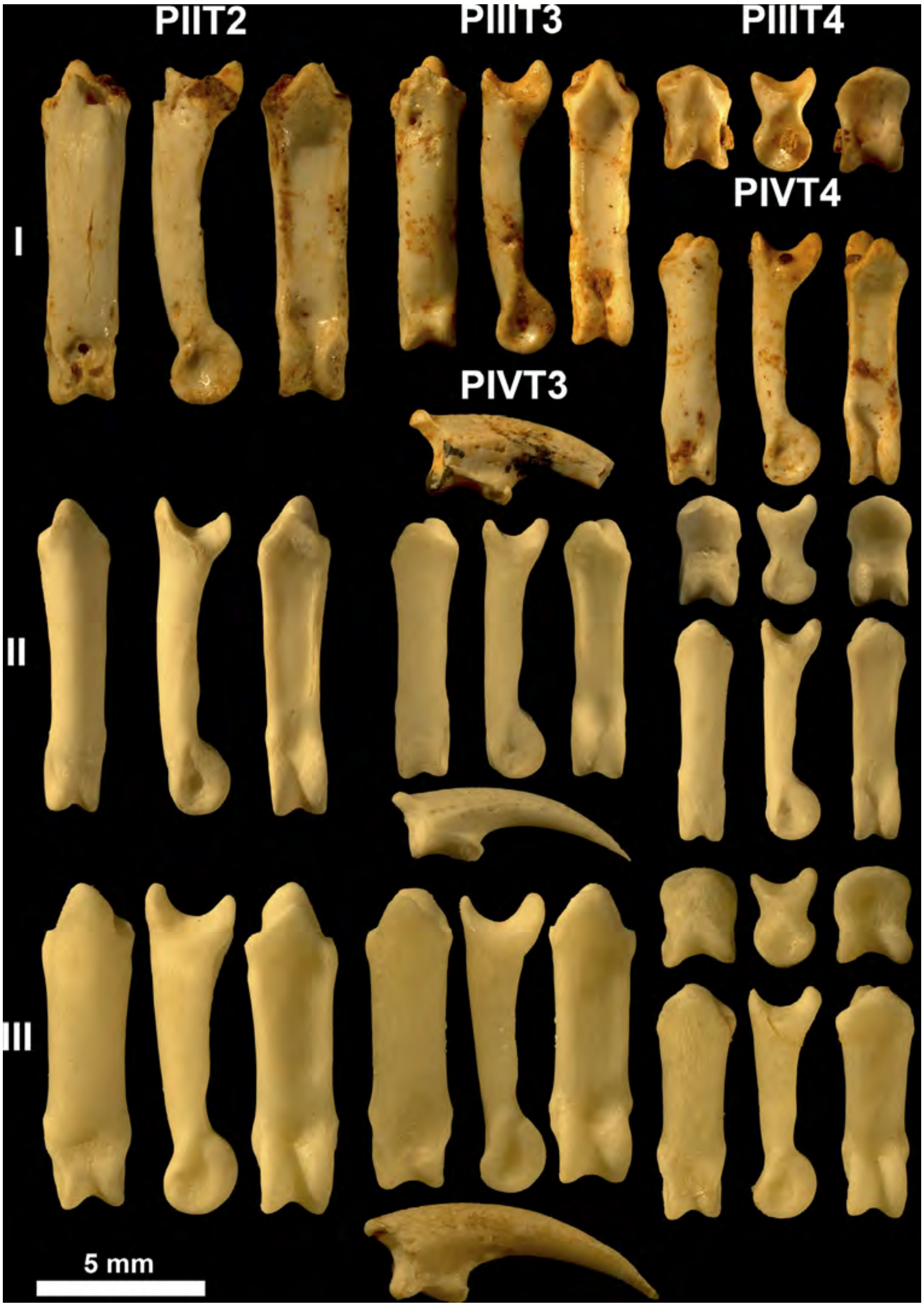

Fig. 5. Comparison of medial and terminal pedal phalanges. PIIT2, phalanx II toe 2; PIIIT3, phalanx III toe 3; PIVT3, phalanx IV toe 3; PIIIT4, phalanx III toe 4; PIVT4, phalanx IV toe 4. Row I: *Otus* sp. from NB-1 [left PIIT2 IMEDEA 107639 in dorsal, medial, and ventral views (from left to right), left PIIIT3 IMEDEA 107637 in dorsal, lateral, and ventral views (from left to right), left PIVT3 IMEDEA 107635 in medial view, right PIIIT4 IMEDEA 107634 in dorsal, medial and ventral views (from left to right), and left PIVT4 IMEDEA 107638 in dorsal, lateral and ventral views (from left to right)]. Row II: *O. scops* (IMEDEA 94019). Row III: *Athene noctua* (IMEDEA 21717).

Fig. 5. Comparaison des phalanges à pédale médiales et terminales. PIIT2, phalange II doigt 2 ; PIIT3, phalange III doigt 3 ; PIVT3, phalange IV doigt 3 ; PIIIT4, phalange III doigt 4 ; PIVT4, phalange IV doigt 4. Rangée I: *Otus* sp. de NB-1 [PIIT2 gauche IMEDEA 107639, en vues dorsale, médiale et ventrale (de gauche à droite), PIIIT3 gauche IMEDEA 107637 en vues dorsale, latérale et ventrale (de gauche à droite), PIVT3 gauche IMEDEA 107635 en vue médiale, PIIIT4 droite IMEDEA 107634, en vues dorsale, médiale et ventrale (de gauche à droite) et PIVT4 IMEDEA gauche 107638 en vues dorsale, latérale et ventrale (de gauche à droite)]. Rangée II : *O. scops* (IMEDEA 94019). Rangée III : *Athene noctua* (IMEDEA 21717).

1998), with the exception of a distal fragment of humerus from the early Miocene of Songor (Kenya), tentatively attributed to *Otus* (Walker and Dyke, 2006), and some Burdigalian bones described as *Otus wintershofensis* from Bavaria (Germany; Ballmann, 1969). The bones of *Otus* obtained at NB-1 document the presence of the genus between the Burdigalian and the Quaternary.

4.5. Order Galliformes Temminck 1820

4.5.1. Family Phasianidae Horsfield 1821

4.5.1.1. cf. Coturnix Garsault 1764. Material: IMEDEA 107595, near complete right femur. IMEDEA 107596, proximal fragment of left humerus. IMEDEA 107597, proximal fragment of left femur (Fig. 6). IMEDEA 107598, sternum fragment. IMEDEA 107610, distal fragment of right tarsometatarsus. IMEDEA 107611, proximal fragment of right tarsometatarsus. IMEDEA 107612, apical fragment of premaxilla. IMEDEA 107621, pelvis fragment. IMEDEA 107622, pelvis fragment. IMEDEA 107623, pelvis fragment.

Extant species used to establish comparisons: *Coturnix*, *Alectoris rufa* (see Supplementary Table 2).

A few remains belonging to at least two individuals of a small-sized species of galliform have been obtained at NB-1. These remains have been attributed to cf. *Coturnix* because they are consistent with the size and osteological features presented by Holman (1964), Olson (1976), Fitzgerald (1969), and Dyke et al. (2003), although their fragmentary condition and the lack of a general review of the Mio-Pliocene quails preclude any further analysis. The premaxilla is characteristically short and slightly curved. The proximal end of the humerus displays a well-developed secondary fossa pneumotricipitalis. The femur is elongated and characteristically curved. The shaft diameter of the femur is 2.77 mm, and falls in the range of *Coturnix* (2.18–2.87 mm, $n = 9$).

4.6. Order Charadriiformes Huxley 1867

4.6.1. Undetermined family, genus and species

Material: IMEDEA 107650, proximal fragment of right carpometacarpus.

The general morphology of this single proximal fragment of right carpometacarpus allows us to record the presence of a species of Charadriiformes similar in size to *Philomachus pugnax*, but its preservation state precludes further analysis.

4.7. Order Passeriformes Linnaeus 1758

4.7.1. Indetermined family, genus and species

Material: IMEDEA 107601, distal end of tarsometatarsus. IMEDEA 107602, distal end of tarsometatarsus. IMEDEA 107603, distal fragment of left tarsometatarsus. IMEDEA 107604, near complete right ulna. IMEDEA 107605, right carpometacarpus. IMEDEA 107606, proximal fragment of right carpometacarpus. IMEDEA 107607, proximal fragment of right humerus. IMEDEA 107608, distal fragment of right humerus. IMEDEA 107609, distal fragment of right humerus. IMEDEA 107613, distal end of tibiotarsus. IMEDEA 107614, distal fragment of left tibiotarsus. IMEDEA 107615, proximal fragment of right carpometacarpus. IMEDEA 107624, 14 terminal pedal phalanges. IMEDEA 107649, 173 pedal phalanges.

The presence of Passeriformes at NB-1 is documented by 26 bones. The fragmentary state of most of this material impedes identification beyond the order level, whereas the more complete bones (e.g., phalanges) do not display enough diagnostic features to allow their identification with species. The bones of Passeriformes from NB-1 belong to at least to 5 different species.

Table 3
Vertebrate bones recovered at Na Burguesa-1. The minimum number of individuals (MNI) is indicated for mammals.
Tableau 3
Vertèbres récupérées à Na Burguesa-1. Le nombre minimum d'individus (MNI) est indiqué pour les mammifères.

Taxa	Number of bones	MNI
Soricinae	368	23
BdApocricetus darderi	2174	55
Paraethomys balearicus	161	11
Gliridae	2748	50
Leporidae	470	16
Bovidae	8	2
Anura	47	–
Squamata	968	–

5. Discussion

NB-1 yielded *ca.* 7000 bones, of which most were mammals, including Eulipotyphla (Soricinae), Rodentia (*Apocricetus*, *Paraethomys*, Gliridae), Lagomorpha (Leporidae), and Cetartiodactyla (Bovidae). In addition, four anurans, twelve reptiles, and several birds and bats were recovered as well (Bover et al., 2014). A preliminary study of this material already suggested close ties with the taxa present at the Early Pliocene deposit of Caló den Rafelino (Bover et al., 2014). The lower degree of insular evolution displayed by the NB-1 taxa suggested an Early Pliocene (Zanclean) age for this deposit. Moreover, the rodent species described from NB-1 [*Apocricetus darderi* (closely related to the mainland *A. alberti*; Torres-Roig et al., 2019a), and the first murine ever recorded in the fossil record of the Balearics, *Paraethomys balearicus* (closely related to the mainland *P. meini*)] allow us to establish for the first time a close, direct relationship of some taxa of the *Myotragus* fauna with their continental ancestors, a paleontological evidence that links the origin of the *Myotragus* fauna with the MSC (Mas et al., 2018; Torres-Roig et al., 2019b in press).

In the fossil bird assemblage of NB-1, the presence of three Strigiformes contributes to explain the origin of the site. Numerous authors have highlighted the role of nocturnal raptor birds as accumulators of remains of small vertebrates. Strigiformes (1) normally swallow their entire prey, and (2) the regurgitated bones show little damage and traces of digestion (e.g., Andrews, 1990). Andrews (1990) points out that Barn Owls (*Tyto*) are among the birds that produce the fewest modifications to the bones of consumed prey. The presence of a giant Barn Owl at NB-1, morphologically close to *Tyto robusta*, suggests that at least a part of this deposit should have derived from the accumulation

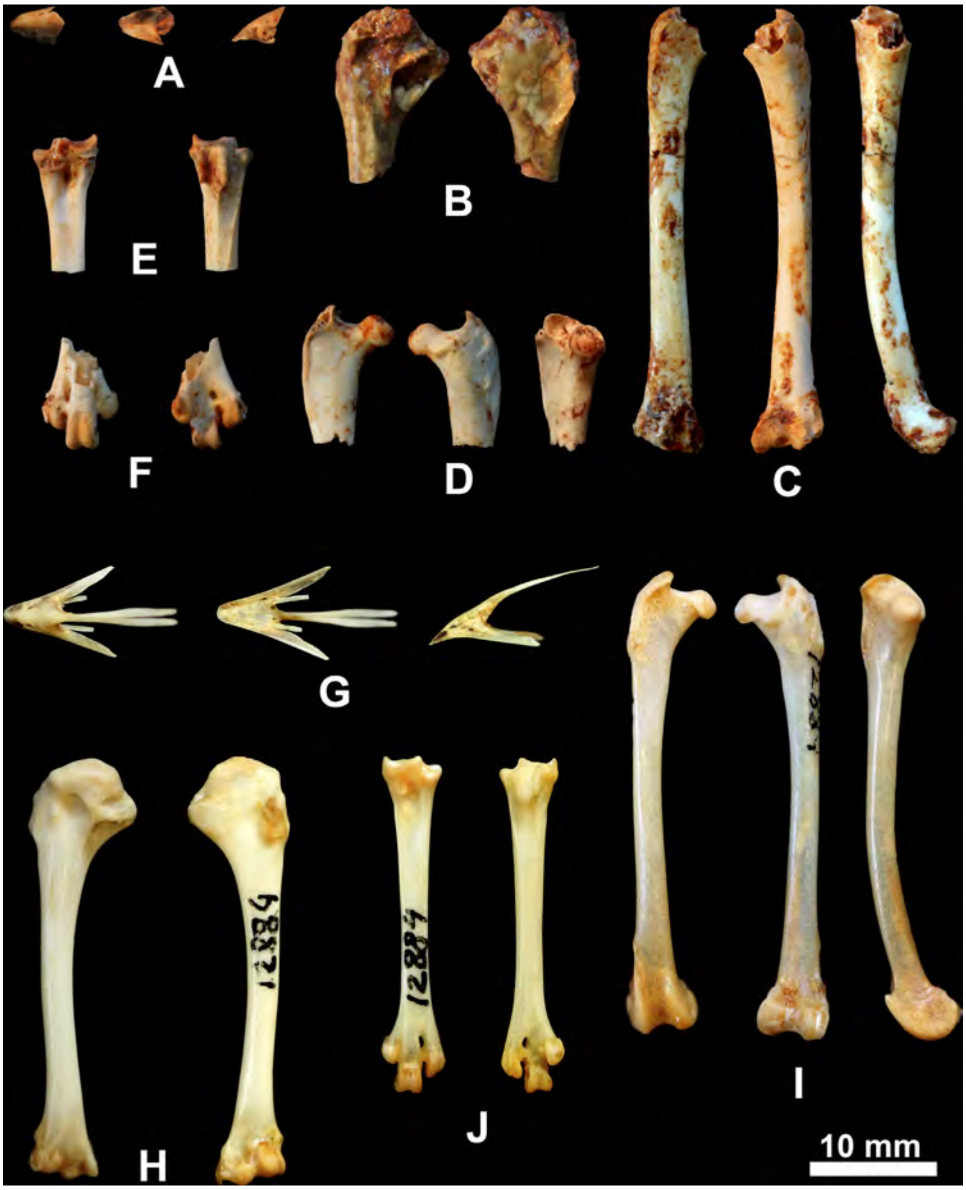

Fig. 6. Comparison of cf. *Coturnix* sp. (specimens **A**–**F**) from NB-1 with *C. coturnix* (specimens **G**–**J**). Specimen **A** (IMEDEA 107612), fragment of premaxilla in dorsal, lateral, and ventral views (from left to right); specimen **B** (IMEDEA 107596), proximal fragment of left humerus in caudal (left) and cranial (right) views; specimen **C** (IMEDEA 107595), right incomplete femur in cranial, caudal, and medial views (from left to right); specimen **D** (IMEDEA 107595), proximal fragment of right femur in cranial, caudal, and medial views (from left to right); specimen **E** (IMEDEA 107611), proximal fragment of right tarsometatarsus in cranial (left) and caudal (right) views; specimen **F** (IMEDEA 107610), distal fragment of right tarsometatarsus in cranial (left) and caudal (right) views; specimen **G** (IMEDEA 12884), premaxilla in dorsal, lateral, and ventral views (from left to right); specimen **H** (IMEDEA 12884), left humerus in caudal (left) and cranial (right) views; specimen **I** (IMEDEA 12884), right femur in cranial, caudal, and medial views (from left to right); specimen **J** (IMEDEA 12884), left tarsometatarsus in cranial (left) and caudal (right) views.

Fig. 6. Comparaison de cf. *Coturnix* sp. (spécimens **A**–**F**) de NB-1 avec *C. coturnix* (spécimens **G**–**J**). Spécimen **A** (IMEDEA 107612), fragment de prémaxillaire en vues dorsale, latérale et ventrale (de gauche à droite) ; spécimen **B** (IMEDEA 107596), fragment proximal d'humérus gauche en vues caudale (gauche) et crânienne (droite) ; spécimen **C** (IMEDEA 107595), fémur droit incomplet en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **D** (IMEDEA 107595), fragment proximal de fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **E** (IMEDEA 107611), fragment proximal de tarsométatarse droit en vues crânienne (gauche) et caudale (droite) ; spécimen **F** (IMEDEA 107610), fragment distal de tarsométatarse droit en vues crânienne (gauche) et caudale (droite) ; spécimen **G** (IMEDEA 12884), prémaxillaire en vues dorsale, latérale et ventrale (de gauche à droite) ; spécimen **H** (IMEDEA 12884), humérus gauche en vues caudale (gauche) et crânienne (droite) ; spécimen **I** (IMEDEA 12884), fémur droit en vues crânienne, caudale et médiale (de gauche à droite) ; spécimen **J** (IMEDEA 12884), tarsométatarse gauche en vue crânienne (gauche) et caudale (droite).

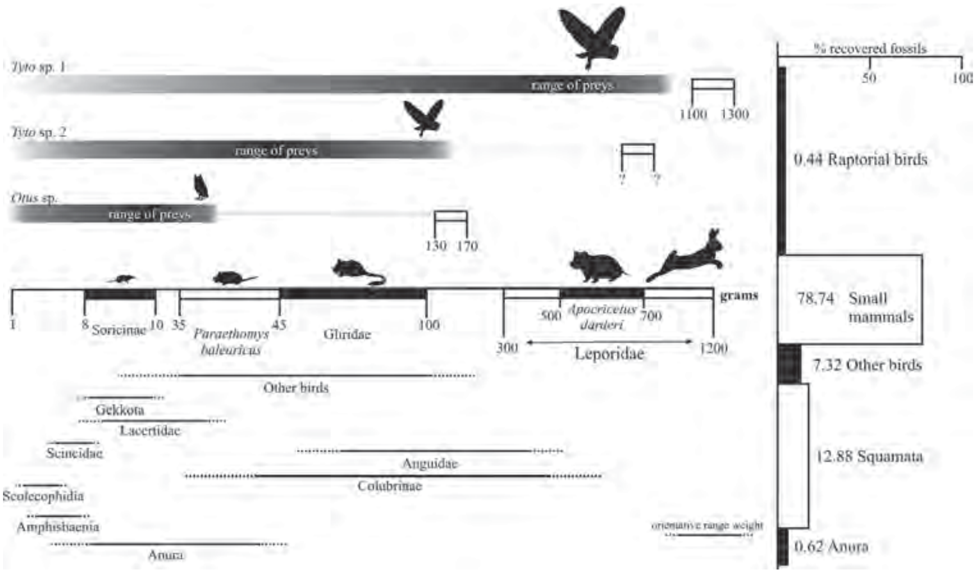

Fig. 7. Schematic diagram showing the potential prey of the Strigiformes based on their body mass estimation (on the left) and the percentages in the composition of the different small vertebrates recovered at site NB-1 (on the right).

Fig. 7. Diagramme schématique montrant les proie potentielles des Strigiformes, sur la base de l'estimation de leur masse corporelle (à gauche) et les pourcentages de composition des différentes petites vertèbres trouvées sur le site NB-1 (à droite).

of its pellets. NB-1 yielded thousands of small vertebrate bones (see Table 3). The microscopic analyses of the surface of the teeth and bones reveal that most of them display no (or negligible) alterations due to ingestion or digestion. Associated material belonging to a same individual has been repeatedly obtained (e.g., associated rodent jaws, associated gecko skeleton, associated vertebrae), despite the difficulties inherent to the extraction of bones with acid. In addition, the preservation of the considerable amount of micromammal bones is remarkably good, including complete or near complete bones (skulls, jaws and long bones), which is a noticeable finding in a hardly cemented karstic fossil site about 5 My old. Although *Tyto* sp. 1 displayed a large body size – an usual trait among insular owls (e.g., Louchart, 2005) – it is not possible to establish if its giantism was the result of its evolution on an island or if it shared its large size with its mainland ancestor.

It is well established that prey size is related to predator size (e.g., Comay and Dayan, 2018; Herrera and Hiraldo, 1976). The size of the giant cricetid *Apocricetus darderi* (estimated body mass in adult stage, 560–730 g), the juvenile specimens of the leporid (estimated body mass, 320–840 g), and the undescribed glirid (estimated body mass at adult stage, 60–100 g) recovered at NB-1 agrees with the prey size expected for *Tyto* sp. 1, a Barn Owl with an estimated body mass of 1190–1360 g (see Supplementary Table 3 and Fig. 7). This size range of prey items (60–840 g) and the large amount of bones from these taxa combined with the unaltered condition of the bones suggest that *Tyto* sp. 1 was a key species in the formation of the fossiliferous deposit. The role of *Tyto* sp. 2 at NB-1 remains unknown, as it could have been acted also as a bioaccumulation agent or have been introduced as a prey by *Tyto* sp. 1. Large-sized owls are known to prey on a wider size range of species than the small-sized owls (e.g., Comay and Dayan, 2018), and thus the large *Tyto* sp. 1 could potentially include smaller prey items, such as the murid (estimated body mass in adult stage, 42 g), some birds, reptiles and amphibians in its diet. However, some of the taxa retrieved from NB-1 suggest that other bioaccumulators could have potentially contributed to the formation of the deposit. Remains of very small-sized taxa (such as a scolecophidian and an amphisbaenid), or large-sized taxa such as adult/subadult hares (four bones), the bovid *Myotragus*, four bones, a large tortoise, one phalanx and a large viper – several bones – are outside of the presumed size range of prey expected for *Tyto* sp. 1 (Fig. 7).

Although some cases of predation by Barn Owls or true owls on small-sized owls (*Otus*) have been recorded (e.g., García et al., 2008), these are rare occurrences (e.g., Mikkola, 1976). Actually, it cannot be ruled out that *Otus* sp. from NB-1 was incorporated into the deposit as a prey by *Tyto* sp. 1 (or even by the smaller *Tyto* sp. 2). Nevertheless, the role of *Otus* sp. as potential bioaccumulator of small vertebrates in NB-1 should be considered. Small mammals like the shrew (with an estimated body mass of 8–10 g) and the murid, small passerines, or small reptiles (geckos, lizards, scolecophidians, small culebrines, amphisbaenids) and amphibians, all them present in the deposit, fall within the prey range of a small-sized owl. The abundance of vertebrates smaller than the estimated size range of *Tyto* spp.'s preferred prey suggests a link with the presence of the small-sized *Otus*. The material available suggests that the hindlimb long bones of *Otus* sp. are slightly larger than those of *Otus scops*, while the measurements of wing bones fall within the range of variability of *Otus scops*. The larger and stouter phalanges of *Otus* sp. compared to those of *Otus scops* are in agreement with its long hindlimb bones. All these features suggest a high terrestriality of *Otus* sp. from NB-1, which could be linked to a preferred predation on small terrestrial vertebrates (like the scolecophidian, the amphisbaenid, etc). A high terrestriality is a widespread trend among insular owls living on islands lacking mammalian predators (e.g., Louchart, 2005).

In summary, at least two of the Strigiformes (*Tyto* sp. 1 and *Otus* sp.) present in the deposit should be considered as bioaccumulation agents of the small vertebrate bones found at NB-1. The third one (*Tyto* sp. 2) could be considered either as a prey of *Tyto* sp. 1 or as another bioaccumulation agent. The differences in size between *Tyto* sp. 1 and *Otus* sp. are great enough that we assume that their prey size ranges differed or showed only a negligible overlap. The predatory role of both genera of strigiforms could have generated an owl pellet deposit showing a prey range wider than expected if it was produced by a single bioaccumulation agent. Thus, according with the available size range of prey, the sample obtained at NB-1 could be considered highly representative of the terrestrial small vertebrate fauna present in the Early Pliocene of Mallorca.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.crpv.2019.08.003.

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Origin, extinction and ancient DNA of a new fossil insular viper: molecular clues of overseas immigration

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Viperinae is a subfamily of viperid snakes whose fossil record in the Mediterranean islands is, until now, restricted to 12 palaeontological deposits on seven islands. Revision of the material excavated 30 years ago from the Middle/Late Pleistocene–Holocene deposit of Es Pouàs [Eivissa (= Ibiza), Balearic Islands, western Mediterranean] revealed about 6000 bones of a small-sized viper across different stratigraphic levels. Its morphological characteristics are different enough to known species of *Vipera* to warrant the description of a new species, but the nearly complete mitochondrial genome obtained from this snake based on a sample dated to 16 130 ± 45 BP, suggested it belonged to a new insular population of Lataste's viper (*Vipera latastei*), ***Vipera latastei ebusitana*** **subsp. nov**. Phylogenetic analysis indicates that the dispersal of the ancestors of *V. l. ebusitana* to Eivissa, most probably from a north-east Iberian population, occurred via overwater colonization < 1.5 Mya, well after the Messinian Salinity Crisis (5.97–5.32 Mya) when land bridges allowed terrestrial colonization of the Balearic Islands by mainland faunas. The morphological differences between *V. l. ebusitana* and the Iberian populations suggest that it is a new dwarf taxon resulting from insular evolutionary processes, becoming extinct shortly after the first human arrival to this island about 4000 years ago.

ADDITIONAL KEYWORDS: ancient DNA – extinction – invasive species – island fauna – Mediterranean – mitochondrial DNA – molecular clocks – new taxa – Quaternary – Serpentes.

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INTRODUCTION

Viperinae Oppel, 1811 (the true vipers) is a subfamily of viperid snakes currently distributed throughout Asia, Africa and Europe, and comprising up to 102 extant species and 13 genera (Phelps, 2010), although the taxonomic status of some species/subspecies remains under discussion (Freitas *et al.*, 2020). The fossil record of viperines in Europe is extensive and begins in the Early Miocene, about 23.8–22.8 Mya (Szyndlar & Rage, 2002). However, true vipers are scarce in the fossil record of the Mediterranean islands, known from only 12 paleontological sites on seven islands (Table 1). These specimens mainly consist of isolated vertebrae, which often defy precise taxonomic assignment. Consequently, the diversity and evolutionary history of Mediterranean vipers are poorly understood and extensively debated. Of particular interest is the identification of self-introduced endemic viper lineages versus those that have potentially been translocated by humans, as this is critical for understanding the assembly of the Mediterranean islands reptile fauna and the origins of fossil taxa.

The Cyclades viper [*Macrovipera lebetina schweizeri* or *M. schweizeri* (Werner, 1935), depending on authors] is often considered the only extant endemic Mediterranean island viperine taxon (Nilson & Andrén, 1988; Stümpel & Joger, 2009), although its presence on the Turkish mainland suggests its Mediterranean distribution may in fact derive from recent anthropic introduction (Stümpel & Joger, 2009; Freitas *et al.*, 2020). Likewise, it is debated whether *Montivipera xanthina* (Gray, 1849) on some Aegean islands (Kurnaz *et al.*, 2018) and *Vipera aspis* (Linnaeus, 1758) on Elba (Masseti & Zuffi, 2011) represent populations introduced by humans or were founded by natural autonomous dispersal, whereas the presence of the latter species on Montecristo island has been interpreted as a human-mediated colonization (Barbanera *et al.*, 2009). The earliest known presence of *M. lebetina lebetina* (Linnaeus, 1758) on Cyprus dates to the ninth millennium BC (Bailon, 1999), probably as the result of human introduction, although its allochthonous character is still under discussion. In contrast, a recently extirpated population of *Vipera latastei* Boscá, 1878 on the Columbretes Islands likely originated as the result of natural dispersal (Marquina *et al.*, 2014; Ruiz Sánchez *et al.*, 2019), as did the populations of *V. aspis* on Sicily (Barbanera *et al.*, 2009; Martínez-Freiría *et al.*, 2020) and *Vipera ammodytes* (Linnaeus, 1758) on the Cyclades (Ursenbacher *et al.*, 2008).

The capacity for members of *Vipera* Laurenti, 1768, in particular, to autonomously colonize Mediterranean islands is also supported by the fossil record of the Balearic Islands, from which a number of putative *Vipera* taxa have been described. The Balearic Islands (western Mediterranean Sea) are the most isolated islands in the

Table 1. Fossil record of Viperinae in the Mediterranean Islands

Taxon	Locality	Site age	Reference
V. latastei subsp. nov.	Es Pouàs (Eivissa)	Late Pleistocene to Holocene	This paper
cf. Vipera sp.	Cova de ca na Reia (Eivissa)	Calabrian	This paper
Vipera sp. (‘OVC’)	Caló den Rafelino (Mallorca)	Pliocene	Bailon *et al.*, 2010
cf. *Vipera natiensis*	Caló den Rafelino (Mallorca)	Pliocene	Bover *et al.*, 2014
Vipera sp. (‘OVC’)	Na Burguesa-1 (Mallorca)	Zanclean	Torres *et al.*, 2014
Vipera natiensis	Punta Nati 12 (Menorca)	Pliocene	Bailon *et al.*, 2002
Vipera sp.	Punta Nati 3 and 12 (Menorca)	Probably Pliocene	Bailon *et al.*, 2002
Viperidae indet.	Punta Nati 2 (Menorca)	Middle Miocene	Bailon *et al.*, 2002
Vipera sp.	Monte Tuttavista (Sardinia)	Late Pliocene–Early Pleistocene	Abbazzi *et al.*, 2004
cf. *Vipera*, *Vipera* sp.	Capo Mannu D1 (Sardinia)	Late Pliocene	Pecorini *et al.*, 1974; Delfino *et al.*, 2011
Vipera sp. *(‘aspis’* group)	Oschiri (Sardinia)	Early Miocene	Venczel & Sanchiz, 2006
Vipera sp. (‘*berus*’ group)	Laghada B (Kos Island)	Pleistocene	Szyndlar, 1991
Viperidae indet. (‘OVC’)	Chios Island	Middle Pleistocene	Schneider, 1975; Szyndlar, 1991
Macrovipera lebetina	Akrotiri Aetokremnos (Cyprus)	Holocene	Bailon, 1999
Viperidae indet.(‘OVC’)	Gargano palaeoisland	Late Miocene–Early Pliocene	Delfino, 2002

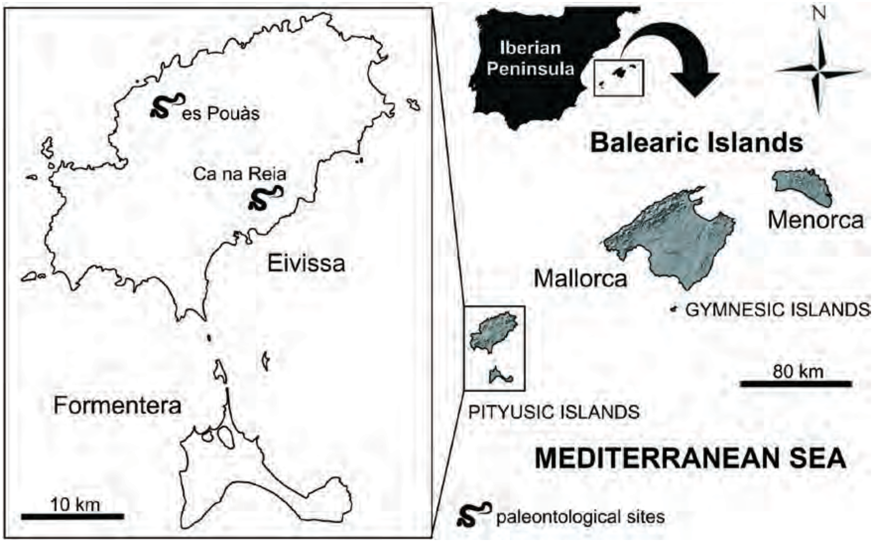

Figure 1. Geographical context of the Pityusic Islands and location of the palaeontological sites of Es Pouàs and Cova de ca na Reia in Eivissa (Balearic Islands, western Mediterranean).

Mediterranean and are composed of two groups (Fig. 1): the western Pityusic Islands (Eivissa, Formentera and surrounding islets) and the eastern Gymnesic Islands (Mallorca, Menorca and surrounding islets). Both groups have remained isolated from the mainland and from each another since the end of the Messinian, 5.33 Mya (Palmer *et al.*, 1999; Bover *et al.*, 2008). The Balearic fossil record of snakes is currently restricted to the Pliocene/Early Pleistocene of the Gymnesics, with the apparent absence of snakes from the Pityusic archipelago an accepted zoological peculiarity (e.g. Boscá, 1883; Compte Sart, 1966; Hinckley *et al.*, 2017). In Menorca, *Vipera natiensis* Bailon *et al.*, 2002 and *Vipera* sp. were described from Pliocene deposits and an indeterminate viperid from a Middle Miocene site (Bailon *et al.*, 2002). In Mallorca, the Pliocene site of Caló den Rafelino yielded two vertebrae of a large viperid attributed to the 'Oriental Vipers Complex' (OVC) (Bailon *et al.*, 2010) and other small vertebrae attributed to cf. *V. natiensis* (Bover *et al.*, 2014), while the Early Pliocene (Zanclean) deposit of Na Burguesa-1 yielded remains of another 'OVC' viper (Bover *et al.*, 2014; Torres *et al.*, 2014). While it is likely impossible to use DNA to establish the relationships between Pliocene taxa and extant species, Pleistocene and Holocene subfossil faunal remains from the Balearic Islands are amenable to ancient DNA analysis (Lalueza-Fox *et al.*, 2000, 2002, 2005a, b; Ramírez *et al.*, 2009; Bover *et al.*, 2018, 2019, 2020).

Ancient DNA studies have been mainly focused on mammalian taxa, especially humans. In contrast, analyses of ancient genetic data from fossil or subfossil reptiles are scarce (but see: Austin & Arnold, 2001, 2006; Austin *et al.*, 2003, 2004; Parham *et al.*, 2004; Arnold & Bour, 2008; Sommer *et al.*, 2009; Kehlmaier *et al.*, 2017, 2020; Seersholm *et al.*, 2018; Mahony *et al.*, 2020). Ancient DNA from snake taxa, in particular, has apparently only been obtained from ethanol or formalin-fixed museum specimens (Ruane & Austin, 2017; Allentoft *et al.*, 2018). In this study we report the presence of fossil viper remains from the Late Pleistocene–Holocene levels of Es Pouàs (Santa Agnès de Corona) and the Early Pleistocene site of Cova de ca na Reia (Santa Eulària des Riu) on the island of Eivissa (Fig. 1). In addition, we present ancient mitochondrial genetic data from the Es Pouàs viper, which allowed us to accurately establish its taxonomic identity and identify its mainland source region, revealing the first recorded overwater colonization of the Balearic Islands by a terrestrial vertebrate postdating the Messinian Salinity Crisis (MSC, Upper Miocene).

MATERIAL AND METHODS

Material

So far, Es Pouàs (Sant Antoni de Portmany, Eivissa) is the most important vertebrate palaeontological site of the Pityusic Islands with a Middle/Late Pleistocene to Holocene chronology. The absence of terrestrial mammals in the fossiliferous record of this cave suggests that the Pityusics were the sole islands over the entire Mediterranean region without terrestrial mammals (e.g. Florit *et al.*, 1989; Alcover *et al.*, 1994; Seguí & Alcover, 1999; McMinn *et al.*, 2005; Guerra, 2015), with the vertebrate fauna apparently only comprising birds, bats and a lizard until the first human arrival about four millennia ago (e.g. Alcover *et al.*, 1981; Alcover, 2008). However, a recent revision of the material excavated from Es Pouàs between 1989 and 1994 revealed *c.* 6000 bones of a small viper in different stratigraphic levels of the grid-squares A2, A3, A4 and A5 [for the topographical survey and reference grid of the site, see: Alcover & Muntaner (1986) and Guerra (2015)] (Table 2). The uppermost prehuman palaeontological level yielded a radiocarbon age of 6130 ± 80 BP (5295–4848 2σ cal BC; UtC-6222, obtained on *Rallus eivissensis* McMinn *et al.*, 2005 bone collagen; grid-square A3 at –60/–80 cm depth), while the lowermost dated level of this grid-square furnished a radiocarbon age of 30 700 ± 600 (34 694–32 523 2σ cal BC; UtC-2929, on bird bone collagen; A3, level 8). The viper bones used for the morphological analysis in our study were obtained from grid-squares A3 (from –60/–80 cm to level 8) and A2 (from –70/–90 cm to –350/–370 cm), whereas vertebrae used for molecular analyses came from grid-square A2 (–110/–130 cm). A combined sample of 64 viper vertebrae from this same grid and level (IMEDEA 106583; total weight: 0.53 g) were radiocarbon dated at 16 130 ± 45 BP (17 620–17 320 2σ cal BC; RICH-24981). In addition, a single ophidian caudal vertebra was obtained from Cova de ca na Reia (Santa Eulària del Riu, Eivissa), a palaeontological site assumed to belong to Gelasian/Calabrian (Alcover & Agustí, 1985).

Table 2. Distribution of the 6018 remains of *Vipera latastei ebusitana* at Es Pouàs. All numbers from the IMEDEA collection

Grid	Level (cm)	IMEDEA Number	Bones
	Surface	106559–106576	29 vertebrae
A2	–70/–90	106840	1 vertebra
	–110/–130 (near wall)	106841	2 vertebrae
	–110/–130	106583–106587	116 vertebrae⁽¹⁾
	–110/130 (wall)	106841	2 vertebrae
	–130/–150	106588–106610	688 vertebrae, 2 compound bones, 1 pterygoid
	–150/–170	106611–106616	549 vertebrae
	–170/–190	106617–106683	1.381 vertebrae⁽²⁾, 1 compound bone
	–190/–210	106684–106711	918 vertebrae
	–210/–230	106712–106721	132 vertebrae, 1 compound bone
	–230/–250	106722–106731	161 vertebrae
	–250/–270	106839	5 vertebrae
	–270/–290	106732–106784	1.026 vertebrae, 1 compound bone
	–290/–310	106785–106802	94 vertebrae
	–330/–350	106803–106832	228 vertebrae, 3 compound bones
	–350/–370	106833–106838	8 vertebrae, 1 compound bone
A3	Lower N3 (near wall)	106842	1 vertebrae
	Lower N3	106843	1 vertebra
	Lower N4	106844	6 vertebrae
	N6 (Near wall)	106554, 106556–106558	14 vertebrae
	Upper N6	106845	41 vertebrae
	Interfase N6–N7	106553, 106555	36 vertebrae⁽²⁾
	N7 (near cave wall)	106542–106551	148 vertebrae⁽²⁾
	N7 (far cave wall)	106541	152 vertebrae⁽²⁾
	Upper N7 (far wall)	106533–106540	181 vertebrae, 1 compound bone
	Lower N7 (near wall)	106552	32 vertebrae
	Lower N7 (far wall)	106846	2 vertebrae
	N8A (far wall)	106847	3 vertebrae
A4	–220/–240	106579–106582	50 vertebrae
A5	–100/–120	106577, 106578	28 vertebrae

⁽¹⁾ From this level, 30 vertebrae were used for DNA analysis and 64 for radiocarbon dating.
⁽²⁾ Some of the vertebrae from this level were charred.

All specimens studied here are curated at the vertebrate collection of the Institut Mediterrani d'Estudis Avançats (Esporles, Spain) (acronym: IMEDEA), while a small sample of 12 unnumbered vertebrae has been deposited at the Muséum National d'Histoire Naturelle in Paris. The comparative material of several species of *Vipera* used in this study came from the IMEDEA and Muséum National d'Histoire Naturelle (Paris, France) (acronym: MNHN) collections [*V. ammodytes* (MNHN-ZA-AC 2020–2), *V. aspis* (IMEDEA106926 and MNHN 1967-100), *V. latastei* (IMEDEA 106925 and MNHN-ZA-AC 2020–1), *V. monticola* Saint-Girons, 1954 (RA-MNHN 1961-0334), *V. seoanei* Lataste, 1879 (IMEDEA106927 and MNHN-ZA-AC 2020–3) and *V. ursinii* (Bonaparte, 1835) (MNHN-ZA-AC 1967-277)].

Scanning electron microscope (HITACHI S-3400N) photographs of the specimens were taken at the Scientific and Technical Services of the Universitat de les Illes Balears (Mallorca). The measurements (in mm) of the vertebrae were taken using a Digital Microscope AM7915MZT Dino-Lite Edge. The measurements and nomenclature used in the morphological description of the specimens follow Szyndlar (1984).

BODY-SIZE ESTIMATION

Several vertebral measurements and methods – including regression and maximum likelihood – have been used to estimate body length in snakes (e.g. Head *et al.*, 2009; LaDuke *et al.*, 2010; McCartney *et al.*, 2018), but it is usually required to have a precise identification of the position of the vertebra in the column, which in the case of isolated vertebrae can be a difficult task. The discussion on this topic is beyond the purpose of this paper and an approximate body-length estimate would be informative enough to understand body-size differences between extant *Vipera* and the fossil snake presented here. For this reason, we follow Bailon *et al.* (2002) in estimating body length of the extinct viper from Eivissa using linear regression of the vertebral measurement CL (centrum length) in intermediate trunk vertebrae, which showed a high coefficient of determination ($R^2 = 0.9512$) (see Supporting Information, Table S1). The complete ossification degree of some structures of these vertebrae, especially the thick walls and condyle–cotyle/neural arch ratio, indicated that the material used to estimate the body size was from adult specimens. We estimated total body length (TBL) using the equation $Y = 1.2523X + 4.6234$ obtained from data of nine individuals belonging to six different species of *Vipera*, where e^Y = total length of the viper and X = ln of the vertebrae centrum length (CL).

ANCIENT DNA EXTRACTION AND LIBRARY CONSTRUCTION

All extraction and library construction steps were performed in the ancient DNA laboratory of the Australian Centre for Ancient DNA (ACAD) at the University of Adelaide (Australia). Fifteen vertebrae of the fossil snake from Es Pouàs [grid A2, –110/–130 cm, radiocarbon age 16 130 ± 45 BP (17 620–17 320 2σ cal BC; RICH-24981, McMinn *et al.*, 2005)] were washed three times in 1.5 mL of water, with a final wash using 1.5 mL of absolute ethanol, air dried and UV irradiated for 15 min on each side. Vertebrae were pulverized using a hammer and the 110 mg remaining were digested on a rotary wheel for 1 h in 1 mL of 0.5 mol/L EDTA (pH 8.0) (Life Technologies, Carlsbad, CA, USA). EDTA was removed by pipetting and bone powder was then digested at 55 °C under constant rotation for 24 h in a digestion buffer consisting of 970 mL 0.5 mol/L EDTA and 30 µL Proteinase-K 20 mg/mL (Life Technologies). Supernatant was collected following centrifugation and DNA was bound to suspended silicon dioxide particles (Brotherton *et al.*, 2013) in a modified PB binding buffer [13.6 mL PB buffer (Qiagen, Valencia, CA, USA), 420 µL 3 mol/L sodium acetate (~pH 5) (Sigma-Aldrich, Saint Louis, MO, USA) and 7 µL Tween-20 (Sigma-Aldrich)]. After purification with 80% ethanol, the sample was eluted in 100 µL of TLE (10 mmol/L Tris, 0.1 mmol/L EDTA pH 8.0). A negative control was extracted alongside the samples.

A non-repaired double-stranded DNA library was constructed from this sample following a protocol based on Meyer & Kircher (2010) with modifications used by Llamas *et al.* (2016), which comprised a 7-mer barcode sequence in both truncated P5 and P7 adapters, the use of Platinum Taq Hifi (Invitrogen, Carlsbad, CA, USA) for the first post-Bst PCR library amplification and the use of Amplitaq Gold (Life Technologies) for subsequent amplifications. The final library was sequenced on an Illumina NextSeq using a 150-cycle Mid Output kit (in PE 2 × 75 mode).

READ FILTERING, MAPPING AND CONSENSUS GENERATION

The quality of a total of 24 791 817 resulting raw sequencing reads was analysed using fastQC v.0.11.2 (http://www.bioinformatics.babraham.ac.uk/projects/fastqc). We demultiplexed sequences from the snake sample by filtering both P5 and P7 barcodes (allowing one mismatch) using SABRE v.1.0 (http://github.com/najoshi/sabre). Adapter sequences were trimmed with AdapterRemoval v.2.1.7 (Schubert *et al.*, 2016) using the following parameter values: mismatch rate 0.1, minimum Phred quality 4, quality base 33, trim ambiguous bases (N) and trim bases with qualities equal to or less than the given minimum quality. AdapterRemoval collapsed (merged) paired reads overlapping by at least 11 bp. After trimming, reads shorter than 25 bp were excluded from further analysis. We retained 23 122 029 collapsed reads (~93% of total read pairs) for downstream analysis.

We constructed a draft mitochondrial genome of the snake from Eivissa using a seven-step process (see schematic diagram in Supporting Information, Fig. S1): (1) iterative mapping to two published reference genomes ('Multi-reference Iterative Mapping Approach', MIMA) using BWA (Li & Durbin, 2009); (2) extension of the MIMA reference using MITObim (Hahn *et al.*, 2013); (3) iterative mapping to the MITObim consensus sequence; (4) BLASTn (Altschul *et al.*, 1990) authentication of mapped regions; (5) merging consensus sequences from steps one and three; (6) iterative mapping to merged reference from step five and creation of final consensus sequence; and (7) BLASTn and mapDamage (Jónsson *et al.*, 2013) authentication of final consensus sequence. These steps are described in detail below:

1. In step one, we used a multi-reference iterative mapping approach (MIMA), which involves sequential rounds of mapping, in between which the reference sequence is updated with information from the previous round. Preliminary morphological analysis suggested the ascription of the remains to the genus *Vipera,* based on the well-developed hypoapophysis, inclined post- and pre-zygapophysis and the shape of pterygoid and compound bones (see detailed description below). For this reason, we chose two mitochondrial genome references: *Vipera berus* (Linnaeus, 1758) (GenBank accession number NC_036956) and *Daboia siamensis* (Smith, 1917) [GenBank accession number NC_011391; Garrigues *et al.*, 2005; Wüster *et al.*, 2008; Freitas *et al.*, 2020; mislabelled as *D. russellii* (Shaw & Nodder, 1797) in GenBank according to Freitas *et al.* (2020)]. For each reference, collapsed reads were mapped using BWA v.0.7.17 backtrack algorithm (Li & Durbin, 2009; parameters aln -n 0.001, -o 2, -l 1024). Subsequently, reads with mapping quality lower than Phred 25 were removed using SAMtools v.1.8 (Li *et al.*, 2009) and duplicate reads were filtered using FilterUniqueSAMCons.py (Kircher, 2012). Intermediate 75% majority consensus sequences were generated using GENEIOUS v.11.1.4 (Biomatters, http://www.geneious.com, Kearse *et al.*, 2012), retaining the reference nucleotide for sites with read-depth < 3×. This new consensus was used as the new reference and the process was iterated until no more reads were mapped. The final 75% majority consensus sequences for the iterative mapping against each reference were then generated in GENEIOUS, calling nucleotides only at sites with read-depth ≥ 3×. After 16 iterations, 2785 unique reads mapped to the *V. berus* mitogenome (reference coverage = 76%; mean depth = 9×), whereas after 13 iterations, 1080 unique reads mapped to the *D. siamensis* mitogenome (reference coverage = 33% coverage; mean depth = 3.2×). The consensus sequences generated from iterative mapping against the two different references were identical for regions where they overlapped. We aligned these consensus sequences with the *V. berus* mitogenome using the MUSCLE algorithm implemented in GENEIOUS and created a new merged reference by retaining nucleotides called from our sequence data and filling any gaps with the corresponding nucleotides from *V. berus*. The merged reference was then used for six rounds of iterative mapping (as described above) after which 2918 unique reads were retained (reference coverage = 78.2%; mean depth = 9.4×). We then generated a 75% majority consensus, retaining the reference nucleotide (*V. berus*) in positions with coverage depth < 3×.
2. In step two, we used the MITObim pipeline v.1.8 (Hahn *et al.*, 2013) with default parameters to map all collapsed reads to the consensus generated at the end of step one (see above). MITObim maps all reads to a reference seed using MIRA (Chevreux *et al.*, 1999) and then iteratively attempts to extend mapped contigs. After 11 iterations of mapping, we converted the MAF formatted output file to SAM file format using 'miraconvert' in MIRA, then removed duplicate reads using FilterUniqueSAMCons.py, before remapping the 2966 retained reads using the GENEIOUS read mapper (maximum mismatches per read = 10%; minimum mapping quality = Phred30; maximum gaps per read = 10% read length; maximum gap length = 10 bp; minimum overlap = 25 bp; word size = 12). We then generated a 75% majority-rule consensus sequence, retaining the reference nucleotide for sites with coverage depth < 3×.
3. In step three, we used the consensus sequence from step two as the reference for another round of iterative mapping using BWA (as described in step one). After three iterative rounds of mapping, we retained 3261 unique reads (reference coverage = 85.3%; mean depth = 10.6×). We then generated a 75% majority-rule consensus sequence, calling nucleotides only for sites with coverage depth ≥ 3×.
4. All overlapping fragments in the consensus sequences from steps one and three were identical. However, some fragments were represented in the consensus of step three but not in the other consensus (from step one). We analysed these new

fragments using BLASTn in order to verify the authenticity of the sequences. Fifteen fragments were analysed and all of them matched most closely to species of the genus *Vipera* (generally with Query Cover > 93% and Identity > 85%).

5. We combined the information from the consensus sequences from steps one and three to create a new merged reference, retaining the *Vipera berus* mitogenome nucleotide only where there was no coverage from our previously mapped reads.
6. In step six, we used the consensus sequence from step five as the reference for a final round of iterative mapping. After two iterations we retained 3339 unique reads mapped (reference coverage = 86.3%; average depth = 10.8×) and generated a final consensus, as described above (i.e. 75% majority threshold, nucleotides called only where coverage depth was ≥ 3×).
7. We analysed the final consensus sequence from step six, including degenerate nucleotides, using BLASTn. The top hit was *Vipera berus* (Query Cover = 76%; Identity = 92.7%). Misincorporation and DNA fragmentation patterns in unique mapped reads were assessed using mapDamage v.2.0.8 (Jónsson *et al.*, 2013) (Supporting Information, Fig. S2), which displays the expected damage pattern observed in ancient samples (e.g. Briggs *et al.*, 2007). Consequently, we used this consensus sequence for all downstream analyses.

PHYLOGENETIC AND HAPLOGROUP NETWORK ANALYSES

Following previously published phylogenetic analyses (e.g. Wüster *et al.*, 2008; Freitas *et al.*, 2020), we selected genetic data from the Viperinae genera *Vipera*, *Montivipera* Nilson *et al.*, 1999, *Macrovipera* Reuss, 1927 and *Daboia* Gray, 1842 available in GenBank to construct two alignments (Supporting Information, Appendices S1 and S2) for maximum likelihood (ML) and Bayesian inference (BI) phylogenetic analyses:

Dataset 1

We downloaded previously published *12S_rRNA*, *16S_rRNA*, *COI*, *Cytb*, *ND2* and *ND4* sequences (see Supporting Information, Table S2) and aligned them to our Eivissan viper data using the MUSCLE algorithm as implemented in GENEIOUS. Whenever possible, we selected isolated gene sequences from the same individual, or at least from the same geographic region for the same species, resulting in an alignment with 34 samples, comprising a single representative per species.

Dataset 2

As the preliminary results using Dataset 1 (see Supporting Information, Fig. S3) indicated that the snake from Eivissa was within the clade comprising *Vipera latastei/monticola*, we substituted the *V. latastei* and *V. monticola* sequences used in Dataset 1 with six sequences representing different populations of *V. latastei* from the Iberian Peninsula and a *V. latastei / monticola* from Morocco (see Supporting Information, Table S2), increasing the dataset to 39 samples.

We divided our alignments into *12S_rRNA*, *16S_rRNA*, as well as first-, second- and third-codon positions of protein-coding genes (PCG). Ambiguous regions of rRNAs were removed using stringent default parameters in Gblocks (Castresana, 2000), which kept 213 out of 365 bp (58%) of *12S_rRNA* and 327 out of 425 bp (76%) of *16S_rRNA*. Consequently, the final alignment was 4164 bp in length (213 bp *12S_rRNA*, 327 bp *16S_rRNA*, 840 bp *COI*, 1104 bp *Cytb*, 1002 bp *ND2* and 678 bp *ND4*). We then determined the best partitioning scheme and substitution models for each dataset using PartitionFinder v.2.1.1 (Lanfear *et al.*, 2016; see Supporting Information, Table S3). We performed a partitioned maximum likelihood analysis in RAxML v.8.2.11 (Stamatakis, 2014), with node support values estimated by performing 1000 bootstrap replicates. We also performed a partitioned MrBayes v.3.2.3 analysis (Ronquist *et al.*, 2012), comprising four separate runs of four Markov chains each using default priors. Each chain ran for 10^7 generations sampling trees and parameter values every 10^4 generations. Topological convergence was assessed using the average standard deviation of clade (split) frequencies (< 0.02), while convergence in individual parameter values was assessed through broadly overlapping distributions and effective sample sizes > 200 in TRACER v.1.6. All sampled trees were summarized as a majority-rule consensus tree after discarding the first 10% of trees as burn-in.

A partitioned molecular dating analysis was performed on both datasets using BEAST v.1.8.4 (Drummond *et al.*, 2012), with a Birth–Death tree prior and a single lognormal relaxed clock. The calibration of phylogenetic trees for Viperidae Oppel, 1811 using fossil records is controversial given the lack of remains for some groups and/or regions, as well as the ambiguity of associating fossil remains to living taxa (see: Stümpel *et al.*, 2016; Martínez-Freiría *et al.*, 2017; Freitas *et al.*, 2020). Most authors recognize these difficulties and generally use a combination of fossil remains, palaeogeography and/or secondary calibration points to date viperid phylogenetic trees (e.g. Wüster *et al.*, 2008; Ferchaud *et al.*, 2012; Velo-Antón *et al.*, 2012; Zinenko *et al.*, 2015; Alencar *et al.*, 2016; Stümpel *et al.*, 2016; Zheng & Wiens, 2016;

Martínez-Freiría *et al.*, 2017; Šmid & Tolley, 2019). Our molecular dating strategy relies on constraining the age of the root of the tree – i.e. the split between *Vipera*–*Daboia* and *Macrovipera*–*Montivipera* – in accordance with the results of Zheng & Wiens (2016). Thus, we constrained the age of the root node using a lognormal prior with a mean of 25.5 Mya and standard deviation of 0.1 (for a similar dating approach, see: Freitas *et al.*, 2020; Martínez-Freiría *et al.*, 2020). Four analyses were run for 10^7 generations sampling every 10^4 generations, discarding the first 10% of samples as burn-in. Convergence was assessed through combined analysis of four independent runs where parameters showed effective sample sizes > 200 as calculated using TRACER v.1.6 (http://tree.bio.ed.ac.uk/software/tracer/). Individual run outputs were combined using LogCombiner v.1.8.4 and a final maximum clade credibility tree was generated using TreeAnnotator v.1.8.4 (Rambaut & Drummond, 2010).

To evaluate the position of the snake from Eivissa within the diversity of *Vipera latastei/monticola*, we aligned the *Cytb* (270 bp) and *ND4* (602 bp) sequences available for *V. latastei/monticola* from Velo-Antón *et al.* (2012), Martínez-Freiría *et al.* (2015, 2020) and Freitas *et al.* (2018) (see Supporting Information, Table S4), including the corresponding sequences for the snake from Eivissa and *Vipera aspis* as outgroup (*Cytb* accession number JX649673 and *ND4* accession number JX649606). The alignment of 872 bp (Supporting Information, Appendix S3), with and without outgroup, was analysed using RAxML, and the resulting tree without outgroup was used to generate a haplogroup network using Fitch algorithm in Fitchi (Matschiner, 2015) (Fig. 2; Supporting Information, Fig. S4). The same dataset was used to graphically depict the pairwise distances between different *V. latastei/monticola* sequences using the heatmap similarity (%) implemented in GENEIOUS.

RESULTS

PHYLOGENETIC ANALYSES

The partial mitochondrial genome sequence for the *Vipera* from Eivissa has a total length of 16 381 bp (GenBank Accession Number MT527189). Up to 3248 nucleotides are degenerate (3181 N, 45 Y and 22 R), precluding the clear annotation of several genes. However, alignment against the mitochondrial genome of *Vipera berus* (NC_036956, total length 16 370 bp) shows that our new sequence has the typical mitochondrial structure of 13 protein-coding genes, 22 tRNA genes (although *tRNA-Thr* has not been recovered), two rRNA genes and two control regions.

The results of our phylogenetic analyses agree with those of previously published Viperinae molecular studies using mitochondrial and nuclear data (Fig. 3; Supporting Information, Figs S3, S5, S6). We recapitulate with high support [i.e. Bayesian posterior probability (PP) = 1.0; maximum likelihood bootstrap (MLB) > 95%] the monophyly of *Daboia*, *Macrovipera*, *Montivipera*, *Vipera* and clades comprising *Daboia/Vipera* and *Macrovipera/Montivipera* (e.g. Garrigues *et al.*, 2005; Wüster *et al.*, 2008; Alencar *et al.*, 2016; Šmíd & Tolley, 2019). We also recover the expected relationships among the *Vipera aspis*, *V. berus* and *V. ursinii* species groups within *Vipera*, as well as the basal position of *V. ammodytes* (e.g. Zinenko *et al.*, 2015; Alencar *et al.*, 2016; Šmíd & Tolley, 2019). Likewise, the relationships among the *Montivipera raddei* (Boettger, 1980) and *M. bornmuelleri* (Werner, 1898) species groups, as well as the *M. xanthina* clade within *Montivipera*, are consistent with the results of past studies (e.g. Alencar *et al.*, 2016; Stümpel *et al.*, 2016; Šmíd & Tolley, 2019), as are the relationships among the monophyletic clade comprising *Daboia mauritanica* (Gray, 1849)/*D. palaestinae* (Werner, 1938) and *D. siamensis* (Šmíd & Tolley, 2019). In our analyses of Dataset 1 (Supporting Information, Figs S3, S6), *Vipera latastei* is the sister-taxon of the snake fossil remains from Eivissa (PP = 1, MLB = 100), within the *V. aspis* species group. In our analyses of Dataset 2 (Fig. 3; Supporting Information, Fig. S5), which includes more representatives of *V. latastei/monticola*, the Eivissan viper falls within the variability of the East CNS [East Central-North-South clade, *sensu* Martínez-Freiría *et al.* (2020), which is named the NE-SE-CN clade by Velo-Antón *et al.* (2012)] *V. latastei* populations (PP = 1.0, MLB = 100). This result raises the possibility that the extinct Eivissan viper should be considered an extinct insular population derived from the eastern Lataste's viper.

Our calibrated trees (Fig. 3; Supporting Information, Fig. S6) also agree with divergence ages obtained for comparable nodes reported by other authors using diverse calibration points (e.g. Wüster *et al.*, 2008; Pook *et al.*, 2009; Velo-Antón *et al.*, 2012; Pyron & Burbrink, 2014; Alencar *et al.*, 2016; Zheng & Wiens, 2016; Šmíd & Tolley, 2019), except for Fenwick *et al.* (2012) who generally obtained younger ages for some nodes (Supporting Information, Fig. S7). The split between the Eivissan viper sample and its nearest relative in Dataset 1 (*Vipera latastei*) was estimated at 2.67 Mya (95% highest posterior density, HPD = 1.83–3.55 Mya) (Supporting Information, Fig. S6). However, the representative of *V. latastei* used in Dataset 1 was a combination of sequences from the western Iberian clades CW-S and CNW-SW (*sensu* Velo-Antón *et al.*, 2012; accession numbers JX649564, KY762037,

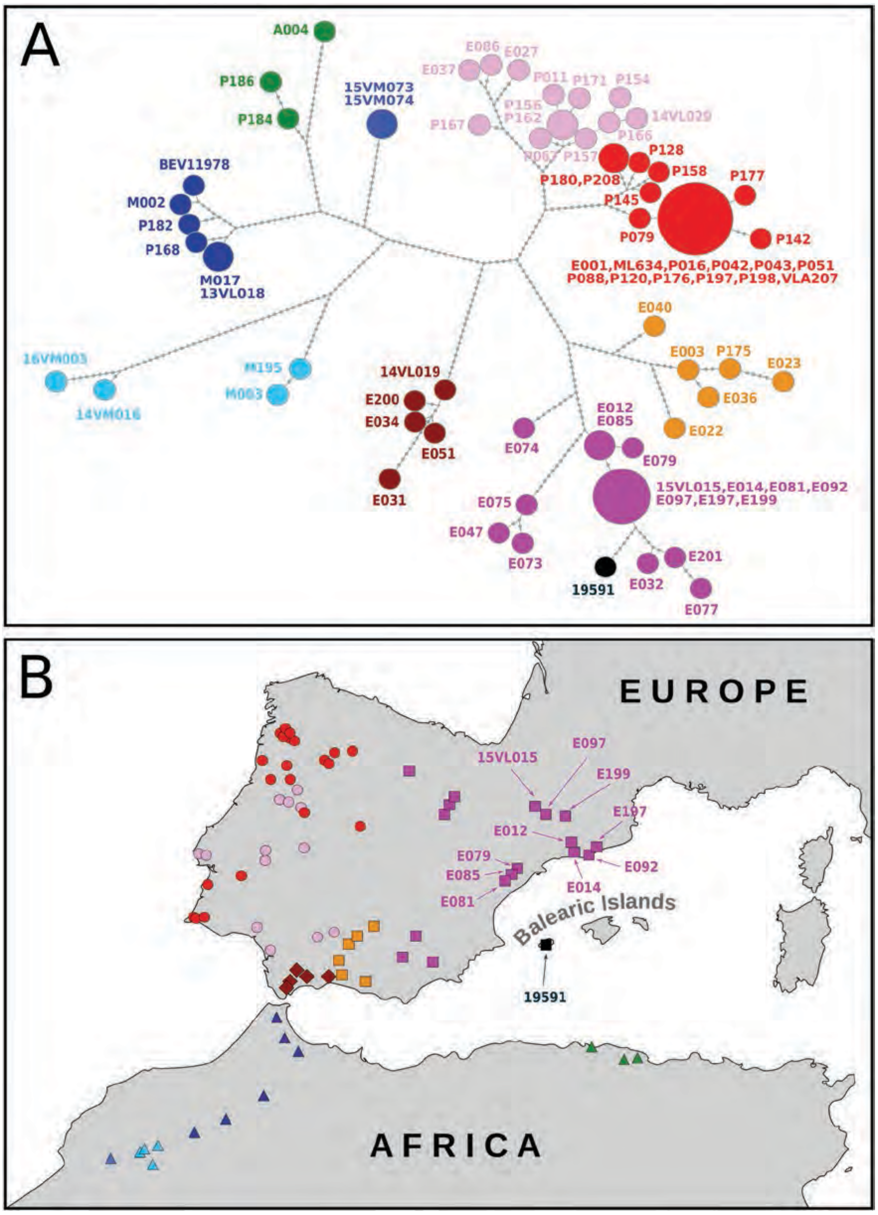

Figure 2. Haplogroup network analysis of 76 *Vipera latastei/monticola* individuals and the *V. latastei ebusitana* (15951, in black) sequences (270 bp *Cytb* + 602 bp *ND4*). A, network estimated using Fitchi algorithm. B, geographical location of individuals including identification numbers for those sequences more similar to *V. latastei ebusitana* according to network analysis. See Supporting Information, Table S4 for details about geographical origin of samples and accession numbers.

KY762066 and MG875549) and from unknown origin within Spain (AY21074).

Our analyses of Dataset 2 suggest the Eivissan viper forms a clade with the East CNS samples (Fig. 3; Supporting Information, Fig. S5), which, according to our data, diverged 0.97 Mya (95% HPD = 0.67–1.31 Mya), in concordance with the < 1.5 Mya age calculated by Velo-Antón *et al.* (2012) and Martínez-Freiría *et al.* (2020). While our node age estimates within *V. latastei* could possibly be biased by violation of the Birth–Death tree prior in BEAST (which assumes samples belong to different species) and the time-dependency of molecular

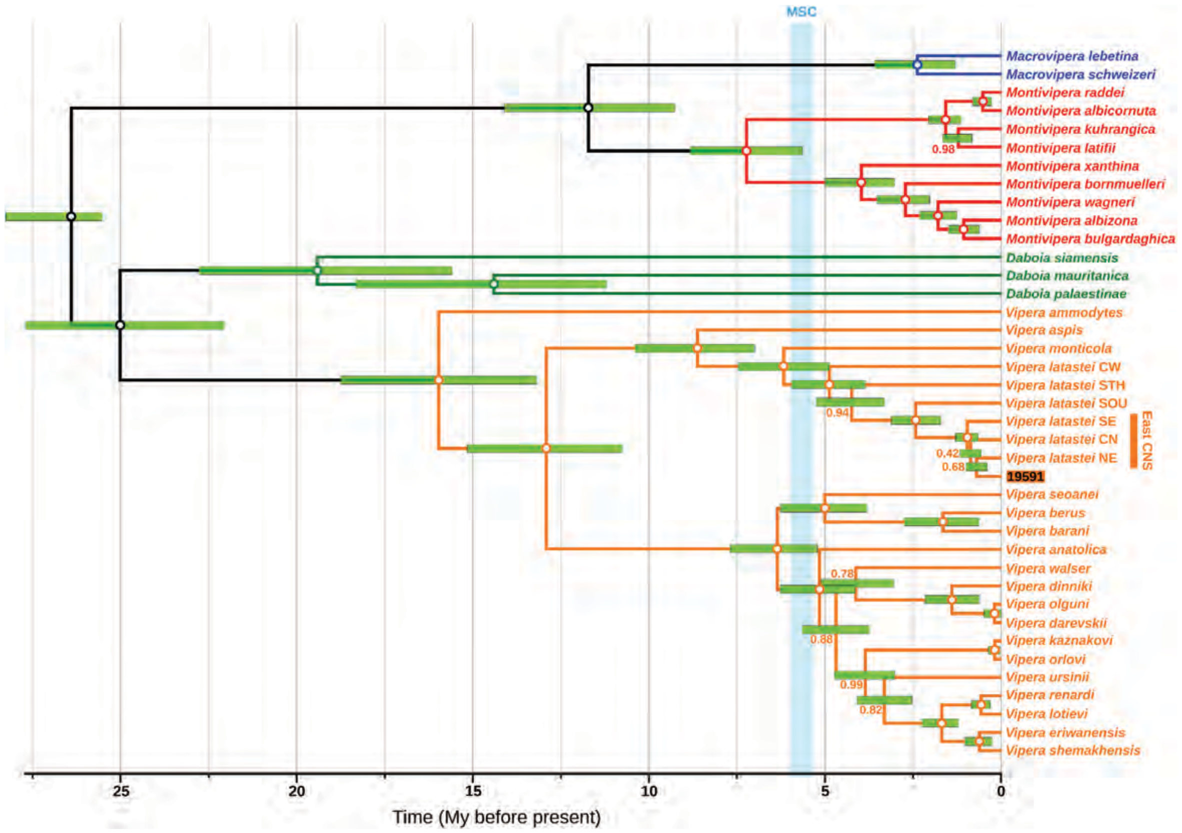

Figure 3. Phylogenetic position of *Vipera latastei ebusitana* (sample 19591) within Viperinae based on mitochondrial sequences (4164 bp) and using BEAST. Nodes are labelled with Bayesian posterior probabilities (PP) and circles in nodes indicate PP = 1. Green bars represent 95% highest posterior density (HPD) intervals. Messinian Salinity Crisis (MSC) is indicated by blue shading. See Supporting Information, Table S2 for information about individual samples and accession numbers. Time in million years before present (BP). *V. latastei* individuals from west (W), south (STH), eastsouth (SOU) and east CNS (SE, CN, NE) populations.

rates (e.g. Subramanian & Lambert, 2011), we believe any effect of these biases is likely to be minimal because the *V. latastei* samples in Dataset 2 represent highly divergent populations (some representing subspecies level taxa) and our node ages are broadly consistent with previously published estimates. Within the East CNS clade, the split between the Eivissan viper and its sister-taxon (*V. latastei* individual from the NE population) is 0.71 Mya (95% HPD = 0.41–1.01 Mya), but this node is poorly supported (PP = 0.68). Importantly, either estimate substantially postdates the last possible opportunity for colonization by means of a land bridge between the Balearic Islands and the Iberian Peninsula during the Messinian Salinity Crisis (MSC, 5.97–5.32 Mya; Krijgsman *et al.*, 1999; Manzi *et al.*, 2013).

We cannot establish a clear placement of the Eivissan viper within the East CNS *Vipera latastei* populations using maximum likelihood or Bayesian inference phylogenetic analyses, but the haplogroup network (Fig. 2) suggests that it should be considered as a separate population, being more genetically similar (> 98% similarity; Supporting Information, Fig. S8) to the individuals from the north-east Iberian east-CNS population (i.e. from localities in Tarragona, Castelló, Barcelona, Huesca and Lleida). The east-CNS population diverged from the east-south population about 2.66 Mya and diversified about 1.13 Mya (Velo-Antón *et al.*, 2012; Martínez-Freiría *et al.*, 2020).

TAXONOMIC STATUS OF THE EIVISSAN VIPER

Island biology is a key discipline for evolutionary studies. The theory of evolution was born on islands and a lot of its stronger documentation comes from islands. Species arriving on an isolated island after crossing a sea barrier start to evolve on the island from a first colonizer propagule, which initially does not differ from its mainland ancestors. Although the split from its ancestral mainland species (and its consequent reproductive isolation) can be established at the time of the arrival on the island, it is obvious that the colonizers are exactly the same as those of the population from which they come. From a morphological and genetic point of view both belong to the same species. The evolutionary adaptation to the new ecological conditions of the island (together with the ecological transformations of the insular ecosystems produced by the colonizers and their descendants) leads to the rise on the island of a new differentiated taxon through the speciation process. Within this process, two questions arise: How long does it take for a distinct new taxon to originate? What kind of differences are necessary for the derived population to be considered a different taxon?

The origin of a new species on islands can be exceptionally quick [e.g. Lamichhaney *et al.* (2017) argue that speciation may occur over only a few generations through 'hybrid speciation'], although it seems reasonable to expect that it usually takes longer. However, overall there are few data on the minimum time that would be necessary to originate a new species. Hume & Martill (2019) documented that *Dryolimnas cuvieri aldabranus* (Pucheran, 1845), the Aldabran flightless rail, evolved on Aldabra in less (perhaps much less) than 100 000 years. If we restrict the question to ophidians, we can estimate the age of new taxa through geological and genetic data. For example, among the Galápagos Islands, the youngest island inhabited by a snake is Fernandina (with a geological age of subaerial lava 0.1–0.03 Myr), where a differentiated subspecies of *Pseudalsophis occidentalis* (Van Denburgh, 1912) exists. It derived from *P. occidentalis* from Isabela (with the geological age for subaerial lava of 0.8–0.5 Myr). From these geological ages, the origin of the Fernandina subspecies should be no older than 100 000 years and could be as young as 30 000 years. The presumed origin of the species *P. occidentalis* occurred as long as 800 000 years ago, but perhaps as recently as 500 000 years. In the Comoros in the Indian Ocean, an endemic subspecies of *Lycodrias cococola* Hawlitschek, Nagy & Glaw, 2012 arose on Grande Comoro, an island 10 000 years old. Together, these data suggest that a recognizable subspecies can arise in as little as tens of thousands of years, although the origin of a distinct species probably requires more time.

Although morphological differences between the Eivissan viper and Lataste's viper could be large enough to probably consider them as different species, the genetic analysis confirms that the Eivissan viper derived from the mainland *Vipera latastei*. Thus, as a conservative compromise, we present it here as a morphologically highly different subspecies of *V. latastei*.

SYSTEMATIC PALAEONTOLOGY

SERPENTES LINNAEUS, 1758

VIPERIDAE OPPEL, 1811

VIPERA LAURENTI, 1768

VIPERA LATASTEI BOSCÁ, 1878

VIPERA LATASTEI EBUSITANA TORRES-ROIG, ALCOVER & BAILON **SUBSP. NOV.**

Zoobank registration: urn:lsid:zoobank.org:act:FA06E236-786D-46BE-A4A0-7AAC973BCFF6

Etymology: Ebusitana from Latin *Ebusus*, an adaptation of Ibosim, the Phoenician name for the island of Eivissa. We propose the common names 'escurçó nan d'Eivissa' (Catalan), 'víbora enana de Ibiza' (Spanish) and 'Eivissan dwarf viper' (English).

Holotype: Complete middle trunk vertebra IMEDEA 106587 (Fig. 4).

Paratypes: Cervical vertebrae (IMEDEA 106535, 106568, 106615, 106618, 106628, 106661, 106689, 106702, 106707, 106713, 106769, 106778), anterior trunk vertebrae (IMEDEA 106579, 106649, 106686, 106693, 106705, 106720, 106750, 106768), middle trunk vertebrae (IMEDEA 106544, 106558, 106564, 106567, 106619, 106629, 106637, 106646, 106652, 106660, 106685, 106691, 106748, 106766, 106777, 106779, 106789) and posterior trunk vertebrae (IMEDEA 106551, 106576, 106621, 106651, 106668, 106711, 106718), pterygoid fragment (IMEDEA 106589) and compound bones (IMEDEA 106534, 106590, 106591, 106644, 106721, 106784, 106829, 106830, 106831, 106838).

Type locality and horizon: Es Pouàs (Sant Antoni de Portmany, Eivissa, Pityusic Islands), grid square A2, level –110/–130 cm.

Chronology: At least Late Pleistocene–Holocene. A sample of 64 vertebrae (IMEDEA 106583) has been dated by at the C14 Laboratory of the Institut Royal du Patrimoine Artistique/Koninklijk Instituut voor het Kunstpatrimonium of Brussels (RICH-24981: 17 620–17 320 2σ cal BC; Late Pleistocene).

Additional referred material: Es Pouàs (Sta. Agnès de Corona, Eivissa): 5925 vertebrae numbered in groups from different levels (see Table 2).

Diagnosis: The following combination of diagnostic characters is exclusive of *Vipera latastei* subsp. *ebusitana*. A Lataste's viper subspecies smaller than the extant Iberian populations of this species, with a body size

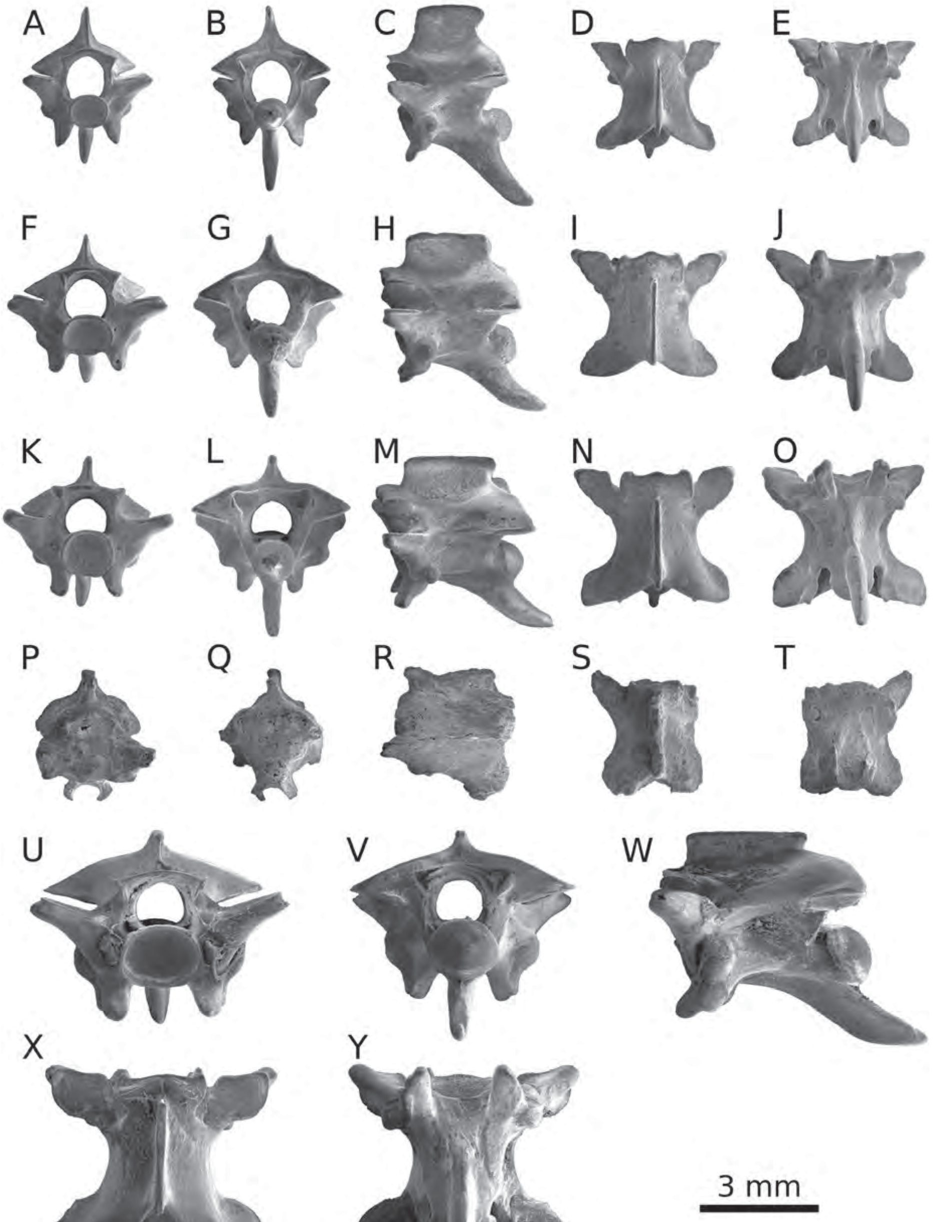

Figure 4. Vertebrae from Eivissan extinct snakes and extant mainland *Vipera latastei*. A–E, cervical vertebra (IMEDEA 106535), F–J, anterior trunk vertebra (IMEDEA 106693) and K–O, middle trunk vertebra (holotype, IMEDEA 106587) from *Vipera latastei ebusitana*. P–T, caudal vertebra (IMEDEA 106848) attributed to cf. *Vipera*. U–Y, middle trunk vertebra (IMEDEA 106925) from mainland *Vipera latastei*. Anterior views (A, F, K, P, U), posterior views (B, G, L, Q, V), lateral views (C, H, M, R, W), dorsal views (D, I, N, S, X) and ventral views (E, J, O, T, Y). Scale bar: 3 mm.

similar to that of the *V. latastei*/*monticola* populations from the High Atlas, the cotyle and especially the condyle, of the trunk vertebrae are characteristically rounded; the diameter of the condyle is very similar to that of the neural canal and proportionally smaller than that of mainland populations of *V. latastei*. The diapophysis is prominent and subspherical. The subcentral ridge is poorly developed. In dorsal view, the trilobular zygosphene displays a central lobule with the same height (or slightly higher) than the lateral ones. The predominantly acute prezygapophyseal processes are short. The articular facets of the zygantrum are generally partially visible as two small tips in dorsal and ventral views. The pterygoid (essentially the anterior branch) is proportionally short and wide and possesses a compacted dentition. The compound bone has a vertical and rectilinear prearticular crest.

Measurements: See Tables 3 and 4.

Description of the type material

Vertebrae: Around 6000 trunk and cervical vertebrae have been recovered from different stratigraphic levels of Es Pouàs, but for the description up to 45 specimens, including 33 trunk vertebrae and 12 cervical vertebrae, have been selected on the basis of best-preservation conditions.

Cervical vertebrae: The cervical vertebrae display the following characteristics: the cotyle and the condyle are notably smaller than the neural canal (Fig. 4A, B), the neural spine is higher than long (Fig. 4C), the centrum length is shorter than that of the trunk vertebrae (Fig. 4C), the hypapophyses are straight, elongated and quite vertically oriented (Fig. 4C), and the prezygapophyseal processes are more reduced than those of the trunk vertebrae (Fig. 4D, E)

Trunk vertebrae: The trunk vertebrae analysed are characterized by their small size, with a centrum length 2.29–3.19 mm in adult specimens ($N = 33$; $CL_{mean} = 2.74$ mm). In anterior view (Fig. 4F, K), the zygophene presents a slight convex dorsal surface and is slightly wider than the cotyle. The prezygapophyseal facets are inclined upward. The cotyle is slightly wider than high and the diameter is similar to that of the neural canal. On each side of the cotyle there is a

Table 3. Measurements (in mm) and indices of the intermediate trunk vertebrae of *Vipera latastei ebusitana*

Trunk vertebrae	*N*	Min	Mean	Max	SD
Measurements					
CL	18	2.29	2.74	3.19	0.27
CTH	18	0.85	1.00	1.13	0.09
CTW	18	1.07	1.22	1.33	0.08
GH	15	3.58	4.15	5.50	0.57
LNS	7	1.61	1.92	2.27	0.23
MLV	18	2.85	3.34	3.95	0.37
MW	17	3.30	3.92	4.72	0.47
PO-PO	15	2.97	3.50	4.30	0.45
PR-PR	18	2.97	3.62	4.39	0.46
WIC	18	1.63	1.96	2.40	0.24
ZW	16	1.48	1.74	1.98	0.15
Indices					
CL/WIC	18	1.24	1.40	1.55	0.08
CL/ZW	16	1.44	1.56	1.69	0.08
CTW/CTH	18	1.14	1.23	1.35	0.06
CTW/WIC	18	0.54	0.63	0.73	0.05
PO-PO/WIC	15	1.65	1.80	1.90	0.07
PR-PR/MLV	18	1.02	1.08	1.14	0.03
PR-PR/WIC	18	1.67	1.84	1.94	0.06
ZW/WIC	16	0.80	0.90	0.98	0.05

Abbreviations: CL, centrum length. CTH, cotyle height. CTW, cotyle width. GH, greatest height of the vertebra. LNS, length of the neural spine. MLV, maximum length of the vertebra. MW, maximum width. PO-PO, width between the outer edges of postzygapophyseal articular surfaces. PR-PR, width between the outer edges of prezygapophyseal articular surfaces. WIC, width of the interzygapophyseal constriction. ZW, zygosphene width.

Table 4. Measurements (in mm) and indices of the cervical vertebrae of *Vipera latastei ebusitana*

Cervical vertebrae	*N*	Min	Mean	Max	SD
Measurements					
CL	11	2.10	2.45	3.03	0.25
CTH	11	0.77	0.92	1.03	0.08
CTW	11	0.95	1.08	1.29	0.11
GH	11	3.89	4.62	5.63	0.52
LNS	6	1.32	1.62	1.75	0.16
MLV	11	2.43	2.92	3.69	0.35
MW	11	2.62	3.47	4.41	0.46
PO-PO	9	2.67	3.23	4.12	0.47
PR-PR	11	2.60	3.26	4.19	0.44
WIC	10	1.48	1.77	2.23	0.22
ZW	11	1.40	1.61	1.98	0.17
Indices					
CL/WIC	10	1.30	1.39	1.44	0.04
CL/ZW	11	1.42	1.52	1.63	0.07
CTW/CTH	11	1.05	1.17	1.28	0.06
CTW/WIC	10	0.56	0.61	0.68	0.03
PO-PO/WIC	9	1.75	1.81	1.93	0.07
PR-PR/MLV	11	1.05	1.11	1.17	0.03
PR-PR/WIC	10	1.74	1.83	1.96	0.08
ZW/WIC	10	0.85	0.91	0.97	0.04

Abbreviations: CL, centrum length. CTH, cotyle height. CTW, cotyle width. GH, greatest height of the vertebra. LNS, length of the neural spine. MLV, maximum length of the vertebra. MW, maximum width. PO-PO, width between the outer edges of postzygapophyseal articular surfaces. PR-PR, width between the outer edges of prezygapophyseal articular surfaces. WIC, Width of the interzygapophyseal constriction. ZW, zygosphene width.

shallow paracotylar depression with a well-developed paracotylar foramen. The parapophyseal process is well developed, subtriangular and with a blunt apex.

In posterior view (Fig. 4G, L), the neural arch is dorsoventrally compressed. The zygantrum is deep and shows well-developed articular facets. The postzygapophysis is inclined upward. The condyle is subcircular and its diameter is slightly smaller than the diameter of the neural canal.

In lateral view (Fig. 4H, M), the neural spine is considerably longer than high. The anterior margin is vertical and higher than the posterior and the latter is inclined backward. Just below the interzygapophyseal constriction margin (= interzygapophyseal ridge or margo lateralis) there is a small lateral foramen on a flat surface lateroventrally inclined. The hypapophysis is posteroventrally directed, exceeding the posterior margin of the condyle. The anteroventral margin of the hypapophysis displays an open sigmoidal shape, while the posterodorsal is practically rectilinear, especially in the anterior trunk vertebrae. The prezygapophyseal processes have a circular section. Diapophyses and parapophyses of similar size; the diapophyses are subspherical and more prominent than the parapophyses. These are oval with a diffuse contour and are distally extended by a ridge on the lateral edge of the parapophyseal process. The parapophyseal processes are anteroventrally projected and anteroposteriorly flattened.

In dorsal view (Fig. 4I, N), these vertebrae have a weak interzygapophyseal constriction. The anterior margin of the zygosphene is trilobulate, the lateral lobes have a more acute profile and generally they display a similar degree of development (or slightly less developed) than the central one. The articular surfaces of the prezygapophysis have a subrhomboidal shape. The prezygapophyseal processes, which are short (around one-sixth of the total length of the prezygapophyseal surfaces) and with a blunt or slightly sharp apex, are anterolaterally oriented. The neural spine is thin and it anteriorly reaches about half of the total length of the zygosphene and posteriorly exceeds the neural arch. The back end of the articular facets of the zygantrum are sometimes visible and displayed as two small tips. The posterior neural wings lack the epizygapophyseal spines. The posterior notch is shallow with a posterior angle between 90° (anterior trunk vertebra) and 120° (posterior trunk vertebra).

In ventral view (Fig. 4J, O), the centrum is longer than wide (centrum length/centrum width 1.3–1.5) and displays a subtriangular shape with a convex ventral surface and a diffuse subcentral ridge, especially in the posterior half of the vertebrae. The basis of the hypapophysis extends anteriorly as a haemal keel that becomes wider until it reaches the basis of the cotyle. On each side of the haemal keel there is a small subcentral foramen. The parapophyseal processes are well developed, subrectangular with a round anterior limit. A narrow and well-marked groove separates them from the cotyle. The diapophysis presents a globular shape and the parapophysis is reduced and it is closely placed to the lateroventral margin of the parapophyseal process. The postzygapophyseal facets display an ovoid to subrectangular shape and are well developed. The condyle presents a well-defined precondylar constriction.

Pterygoid: IMEDEA 106589 is an anterior fragment of a right pterygoid that measures 3.52 mm from the anterior branch (or palatal process) to the anterior limit of the ectopterygoid process and 0.44 mm width in the middle point (Fig. 5). The anterior end (= insertion area with the palatine) is bilobed with anterolateral and anteromedial processes, the first slightly more developed. Its anterior region is compressed lateromedially, then it is flattened in lateral view from the ectopterygoid process to the posterior region. Posteriorly, and in dorsal view, the impression of the posterior branch of the ectopterygoid is visible on the ectopterygoid process. The ectopterygoid process is well developed, starting at the pterygoid flange and becoming wider backwards. In ventral view, the ectopterygoid process is placed between the position of the seventh and the eighth teeth, displaying a set of teeth close to each other with a ratio number of teeth/length from the anterior tip to the ectopterygoid process (7/3.52) = 1.99.

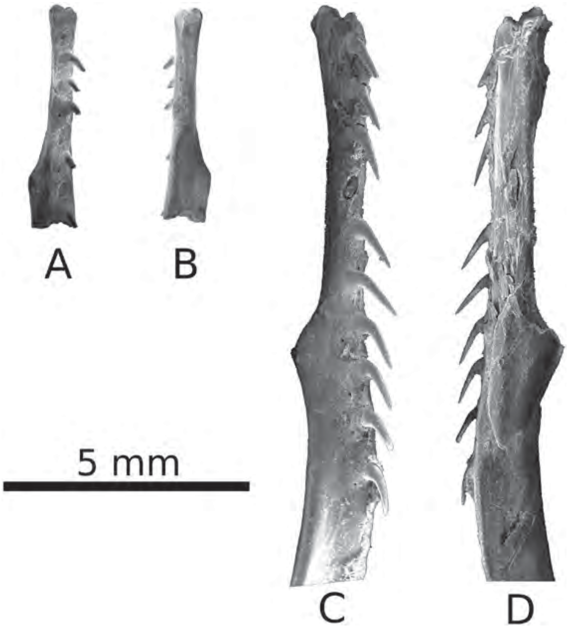

Figure 5. *Vipera latastei* pterygoids. A–B, *Vipera latastei ebusitana* (IMEDEA 106589) from Es Pouàs. C–D, mainland *Vipera latastei* (MNHN-ZA-AC 2020–1). Ventral views (A, C) and dorsal views (B, D). Scale bar: 5 mm.

Compound bones: Ten fragmented compound bones have been recovered from Es Pouàs, and only IMEDEA 106831 is a near-complete specimen (Fig. 6). All of them display the typical viperid pattern, i.e. mandibles characterized by long compound bones strongly curved with well-prominent prearticular crests and low surangular crest (ratio between maximum height of the prearticular crest and surangular crest between 3 and 4). The near-complete specimen IMEDEA 106831 has a maximum length of 9.80 mm (estimated total mandibular – i.e. compound bone + dentary – ~ 13.4 mm), and its prearticular crest has a maximum height of 1.80 mm, whereas this measure is 1.86 mm in IMEDEA 106721. The prearticular crest is vertical and, in dorsal view, rectilinear; the mandibular fossa is narrow and deep. The retroarticular process is well developed, slightly longer than the glenoid fossa, it is medially curved and with a blunt end. In lateral view, the mental foramen has an elliptical shape and it is open frontwards. In medial view, the infraglenoidal groove is well developed.

BODY-SIZE ESTIMATION

Our estimation of the body size of the Eivissan viper using the most complete vertebrae – including the largest available vertebrae – indicates an adult average total length of 36 cm (29–44 cm, $N = 18$). Following Boback (2003), we used the comparison between the maximum total lengths to establish unequivocally the condition of dwarfism of the Eivissan viper in comparison to the Iberian populations from which it derives. We compared these measurements with the data for *Vipera latastei* European populations obtained in the literature (maximum total length above 70 cm; Brito *et al.*, 2006, Martínez-Freiría *et al.*, 2014), especially in the Iberian origin populations of *V. l. ebusitana* (maximum total length 71.9 cm; Brito *et al.*, 2006).

DIFFERENCES BETWEEN *VIPERA LATASTEI LATASTEI* AND *VIPERA LATASTEI EBUSITANA*

Eivissan *Vipera latastei ebusitana* differs morphologically from the Iberian *V. latastei latastei*

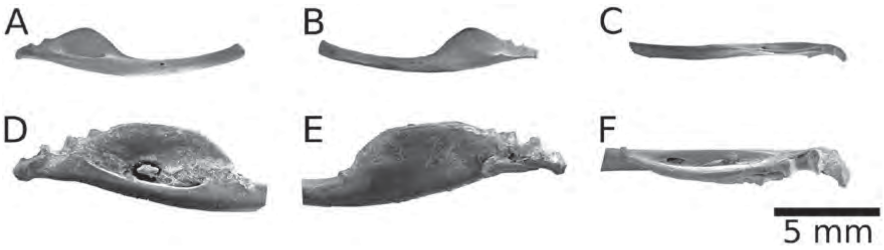

Figure 6. *Vipera latastei* compound bones. A–C, *Vipera latastei ebusitana* (IMEDEA 106831) from Es Pouàs. D–F, mainland *Vipera latastei* (MNHN-ZA-AC 2020–1). Lateral views (A, D), medial views (B, E) and dorsal views (C, F). Scale bar: 5 mm.

in the following traits: the trunk vertebrae of the fossil present a smaller and more rounded cotyle and condyle (Fig. 4F, G, K, L). The latter has a diameter similar or slightly smaller than the neural canal (Fig. 4G, L). In *V. l. latastei* the cotyle and the condyle are subelliptical and the condyle has a larger diameter than that of the neural canal (Fig. 4U, V). Anterior and posterior parts of the neural arch have a similar height in *V. l. ebusitana* (Fig. 4H), whereas in *V. l. latastei* it is higher posteriorly (Fig. 4W). The diapophyses of *V. l. ebusitana* are well developed and present a subspherical shape, whereas the parapophyses are indistinct from the parapophyseal process (Fig. 4H, M). In *V. l. latastei* the diapophyses are elongated dorsoventrally and the parapophyses have a diffuse outline but are well defined (Fig. 4W). The subcentral ridge is poorly developed in *V. l. ebusitana* (Fig. 4H, M), whereas in *V. l. latastei* it is well marked (Fig. 4W). The zygosphene is trilobulate in both taxa, but in *V. l. ebusitana*, the central lobule is similar or slightly longer than the lateral ones (Fig. 4D, I), whereas in *V. l. latastei* the lateral lobules are more developed than the central one (Fig. 4X). Similarly, *V. l. ebusitana* and *V. l. latastei* have short prezygapophyseal processes, but in the first these processes are generally more acute than in the second (Fig. 4I, N, X). In *V. l. ebusitana* the articular facets of the zygantrum are extended posteriorly forming two small spines visible in the dorsal/ventral view of the vertebra (Fig. 4N), whereas in *V. l. latastei* the zygantrum remains completely covered (hidden) by the neural arch (Fig. 4X). The anterior branch of the pterygoid of *V. l. ebusitana* is proportionally shorter and wider than in *V. l. latastei* (length/width = 7.1 mm/0.81 mm). Moreover, *V. l. ebusitana* presents a ratio teeth number/length (7/3.52 = 1.99) higher than in *V. l. latastei* (ectopterygoid process located between the eighth and ninth teeth; 8/7.10 = 1.13). The compound bone displays a vertical and, in dorsal view, a rectilinear prearticular crest in *V. l. ebusitana* (Fig. 6C), whereas in *V. l. latastei* this pre-articular crest is slightly medially inclined and curved medially in dorsal view (Fig. 6F).

The caudal vertebra from Cova de ca na Reia

The posterior caudal vertebra IMEDEA 106848 from Cova de ca na Reia is in a poorly preserved condition. Just a good portion of the neural crest, a part of the left prezygapophysis, a small portion of the postzygapophyses and the base of the neural spine is preserved, while the anterior margin of the zygosphene is eroded. The cotyle, the condyle and the pleurapophyses also are totally eroded.

The total ventral length of this fragmented vertebra is 1.92 mm. In anterior view, the dorsal surface of the zygosphene is convex (Fig. 4P). The neural arch is moderately flattened in posterior view (Fig. 4P, Q). The neural spine is considerably thick (Fig. 4P, Q, S) and longer than high (Fig. 4R). The hemapophyses are clearly individualized in the posterior half of the centrum and converging anteriorly (Fig. 4T). Despite the hemapophyses are incomplete the left one is clearly incurved, i.e. the concavity is on the inner side.

DISCUSSION

Colonization of Eivissa

The chronological and stratigraphical data from Es Pouàs confirm the presence of the Eivissan dwarf viper (*Vipera latastei ebusitana*) over at least *c.* 30 000 years, which, combined with its distinctive morphological and genetic characteristics, suggest that it should be considered a new taxon resulting from rapid evolutionary process under insular conditions. The genetic approach presented here suggests that the Eivissan dwarf viper diverged from the east CNS mainland *V. latastei* about 1 Mya (east CNS crown age: mean = 0.97 Mya; 95% HPD = 0.67–1.31 Mya), consistent with the east CNS clade node ages estimated by other authors (i.e. < 1.5 Mya; Velo-Antón *et al.*, 2012; Martínez-Freiría *et al.*, 2020). Thus, our data allow us to conclude that the ancestors of the Eivissan dwarf viper arrived in Eivissa between 1.31 Mya (upper bound of the East CNS crown age 95% HPD) and *c.* 30 000 (first appearance of this taxon in the fossil record). This conservative date range suggests colonization of the island was via an overseas dispersal event, because the last land connection between Iberia and the Balearic Islands occurred 5.6–5.33 Mya (e.g. Mas *et al.*, 2018). Such overseas colonization is widely reported for reptiles arriving on islands, such as the Canary Islands (e.g. *Gallotia* Boulenger, 1916, Cox *et al.*, 2010; or a boid snake on Lanzarote, Barahona *et al.*, 1998) and the Galápagos Islands [e.g. *Pseudalsophis*, Zaher *et al.*, 2009 (Zaher *et al.*, 2018)]. The current distance between Eivissa and Iberia is only about 90 km, which reduced to *c.* 70 km during Pleistocene glacial periods, and so could plausibly have been overcome by rafting on flotsam (as demonstrated by the dispersal of snakes to isolated islands like Galápagos, and other oceanic islands).

The poor preservation condition of the caudal vertebra from the deposit Cova de ca na Reia precludes its accurate taxonomic identification. Consequently, its attribution to *Vipera* is only tentative and we designate it as cf. *Vipera* on the basis of the curvature of the hemapophyses. Direct comparison between available caudal vertebrae of different Colubridae [*Hemorrhois hippocrepis* (Linnaeus, 1758), *Macroprotodon mauritanicus* Guichenot, 1850 and *Zamenis scalaris* (Schinz, 1822)] and of different species of *Vipera* has allowed us to verify that the hemapophyses in *Vipera* are medially arched, as observed in the Cova de ca na Reia specimen, whereas in the different species of Colubridae *s.l.* the hemapophyses are vertically oriented. All points indicate that it represents the ancestor of the Es Pouàs viper, although this needs further confirmation. If the vertebra from the Cova de ca na Reia site actually belongs to the ancestor of the new subspecies described here (*Vipera latastei ebusitana*), its presence in this site (in combination with our molecular dating results) would restrict the age of this deposit to the Calabrian, whereas it was previously tentatively attributed to the Gelasian/Calabrian on the base of its associated malacological fauna.

Extinction chronology and causes

Fossils of *V. l. ebusitana* have been retrieved over a wide range of pre-human levels in the Es Pouàs deposit (at least between 5295 and 32 523 BC), while it is apparently absent at levels postdating the first evidence of human presence (i.e. postdating 2139 BC; Alcover, 2008). The extinction of the species presumably occurred between 2139 and 5295 BC. The sole notable event occurring on Eivissa during this time period was the arrival of humans. Climate-related causes of the extinction of the Eivissan dwarf viper can be excluded because no remarkable climatic changes occurred during this interval, leaving therefore only human-driven impacts as potential causes of its disappearance.

The impact of first human settlers on the Eivissan ecosystems could derive from three main causes (or their combined effect), which are known to affect populations of snakes everywhere: (1) transformation/depauperation of ecosystems (e.g. Henderson & Powell, 1996; Bailon *et al.*, 2015; Bochaton *et al.*, 2015, 2019), (2) direct hunting of the species (e.g. Tóth *et al.*, 2010) and (3) introduction of alien species (e.g. Steadman, 1986; Henderson, 1992; Powell, 1999, 2002).

Although all these human activities could have potentially contributed to the extinction process, the first two impacts should have only had a limited effect on the extinction of the vipers due to the size and rocky landscape of the island. Thus, excluding these potential causes for extinction, the introduction by humans of alien species emerges as the most plausible cause for Eivissan viper extinction.

First human settlers introduced several mammals, but there is no record of introduction of reptiles during all the Eivissan prehistory, which precludes the introduction of specific reptile diseases as a possible cause for the Eivissan dwarf viper extinction. The first introduced mammals exclusively consist of five domesticated taxa (cow, sheep, goat, pig and dog) and two wild rodents (wood mouse and garden dormouse) (Alcover, 2008). Among these introduced mammals, just dogs, pigs and rodents should be considered as potential snake predators. Dogs presumably arrived with the first settlers to Eivissa, but there is no evidence that they ever became feral. Although dogs can potentially kill snakes, the dog population density should have been high enough to have a noticeable effect on the viper population, but there is no record of it (Valenzuela, 2015). The same applies to *Sus scrofa* Linnaeus, 1758: although they are potential consumers of vipers (e.g. Maritz *et al.*, 2016), the density of feral pigs required to produce the extinction of vipers should have been high, which is not supported by the archaeological record.

Thus, only the two rodents could be considered as potential causes of the extinction of the Eivissan dwarf viper. Without mammal predators, the increase of populations of both rodents should have been explosive after their arrival, as occurs invariably with invasive rodents on territories without mammals (e.g. Hardouin *et al.*, 2010; Nathan *et al.*, 2015). Both species include animal items in their diet. However, the wood mouse can be reasonably excluded as a potential predator of the Eivissan dwarf viper, because it only occasionally predates on small invertebrates, while no records of predation on small vertebrates exist (e.g. Hansson, 1985).

Eliomys quercinus (Linnaeus, 1758) emerges as the potential agent causing the extinction of the Eivissan dwarf viper. In contrast to the wood mouse, it is well documented that the garden dormouse predates on small vertebrates, including lizards and small mammals (e.g. Kahmann & Lau, 1972). It also has a high resistance to viper venom (Phisalix, 1930, 1931; Storch, 1978). Rodents are considered prolific invasive species (e.g. Atkinson, 1985; Drake & Hunt, 2009), especially in the absence of predatory mammals, and founder populations on an island would have quickly increased (e.g. Hardouin *et al.*, 2010; Nathan *et al.*, 2015). The high adaptability of *E. quercinus* to the range of habitats of Eivissa could have also contributed to the rapid increase of its populations. In addition, vipers are viviparous and produce a reduced number of small-sized young, which should have been an easily available resource for the garden dormouse.

Alien rodents introduced into the Balearics by humans have been considered as key elements in the transformation of pristine ecosystems (Traveset *et al.*, 2009). Here we propose that the introduction of the garden dormouse likely played a pivotal role in the extinction of the Eivissan dwarf viper, although the effect of other human-caused environmental alterations will have played an additional role in the decline of this species.

Body-size evolution

The dwarfism of the Eivissan viper [with an adult total length estimated at 36 cm (29–44 cm, $N = 18$)] is most probably related to the influence of island selective forces, such as the size of available prey. The diet of adult specimens of *V. latastei* in the Iberian Peninsula is based mainly on small mammals, and on lizards for juvenile vipers (Martínez-Freiría *et al.*, 2014). In a similar way to dwarf *Vipera latastei monticola* from the High Atlas (see: Saint-Girons, 1980; Freitas *et al.*, 2018) and *Vipera aspis* from Montecristo Island (Luiselli *et al.*, 2015), geographic isolation and a diet of adults likely restricted to lizards could have led to dwarfism in the Eivissan viper. For comparison, total size estimates using 31 adults of *V. latastei-monticola* from the west and central regions of High Atlas yielded ranges between 33.5 cm (standard deviation 5.13) for male individuals and 32.1 cm (standard deviation 2.09) for female individuals (F. Martínez-Freiría, unpublished data).

The evolution of body size in insular snakes has been analysed by many different authors. Case (1978) found a general trend – with a few exceptions – towards dwarfism of snakes on islands, whereas Boback (2003) and Boback & Guyer (2003) described an evolutionary trend towards gigantism in colubrids and towards dwarfism in viperids, the latter recorded in extant individuals of nine species of *Crotalus* Linnaeus, 1758, one species of *Bothrops* Wagler, 1824 and two species of *Vipera*. No examples of evolution towards dwarfism had been recorded among fossil viper species so far, and thus the case presented here is the first palaeontological evidence supporting the evolutionary trend towards dwarfism in island viperids postulated by Boback (2003) and Boback & Guyer (2003).

CONCLUSION

Traditionally, three morphological complexes are identified within the species formerly included in the genus *Vipera* (Szyndlar, 1991): the 'Oriental vipers complex' (OVC), including the largest species currently in genera *Macrovipera*, *Montivipera* and *Daboia*; the '*aspis* complex', including *V. ammodytes*, *V. latastei*, *V. aspis* and others; and the '*berus* complex', including smaller members of the genus such as *V. berus*, *V. ursinii* and others. Typically, vertebrae of the '*berus* complex' can be defined as small, elongate and characterized by low neural spines and hypapophyses, whereas those of the 'OVC' are large, relatively short and have high spines and hypapophyses. Vertebrae of the '*aspis* complex' (in which *V. latastei* is included) display intermediate conditions between the '*berus* complex' and the 'OVC'. Although morphological differences in skeletal remains among these complexes should be clear, the morphology within each complex is highly homogeneous. In addition, differences in the vertebral morphology between the extant species of the '*berus*' and '*aspis*' complexes could be related to body size. Thus, the proper identification of isolated vertebrae, and the resolution of phylogenetic relationships from a morphological approach is usually difficult. The distinctive morphology and size of the fossil viper remains from Eivissa described in this paper could have been potentially enough to describe a new species belonging to *Vipera* within the '*aspis* complex'. However, DNA sequences have instead allowed its attribution to a new subspecies of *V. latastei*, the identification of the mainland origin population and thus the establishment of an insular evolutionary scenario for the phenotypic differences observed in the vertebrae recovered from the deposit of Es Pouàs.

For these reasons, whenever possible, the combination of morphological and ancient DNA approaches proposed here is important for properly establishing the appropriate taxonomic and phylogenetic attribution of fossil viper vertebrae.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. Graphic illustrating the different steps in the multi-reference iterative mapping approach (MIMA) for the obtaining of the partial mitochondrial genome sequence for *Vipera latastei ebusitana*.
Figure S2. Results of mapDamage analyses of unique reads from *Vipera latastei ebusitana* in the multi-reference iterative mapping approach (MIMA). Substitution (four top panels) and misincorporation (two bottom panels) panels display the pattern typically observed in ancient samples.
Figure S3. A (left), maximum likelihood and B (right), Bayesian phylogenetic relationships of Viperinae genera *Vipera*, *Montivipera*, *Macrovipera* and *Daboia* available in GenBank using Dataset 1, including *Vipera latastei ebusitana* (sample 19591). The analysis was performed in RAxML and MrBayes using 4164 bp of several mitochondrial genes (see Supporting Information, Table S2 for accession number details and Table S3 for partitioning scheme). Bootstrap values for ML (MLB) and Bayesian posterior probabilities (PP) are given in each node. Nodes with circles indicate MLB = 100 and PP = 1 and nodes without value indicate MLB < 75 and PP < 0.95.
Figure S4. Maximum likelihood (ML) tree of 76 *Vipera latastei/monticola* individuals and the *V. latastei ebusitana* (15951, in black) sequences (270 bp *Cytb* + 602 bp *ND4*) used to build haplogroup network of Figure 2. Circles in nodes of ML tree indicate Bootstrap values (MLB) = 100, whereas nodes without values MLB < 75. See Supporting Information, Table S4 for details about geographical origin of samples and accession numbers. Haplogroup names following Freitas *et al.* (2018) for African populations and Martínez-Freiría *et al.* (2020) for Iberian populations (CNW-SW and CW-S sub-groups within West populations following Velo-Antón *et al.*, 2012).
Figure S5. A (left), maximum likelihood and B (right), Bayesian phylogenetic relationships of Viperinae genera *Vipera*, *Montivipera*, *Macrovipera* and *Daboia* available in GenBank using Dataset 2, including *Vipera latastei ebusitana* (sample 19591) and individuals of *V. latastei* from different populations. The analysis was performed in RAxML and MrBayes using the same gene sequences as Dataset 1 genes (see Supporting Information, Table S2 for accession number details and Table S3 for partitioning scheme). Bootstrap values for ML (MLB) and Bayesian posterior probabilities (PP) are given in each node. Nodes with circles indicate MLB = 100 and PP = 1, whereas nodes with no data indicate MLB < 75 and PP < 0.95. *V. latastei* individuals from west (W), south (STH), east-south (SOU) and east CNS (SE, CN, NE) populations.
Figure S6. Phylogenetic position of *Vipera latastei ebusitana* (sample 19591) within Viperinae based on mitochondrial sequences (4164 bp) and using BEAST and Dataset 1. Nodes are labelled with Bayesian posterior probabilities (PP) and circles in nodes indicate PP = 1. Green bars represent 95% highest posterior density (HPD) intervals. Messinian Salinity Crisis (MSC) is indicated by blue shading. See Supporting Information, Table S2 for information about individual samples and accession numbers. Time in million years before present (BP).
Figure S7. Comparison of split-ages for the different nodes in trees estimated in this paper and previous analyses published elsewhere (see references in the figure).
Figure S8. Heatmap of pairwise similarity between the *Vipera latastei ebusitana* and *V. latastei/monticola Cytb* (270 bp) and *ND4* (602 bp) sequences from Velo-Antón *et al.* (2012), Martínez-Freiría *et al.* (2015, 2020) and Freitas

et al. (2018). See Supporting Information, Table S4 for accession numbers of the sequences used. Sequences for the extinct taxon are more similar (> 98% similarity) to the *V. latastei* ones from north-east Iberian east-CNS populations (*sensu* Martínez-Freiría *et al.*, 2020; or NE populations of NE-SE-CN clade *sensu* Velo-Antón *et al.*, 2012). Haplogroup names following Freitas *et al.* (2018) for African populations and Martínez-Freiría *et al.* (2020) for Iberian populations (CNW-SW and CW-S subgroups within west populations following Velo-Antón *et al.*, 2012).

Table S1. Measurements (in mm) of trunk vertebrae and indices of selected *Vipera* species and lineal regression used to estimate total body length (TBL) of *Vipera latastei ebusitana* (see Supporting Information, Table 3 for same measurements in *V. l. ebusitana*). Abbreviations: CL, centrum length. CTH, cotyle height. CTW, cotyle width. GH, greatest height of the vertebra. LNS, length of the neural spine. MLV, maximum length of the vertebra. MW, maximum width. PO-PO, width between the outer edges of postzygapophyseal articular surfaces. PR-PR, width between the outer edges of prezygapophyseal articular surfaces. TBL, total body length. WIC, width of the interzygapophyseal constriction. ZW, zygosphene width.

Table S2. GenBank accession numbers of the different Viperinae sequences used for phylogenetic inference in Datasets 1 and 2.

Table S3. Optimal partitioning scheme inferred with PartitionFinder for a total alignment of 4164 bp (213 bp for *12S_rRNA*, 327 bp for *16S_rRNA*, 840 bp for *COI*, 1104 bp for *Cytb*, 1002 bp for *ND2* and 678 bp for *ND4*) of 34 Viperinae species for Datasets 1 and 2. See Supporting Information, Table S2 for accession number details. Partitioning scheme inferred selecting models implemented in each software (RAxML, MrBayes and BEAST).

Table S4. GenBank accession numbers and details of the different *Vipera latastei/monticola Cytb* (270 bp) and *ND4* (602 bp) sequences used for the haplotype network analysis. Clade names following (1) Velo-Antón *et al.* (2012), (2) Martínez-Freiría *et al.* (2020) and (3) Freitas *et al.* (2018).

Appendix S1. Dataset 1 alignment in PHYLIP format.

Appendix S2. Dataset 2 alignment in PHYLIP format.

Appendix S3. Alignment of *Vipera latastei/monticola* for haplogroup network analysis in PHYLIP format.

4. Bover P., Mitchell K.J., Torres-Roig, E., Llamas B., Thomson V.A., Alcover J.A., Agustí J., Cooper A. i Pons J. 2020. Ancient DNA from an extinct Mediterranean micromammal — *Hypnomys morpheus* (Rodentia: Gliridae)— provides insight into the biogeographic history of insular dormice. *Journal of Zoological Systematics and Evolutionary Research*, 58: 427-438.

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Ancient DNA from an extinct Mediterranean micromammal—*Hypnomys morpheus* (Rodentia: Gliridae)—Provides insight into the biogeographic history of insular dormice

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Abstract

The dormice (Gliridae) are a family of rodents represented by relatively few extant species, though the family was much more species-rich during the Early Miocene. Intergeneric phylogenetic relationships among glirids in some cases remain unresolved, despite extensive molecular and morphological analyses. Uncertainty is greatest with respect to the relationships among fossil taxa and how extinct lineages are related to modern species. The fossil genus *Hypnomys* from the Balearic Islands (western Mediterranean Sea) includes the Late Pleistocene–Holocene species *Hypnomys morpheus*, which has variously been considered a close relative or subgenus of the extant *Eliomys*. In the present study, we sequenced ancient mitochondrial DNA from *H. morpheus*, which suggests a sister relationship with the extant members of *Eliomys*. In addition, the pairwise sequence variation between *Hypnomys* and *Eliomys* is higher than that observed between congeneric glirid species (e.g., many *Graphiurus* spp.), which allows us to reject the hypothesis that *Hypnomys* is a subgenus of *Eliomys*. Our molecular dating analyses suggest that *Hypnomys* and *Eliomys* diverged 13.67 million years ago (95% highest posterior density [HPD] = 7.39–20.07). The relatively early split between these genera together with the molar morphology of early representatives of *Hypnomys* points to a Middle-Late Miocene origin from a continental glirid with a complex molar pattern, such as *Vasseuromys* or a closely related genus.

KEYWORDS
endemic, fossil, Island fauna, mitochondrial DNA, phylogeny

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1 | INTRODUCTION

The dormice (Gliridae) are a family of rodents whose interspecific phylogenetic relationships have been widely discussed. In some cases, these remain unresolved despite analyses using extensive molecular datasets (e.g., Bentz & Montgelard, 1999; Montgelard, Matthee, & Robinson, 2003; Nunome, Yasuda, Sato, Vogel, & Suzuki, 2007) or morphological characters (e.g., Freudenthal & Martín-Suárez, 2013; Storch, 1995; Wahlert, Sawitzke, & Holden, 1993). Within extant Gliridae, Holden (2005) recognizes three subfamilies: Graphiurinae (single genus *Graphiurus* Smuts, 1832, including three subgenera and 15 species), Glirinae (monotypic genera *Glis* Brisson, 1762 and *Glirulus* Thomas, 1906), and Leithiinae (including *Chaetocauda* Wang, 1985, *Dryomys* Thomas, 1906, *Eliomys* Wagner, 1840, *Muscardinus* Kaup, 1829, *Myomimus* Ognev, 1924, and *Selevinia* Belosludov and Bashanov, 1939, with a total of 12 species). A number of glirids have been recorded in the Pliocene–Holocene fossil record of the Mediterranean Islands (van der Geer, Lyras, de Vos, & Dermitzakis, 2010) several of which have been assigned to the subfamily Leithiinae based on morphological characters, including the genus *Hypnomys* Bate, 1918 from the Balearic Islands. However, the phylogenetic relationships of these extinct dormice have not been tested using molecular data, which may provide new evidence to clarify uncertainties about their taxonomy and biogeographical origin.

The extinct genus *Hypnomys* (Rodentia: Gliridae) was originally erected by Bate (1918) to accommodate two species of Pleistocene dormouse discovered in the Balearic Islands: *H. mahonensis* Bate, 1918 and *H. morpheus* Bate, 1918. de Bruijn (1966) initially described an additional species—*H. gollcheri*—from the Pleistocene of Malta, though *H. gollcheri* was ultimately transferred to the newly erected genus *Maltamys* Zammit-Maempel & de Bruijn, 1982 (see Zammit-Maempel & de Bruijn, 1982). Similarly, while Esu and Kotsakis (1980) recorded putative *Hypnomys* remains in the Early Pleistocene deposit of Nuraghe Su Casteddu (Sardinia), this material was later included in *Tyrrhenoglis* Engesser, 1976, an endemic genus from Sardinia (Zammit-Maempel & de Bruijn, 1982). Alcover and Agustí (1985) mentioned remains of a species of Gliridae from Cova de ca na Reia on Eivissa (Pityusic Islands, western Group of the Balearic Islands; presumably from the Lower Pleistocene/Upper Pliocene) that has often been considered to belong to *Hypnomys*, but this material has never been properly studied.

According to Wahlert et al. (1993), members of the subfamily Leithiinae share four morphological characters: posterior emargination or a foramen in the posterior part of the squamosal bone, fenestra in the angle of the mandible, low inclination of the coronoid process relative to the occlusal surface, and one complete transverse valley in the second lower molar. *Hypnomys* possess all of these diagnostic morphological characters (Figure S1), though the fenestra in the angle of mandible is not strictly present in all *Hypnomys*—or other Leithiinae such as *Eliomys*—but in most of them (see Yuste & Calzada, 2009, and pers. obs.). More specifically, a close relationship with *Eliomys* was suggested in the original description of *Hypnomys* (Bate, 1918), on the basis of the general plan of the skull, mandible, and limb bones, and a fenestra in the angle of the mandible. Subsequent studies also suggested that the closest relative of *Hypnomys* was *Eliomys* (Petronio, 1970), *Leithia* Lydekker, 1895 (Mills, 1976), or *Tyrrhenoglis* (Chaline & Mein, 1979). Several authors have since suggested that the Western Mediterranean insular fossil glirids—*Hypnomys*, *Leithia*, *Tyrrhenoglis*, *Maltamys*, and *Eivissia* Alcover & Agustí, 1985—all descended from *Eliomys* (Alcover & Agustí, 1985; Alcover, Moyà-Solà, & Pons-Moyà, 1981; Daams & de Bruijn, 1995; Zammit-Maempel & de Bruijn, 1982). Indeed, Agustí (1980) suggested that *Eliomys* should be considered the most likely ancestor of *Hypnomys*, and Zammit-Maempel and de Bruijn (1982) considered *Hypnomys* (and other insular genera as *Tyrrhenoglis* and *Maltamys*) as a subgenus of *Eliomys*, which is a view that has been widely adopted in the literature (e.g., Alcover & Agustí, 1985; Reumer, 1982, 1994). However, no consensus exists regarding the taxonomy of these fossil glirid taxa.

Though it has never been directly tested, it is generally assumed that the ancestor of *Hypnomys* likely dispersed to the Balearic Islands while they were connected by land to the European mainland during the Late Miocene Messinian Salinity Crisis (MSC) (e.g., Agustí, 1980, 1986; Alcover et al., 1981; Bover et al., 2014; Mas et al., 2018; Moyà-Solà & Pons-Moyà, 1980). The fossil record in Mallorca is consistent with this biogeographical hypothesis, with extensive evidence that a radiation of this endemic clade had occurred by the Pliocene: *Hypnomys/Eliomys* sp. [Early Pliocene (Bover et al., 2014)], *Hypnomys* sp. [Zanclean (Bover et al., 2014)], *H. waldreni* [Piazencian (Reumer, 1979)], *H. onicensis* [formerly *H. intermedius*, Early Pleistocene (Reumer, 1981, 1994)], and *H. morpheus* [Middle Pleistocene-Holocene Bate, 1918)]. Establishing the age of the divergence between this Mallorcan dormouse lineage and its nearest living continental relatives may help in narrowing down its phylogenetic origins by constraining the range of fossil taxa from which it could possibly have descended.

Ancient DNA sequences have been successfully used for phylogenetic analyses of small extinct species (see review in Woods, Marr, Brace, & Barnes, 2017) and can provide information about phylogenetic relationships in situations that are challenging for morphological analyses (e.g., fossil insular species where taxonomic position is frequently obscured by autapomorphies acquired during isolation). Although a close relationship between *Hypnomys* and *Eliomys* based on morphology has been widely accepted, major discrepancies in the attribution of several genera to different Gliridae subfamilies using morphological (e.g., Daams & de Bruijn, 1995; Freudenthal & Martín-Suárez, 2013; Storch, 1995; Wahlert et al., 1993) or molecular characters (e.g., Bentz & Montgelard, 1999; Fabre, Hautier, Dimitrov, & Douzery, 2012; Montgelard et al., 2003; Nunome et al., 2007) suggest that the taxonomic position of *Hypnomys* requires confirmation using genetic data. In this paper, we generate the first DNA sequences for *Hypnomys* and use these to infer its phylogenetic relationship to extant glirids. We also conduct molecular dating analysis to test hypotheses about the biogeographic history of *Hypnomys*—specifically that the temporal origin of the *Hypnomys*

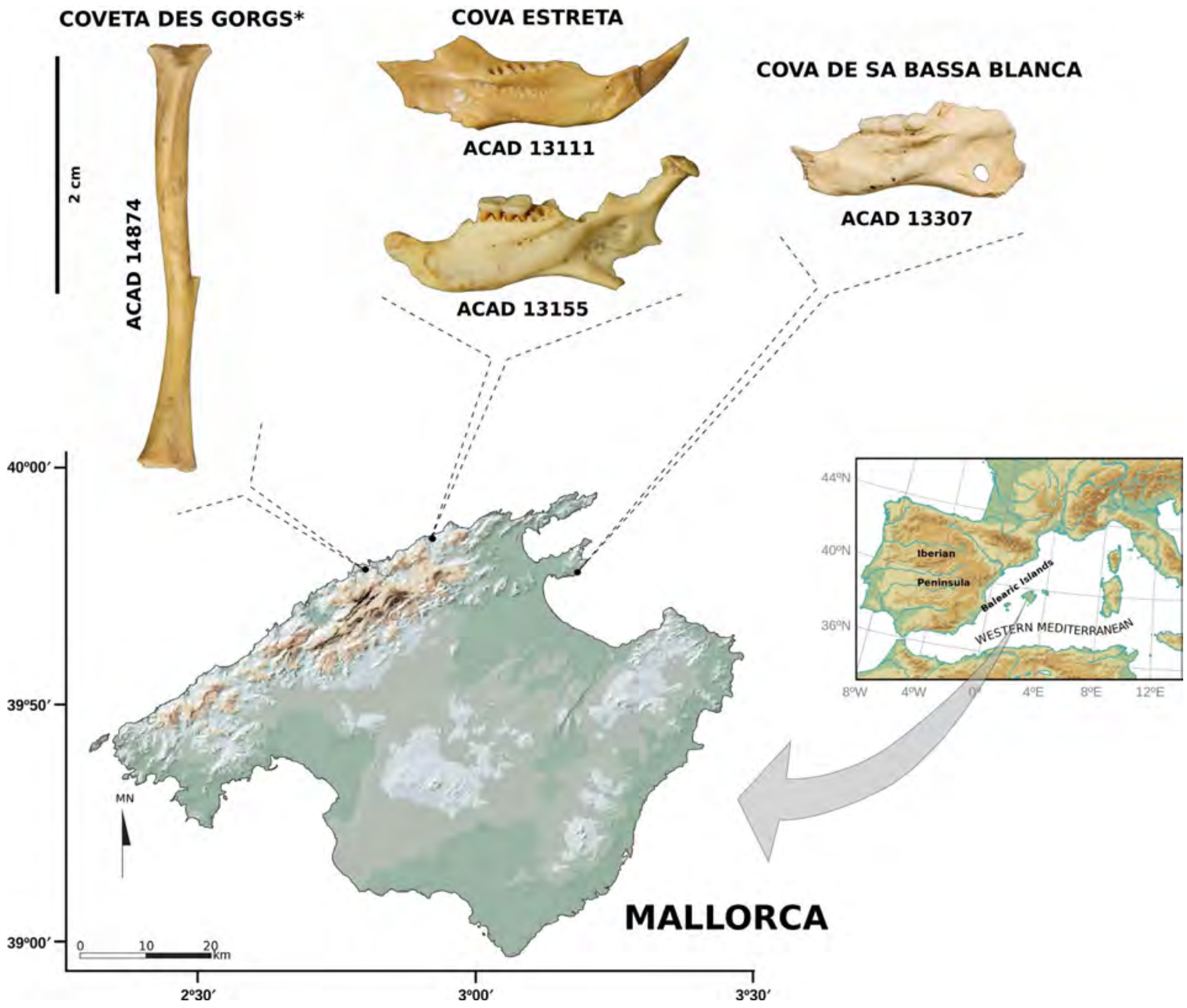

FIGURE 1 Map showing the location of Mallorcan deposits with respective *Hypnomys morpheus* bones used for ancient DNA analysis. ACAD 13111, left mandible. ACAD 13155, right mandible. ACAD 13307, right mandible. ACAD 14874, left tibia. Mandibles ACAD 13111 and 13155 were pooled for DNA extraction. The asterisk indicates the sample that yielded endogenous DNA

lineage coincides with the Messinian Salinity Crisis—and to identify potential ancestral taxa in the fossil record.

2 | MATERIALS AND METHODS

2.1 | Samples

In this study, we attempted to extract DNA from four *Hypnomys morpheus* samples curated at the vertebrate public collection of the Mediterranean Institute for Advanced Studies (IMEDEA, Balearic Islands, Spain) and from three different caves (Figure 1): a pool of two bones [left (ACAD 13111) and right (ACAD 13155) mandibles from Cova Estreta (Pollença) (Encinas & Alcover, 1997)], a right mandible (ACAD 13307) from Cova de sa Bassa Blanca (Alcúdia) (Ginés & Ginés, 1974), and a left tibia (ACAD 14874) from Coveta des Gorgs (Escorca). The exact chronology of these samples could not be established as the specimens were entirely consumed during DNA extraction and could not be radiocarbon dated. Nevertheless, up to three radiocarbon dates have been obtained from remains obtained in the same stratigraphic level of Cova Estreta: *H. morpheus* bone [UtC-5175, 6,357 ± 44 BP, 5,469–5,288 (86.3%) 5,272–5,227 (9.1%) calBC] (Encinas & Alcover, 1997), and a bone [UtC-5171, 5,720 ± 60 BP, 4,716–4,449 calBC] (Encinas & Alcover, 1997) and coprolite [Wk-33010, 4,950 ± 38 BP, 3,798–3,650 calBC] (Rivera et al., 2014) of the extinct bovid *Myotragus balearicus* Bate, 1909. Radiocarbon dates of several bones of *M. balearicus* from the same level (surface) of the Coveta des Gorgs indicate a chronology range from 4,456 ± 33 BP [RICH-21771, 3339–3205 (45.2%) 3,197–3,014 (50.2%) calBC] to 9,164 ± 42 BP [RICH-21974, 8,533–8,516 (2.5%) 8,480–8,285 (92.9%) calBC] (Bover & Alcover, 2003; Bover et al., 2016, 2018; Lalueza-Fox, Shapiro, Bover, Alcover, & Bertranpetit, 2002). No chronology was available for the sample from Cova de sa Bassa

Blanca. Although several rodents are currently living in Mallorca, differences in size and anatomy between them and *Hypnomys* are distinctive enough to clearly discriminate genera in terms of dental, skull, and postcranial morphology (Agustí, 1980; Bover, Alcover, Michaux, Hautier, & Hutterer, 2010; Mills, 1976; Reumer, 1979, 1981, 1982). Up to six rodents currently live on the island as a result of historical introductions (e.g., Alcover, 2010; Bover & Alcover, 2008), including the glirid *Eliomys quercinus* (Linnaeus, 1766), and murids *Mus musculus* Linnaeus, 1758, *Mus spretus* Lataste, 1883, *Apodemus sylvaticus* Linnaeus, 1758, *Rattus rattus* Linnaeus, 1758, and *Rattus norvegicus* Berkenhout, 1769. The first human settlers to the island (around 4,300 years ago, Bover et al., 2016) introduced *E. quercinus* and *A. sylvaticus*, which were putatively involved in the extinction of the only pre-human rodent *H. morpheus* (Bover & Alcover, 2008). The only *H. morpheus* sample that yielded endogenous DNA, tibia ACAD 14874 (see below, sections 2.2 and 3), displays enough diagnostic traits to identify it as unquestionably belonging to the fossil species: The cross-section of the distal half of the diaphysis and the extent of the tibia-ulna synostosis allow the discrimination of Gliridae from Muridae tibiae. In addition, the position and relative size of the trochlear process of the calcaneum and thus its corresponding structure in the tibia are as in other glirids and not expanded distally as in murids (Stains, 1959), and the lateral groove of the tibia resembles that of *Eliomys*, not weakly developed as in murids (Mills, 1976). However, differences in size between the Mallorcan *E. quercinus* and *H. morpheus* allow each to be discriminated from the other (Bover et al., 2010). The tibiae of *H. morpheus* have been illustrated by Alcover and Roca (1975), Alcover et al. (1981) and Bover et al. (2010).

2.2 | Extraction, library preparation, enrichment, and sequencing

Sample processing, DNA extraction, PCR preparation, and library construction were performed at the facilities of the Australian Centre for Ancient DNA (ACAD) at the University of Adelaide (Australia). The samples were cleaned with surgical blades to remove surface contamination and dirt, irradiated with UV for 30 min on each side, wiped with 3% sodium hypochlorite, soaked for 2 min in 80% ethanol to fully remove sodium hypochlorite, air-dried, and finally irradiated again for 15 min on each side. Each sample was placed in a sterilized stainless steel container with an 8-mm tungsten ball and powdered using a Braun Mikrodismembrator U (B. Braun Biotech International, Berlin, Germany) for 5 s at 3,000 rpm. We obtained 190 mg for the pool of ACAD 13111 and 13155, 150 mg of bone powder for sample ACAD 13307, and 180 mg for sample ACAD 14874. The bone powder for each sample was decalcified and digested overnight at 55°C on a rotary wheel in 4 ml 0.5 M EDTA (pH 8.0) (Life Technologies, Carlsbad, CA, USA), 200 µl of 10% SDS (Life Technologies), and 40 µl of 20 mg/ml Proteinase K (Life Technologies). DNA extraction was performed using a modified QG buffer [15.5 ml QG buffer (Qiagen, Valencia, CA, USA), 1.3% Triton X-100 (Sigma-Aldrich, Saint Louis, MO, USA), 25 mM NaCl (Sigma-Aldrich), and 0.17 M sodium acetate (Sigma-Aldrich)] and suspended in 100 µl of silicon dioxide solution (Brotherton et al., 2013). Samples were then purified using 80% ethanol, and bound DNA was eluted in 200 µl TLE buffer (10 mM Tris, 0.1 mM EDTA, pH 8). A negative control was included for all extractions. No other glirids have ever been processed in the ancient DNA laboratory at ACAD before.

A PCR was performed to screen for the presence of DNA using primer pairs Mamm_12S_E and Mammal_12S_H (Macqueen, Seddon, Austin, Hamilton, & Goldizen, 2010) to amplify a ~95 bp fragment of mitochondrial *12S ribosomal RNA* gene (*12S*). Two microliters of template was used in the PCR (final volume 25 µl), which contained: 1 × Platinum Taq High Fidelity Buffer (Invitrogen, Carlsbad, CA, USA), 3 mM $MgSO_4$, 0.4 µM each primer, 0.25 mM each dNTP, 1.25 U Platinum Taq HiFi (Invitrogen), 2 mg/ml rabbit serum albumin (RSA, Sigma-Aldrich). PCR cycling conditions were as follows: initial denaturation at 94°C for 2 min; 50 cycles of denaturation at 94 °C for 20 s (s), primer annealing at 55°C for 15 s, elongation at 68°C for 30 s; and a final elongation step at 68°C for 10 min. PCR products were visualized under UV light on a 3.5% agarose gel stained with Gel-Red (Jomar Bioscience, Kensington, Australia). PCR products were purified using Agencourt AMPure XP magnetic beads (Beckman Coulter, Brea, CA, USA) according to the manufacturer's protocol. Both strands were sequenced using the BigDye 3.1 Terminator Kit (Applied Biosystems, Foster City, CA, USA). Dye terminators were removed using the Agencourt CleanSEQ magnetic particle solution (Beckman Coulter), and DNA sequencing was performed on 3130xl and 3730xl Genetic Analyzers (Applied Biosystems).

Of the three *H. morpheus* samples analyzed, only ACAD 14874 (Coveta des Gorgs) yielded a positive PCR amplification. Sanger sequencing of the purified amplicon from ACAD 14874 produced a 95-bp fragment after primer trimming. The first BLASTn (Altschul et al., 1997) hit of this sequence against the NCBI nucleotide database (accessed January 10, 2019) was the garden dormouse *Eliomys quercinus* (coverage 98%, identity 95%, *E*-value 6e-32), whereas a second hit was the Asian garden dormouse *Eliomys melanurus* (Wagner, 1840) (coverage 100%, identity 93%, *E*-value 4e-29).

We constructed a double-stranded DNA sequencing library from ACAD 14874 following the protocol described by Meyer and Kircher (2010) using modifications as in Llamas et al. (2016), which uses truncated Illumina adapters with a P5 5-mer barcode and Platinum Taq HiFi (Invitrogen) for post-*Bst* amplification. Enrichment of this library for mtDNA was performed using the protocol described by Mitchell et al. (2016). We performed two parallel enrichment reactions of the DNA library. Following amplification with full-length Illumina sequencing adapters, the molecules retained after enrichment were sequenced on an Illumina HiSeq (Fast Run 2x100 PE), an Illumina MiSeq (2x150 PE), and a NextSeq (2x75 PE) runs.

2.3 | Sequencing data processing and sequence assembly

Resulting reads were demultiplexed according to P5 barcode sequences using Sabre v.1.0 (https://github.com/najoshi/sabre) allowing one mismatch (option -m 1), adapter sequences were removed using AdapterRemoval v.2.1.7 (Schubert, Lindgreen, & Orlando, 2016), and paired reads were collapsed in a single read when overlapping by 11 nucleotides. A concatenated file of 2,136,646 collapsed reads from the three sequencing runs was used to iteratively map to different references. To date (April 2019), the only available complete mitochondrial genomes from glirids available in GenBank are from *Glis glis* (Linnaeus, 1766) and *Graphiurus kelleni* (Reuvens, 1890), and in general, mitochondrial sequences for the Gliridae are scarce, with *cytochrome b* (*CYTB*) and *12S* genes as the most represented genes across the family. For this reason, we mapped our sequencing reads to the putatively closest relative of *Hypnomys*, *Glis glis* (complete mitochondrial genome, GenBank accession number NC_001892), and the longest available *CYTB* and *12S* sequences for genus *Eliomys* (*E. quercinus*: *CYTB* accession number GQ453668, *12S* accession number Y16896; *E. melanurus*: *CYTB* assembly of sequences HE614010 and KF422705, *12S* accession number AJ536350; see Table 1 for details on references and mapping results) using BWA v.0.7.17 (Li & Durbin, 2009) with the recommended parameters for ancient DNA (aln -l 1,024, -n 0.01, -o 2). Reads with a mapping quality Phred score above 25 were filtered using SAMtools v.1.8 (Li et al., 2009), and duplicates removed using FilterUniqueSAMCons.py (Kircher, 2012). Mapping results were visualized using Geneious v.11.1.4 (Biomatters, http://www.geneious.com, Kearse et al., 2012), with 75% majority intermediate consensus sequences generated in Geneious using the reference to call nucleotides in positions with coverage read-depth < 3. This consensus was then used as reference for a new round of mapping. The process was iterated until no more unique reads were mapped to the reference. We generated final 75% majority consensus sequences with nucleotides only called in positions with coverage read-depth ≥ 3x. Nucleotide misincorporation and DNA fragmentation patterns were assessed using mapDamage v.2.0.2 (Jónsson, Ginolhac, Schubert, Johnson, & Orlando, 2013).

We recovered up to 3,501 bp of the *Hypnomys morpheus* mitochondrial genome after 18 mapping iterations to *Glis glis* mitogenome (Table 1), including nine complete *transfer RNA genes* [*Cysteine* (*Cys*), *Glutamine* (*Gln*), *Glutamic acid* (*Glu*), *Isoleucine* (*Ile*), two *Leucines* (*Leu1*, *Leu* 2), *Methionine* (*Met*), *Tyrosine* (*Tyr*), *Valine* (*Val*)], fragments of six protein coding genes [*NADH dehydrogenase subunit 1* (*ND1*) (65 bp, two fragments), *NADH dehydrogenase subunit 2* (*ND2*) (17 bp, one fragment), *NADH dehydrogenase subunit 5* (*ND5*) (40 bp, one fragment), *NADH dehydrogenase subunit 6* (*ND6*) (43 bp, one fragment), *cytochrome c oxidase subunit I* (*COX1*) (259 bp, two fragments), and *cytochrome b* (*CYTB*) (318 bp, one fragment)], and fragments of the two *rRNA* genes [*12S* (697 bp, four fragments) and *16S ribosomal RNA* (*16S*) (1,221 bp, five fragments)]. Sequences obtained for *12S* and *CYTB* genes were aligned to the corresponding sequences from the iterative mapping to isolated *12S* and *CYTB* genes of *Eliomys quercinus* (942 and 361 bp of each gene recovered, respectively) and *E. melanurus* (848 and 590 bp of each gene recovered, respectively). The sequences for each gene overlapped and were identical, and thus, the longest sequence for each gene was selected for the phylogenetic analysis. Despite the low number of unique reads mapping to each reference, mapDamage analyses (Figure S2) displayed damage patterns consistent with ancient samples for unrepaired libraries (Briggs et al., 2007).

2.4 | Phylogenetic analyses

We aligned the *Hypnomys morpheus 12S* (942 bp, GenBank accession number MN153772) and *CYTB* (590 bp, GenBank accession number MN164630) sequences with available data from other glirid and outgroup species (Table 2 for GenBank accession numbers) using MUSCLE (Edgar, 2004) in Geneious. We adjusted the size of each gene in all the 18 species to the length of these genes obtained for *H. morpheus*, and ambiguous regions in the *12S* gene alignment were removed using stringent default parameters in Gblocks v.0.91b (Castresana, 2000), which kept 739 out of the 1,014 bp of the full *12S* alignment (73%). Our final alignment (see Alignment S1) comprised 1,330 bp (591 bp for *CYTB* and 739 bp for *12S*). Partitioning schemes and substitution models (Table 3) in the *12S* region and codon positions in the *CYTB* region were estimated in PartitionFinder v.2.1.1 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016). We inferred a maximum likelihood tree in RAxML v.8.2.11 (Stamatakis, 2014), with node support values estimated by performing 1,000 bootstrap replicates. We also performed a MrBayes v.3.2.3 analysis (Ronquist et al., 2012) with four separate runs of four Markov chains each using default priors. Each chain ran for 10^8 generations sampling trees and parameter values every 10^4 generations. Sampled trees were

TABLE 1 Reference information and iterative mapping results. Up to 2,136,646 sequencing reads from *Hypnomys morpheus* enriched libraries were mapped to the different sequences used as reference

Reference data				Mapping results				
Species	Sequence	GenBank #	Length (bp)	Iterations	Unique reads	Coverage (%)	Coverage depth (x)	Mean Fragment length (bp)
Glis glis	Mitogenome	NC_001892	16,602	18	1,066	23.5	4.8	74.3
Eliomys quercinus	*CYTB*	GQ453668	1,140	14	143	33.3	9.2	73.0
Eliomys quercinus	*12S*	Y16896	963	5	314	99.7	24.2	74.0
Eliomys melanurus	*CYTB*	HE614010 + KF422705	1,003	13	197	61.8	15.0	76.7
Eliomys melanurus	*12S*	AJ536350	967	5	279	94.5	21.3	73.7

TABLE 4 Divergence ages of selected nodes reported in this and previous studies. All ages are in millions of years ago

Node	This paper	Montgelard et al. (2003)	Nunome et al. (2007)	Mouton et al. (2012)	Mouton et al. (2017)
(*E. quercinus, E. melanurus*)	1.91–8.19	7.0 ± 0.9	na	4.87–8.88	5.56–7.49
(*D. nitedula, D. laniger*)	3.85–15.96	16.7 ± 1.8	na	na	na
(*Eliomys, Dryomys*)	14.47–31.84	28.5 ± 2.8	14.5 ± 2.4	na	13.08–24.40
(*Eliomys, Dryomys*), *Myomimus*)	17.56–37.89	38.1 ± 3.6	na	na	na
Leithiinae	20.55–41.36	40.8 ± 3.8	22.3 ± 2.8	9.85–54.36	na
(*Glis, Glirulus*)	16.12–41.34	27.7 ± 3	27.0 ± 2.9	na	na
Graphiurinae	9.00–25.04	8.7 ± 1	na	na	na
Gliridae	26.91–50.08	50.0	28.6 ± 2.9	na	na
(Sciuridae, Gliridae)	50.00–54.72	na	52.7 ± 1.4	na	na

For the 591 bp of *CYTB*, similarity values >93% and >90% were observed between congeneric species within *Eliomys* and *Graphiurus*, respectively. For this same *CYTB* fragment, *H. morpheus* displayed a similarity of 84% and 85% with *E. quercinus* and *E. melanurus*, respectively, comparable to the similarity values observed between members of other glirid genera, for example, *Muscardinus-Glis* (85.2%), *Glirulus-Glis* (84.2%), or *Graphiurus kelleni-Glis* (84%). Similar patterns were observed in our pairwise analysis of the 739 bp of the *12S* gene. The highest similarity values were displayed by pairwise comparison between congeneric species within *Eliomys* (96.6%), *Dryomys* (95.4%), and *Graphiurus* (93%–99.6%). Values around 93% were also observed for pairwise comparison between *Hypnomys-E. quercinus* (93.8%), *Hypnomys-E. melanurus* (93.1%), and *Glirulus-Glis* (93.5%). Finally, where data were available for both *CYTB* and *12S*, the highest values were again observed between congeneric species within *Eliomys* (95.2%) and *Graphiurus* (93%), followed by *Hypnomys-E. quercinus* (89.4%), *Hypnomys-E. melanurus* (89.5%), and *Glirulus-Glis* (89.4%).

Our phylogenetic analyses clearly place our *H. morpheus* within Gliridae and as sister clade of *Eliomys* (Figure 2 and S3). For this reason, we can confidently discard the hypothesis that the tibia belongs to a murid, especially to similar-sized rodents of the genus *Rattus* Fischer de Waldheim, 1803. Furthermore, the position of *H. morpheus* sequences outside the genetic variability of *Eliomys CYTB* gene (Figure S5) clearly shows that there is no reason to interpret our data as a result of a misidentification of an *Eliomys* bone.

4 | DISCUSSION

Our molecular data are fully consistent with a close relationship between *Hypnomys* and *Eliomys*, as suggested by past morphological analyses (e.g., Agustí, 1980, 1981; Bate, 1918; Mills, 1976; Zammit-Maempel & de Bruijn, 1982). The basal placement of *H. morpheus* outside the variability of the modern *Eliomys* species and the pairwise similarity (Figure S4) between the fossil and each of two *Eliomys* species studied here (which display equivalent levels of similarity as that between *Glis* and *Glirulus*; but see *Graphiurus platyops* Thomas, 1897 in comparison with other *Graphiurus* species using *12S* data) suggest that *Hypnomys* should not be considered as a subgenus of *Eliomys*, and the generic status established by Bate (1918) should be retained.

In general, the lowest values of the 95% HPD intervals for node ages (Table 4) are similar to the values obtained by Nunome et al. (2007), whereas the highest values of 95% HPD intervals are similar to those obtained by Montgelard et al. (2003). However, Freudenthal and Martín-Suárez (2013) suggested that the base age of Gliridae (50 Mya) used as a calibration age by Montgelard et al. (2003) was too old and should be replaced by 16 Mya, a view that has subsequently not been followed (e.g., Mouton et al., 2017). Despite the uncertainties of the node ages of our (and other published) calibrated trees, the available *Hypnomys-Eliomys* divergence estimate of 13.67 Mya (95% HPD = 7.39–20.07 Mya) allows us to identify three possible palaeobiogeographic scenarios for the origin of the *Hypnomys* lineage in the Balearic Islands.

The first possible origin for *Hypnomys*, which is the most commonly accepted hypothesis (e.g., Agustí, 1980; Alcover et al., 1981; Bover et al., 2014; Colom, 1978; Mas et al., 2018; Moyà-Solà & Pons-Moyà, 1980), involves a split from a continental ancestor during the Late Tortonian/Early Messinian (Figure 2) and its arrival into the Balearic Islands during the Messinian Salinity Crisis (MSC, 5.97–5.33 Mya; Krijgsman, Hilgen, Raffi, Sierro, & Wilson, 1999; Manzi et al., 2013). According to Agustí (1986) and Bover, Quintana, and Alcover (2008), the putative continental ancestor would be the fossil species *Eliomys intermedius* Priant, 1953 or *E. truci* Mein and Michaux, 1970, both representatives of the lineage *E. truci-E. yevesi-E. intermedius-E. quercinus* (Mansino, García-Álix, Ruiz-Sánchez, & Montoya, 2015). However, preliminary morphological analysis of the earliest known representative of the *Hypnomys* lineage (currently under analysis) obtained from the Early Pliocene Zanclean site of Na Burguesa-1 (NB-1) on Mallorca conflicts with this hypothesis. The NB-1 glirid shows an unexpectedly complex dental pattern (Figure 3), whereas proposals that *Hypnomys* descends from fossil *Eliomys* species (e.g., Agustí, 1980, 1981, 1986; Alcover & Agustí,

TABLE 2 Gliridae and outgroup samples and accession numbers. Mitochondrial *12S* and *CYTB* sequences were used in the maximum likelihood and Bayesian inference phylogenetic analyses

Species	*12S*	*CYTB*
Dryomys laniger Felten and Storch, 1968	AJ536349	
Dryomys nitedula (Pallas, 1778)	D89005	KJ739702
Eliomys melanurus (Wagner, 1840)	AJ536350	HE614010 + KF422705
Eliomys quercinus (Linnaeus, 1766)	Y16896	AJ225030
Glirulus japonicus (Schinz, 1845)	D89007	D89001
Glis glis (Linnaeus, 1766)	NC_001892	NC_001892
Graphiurus kelleni (Reuvens, 1890)	HE978360	HE978360
Graphiurus lorraineus Dollman, 1910	AJ536356	
Graphiurus microtis (Noack, 1887)	AJ536352	
Graphiurus murinus (Desmarest, 1822)	AJ536351	AJ225115
Graphiurus ocularis (Smith, 1829)	AJ536355	
Graphiurus parvus (True, 1893)	AJ536353	
Graphiurus platyops Thomas, 1897	AJ536354	
Muscardinus avellanarius (Linnaeus, 1758)	D89006	AJ225117
Myomimus roachi (Bate, 1937)	AJ536348	
Glaucomys volans (Linnaeus, 1758) (outgroup)	AF038020	AF157921
Sciurus aestuans Linnaeus, 1766 (outgroup)	AJ012746	AJ389530

TABLE 3 Optimal partitioning scheme inferred using PartitionFinder. The total alignment consists of 1,330 bp (591 bp for *CYTB* and 739 bp for *12S*) from 19 Gliridae species. See Table 2 for accession number details

	Substitution model		
Partition	RAxML	MrBayes	BEAST
12S, *CYTB*_1	GTR + G	GTR + G	GTR + G
*CYTB*_2	GTR + G	HKY + I	HKY + I
*CYTB*_3	GTR + G	HKY + G	HKY + G

summarized as a majority-rule consensus tree after discarding the first 10% of trees as burn-in (Figure S3).

We implemented a birth-death tree prior and a single relaxed uncorrelated lognormal clock model (with rate multipliers for each of the three partitions, see Table 3) to estimate phylogeny and divergence times using BEAST v.1.8.4 (Drummond, Suchard, Xie, & Rambaut, 2012). To calibrate our analysis, we followed previous studies (e.g., Montgelard et al., 2003; Nunome et al., 2007; Mouton et al., 2017) and constrained the age of the divergence between Sciuridae and Gliridae according to a uniform distribution with a minimum of 50 million years ago (Mya) and a maximum of 55 Mya, corresponding to the earliest known fossil representatives of these families (Hartenberger, 1998). We repeated our analysis four times with different starting trees created using Mesquite v.3.04 (Maddison & Maddison, 2018) based on an ML tree created using IQTREE v.1.6.6 (Nguyen, Schmidt, von Haeseler, & Minh, 2015). Each analysis comprised a chain of 10^8 iterations, sampling every 10^4 iterations. Parameter convergence and sampling was assessed using Tracer v.1.6.1. The first 10% of trees from each chain were removed as burn-in, with the remainder from each chain combined using LogCombiner v.1.8.4 and summarized using TreeAnnotator v.1.8.4 (Rambaut & Drummond, 2010).

We graphically depicted the pairwise distances between different Gliridae sequences using the heatmap similarity (%) implemented in Geneious (Figure S4) for the two different mitochondrial genes available (16 species for the *12S* gene and nine for the *CYTB* and a combination of *CYTB* and *12S*).

We tested the position of *Hypnomys morpheus* in relation to the variation within the *Eliomys* genus using a 370-bp *CYTB* fragment obtained for 48 individuals of *E. quercinus* (accession numbers AJ225030, FM164278, FR848957, FR848958, GQ453668, GQ453669, HE611090-HE611093, HE613976-HE614008, JX457812-JX457816), eight individuals of *E. melanurus* (accession numbers FM164279, FM164280, FR848955, FR848956, HE614009-HE614012), and *Graphiurus kelleni* (accession number HE978360) as outgroup using an unpartitioned IQTREE analysis. The same alignment without the outgroup was used in the haplotype network analysis using Fitchi (Matschiner, 2015). *Eliomys* clades obtained in both IQTREE and Fitchi analyses (Figure S5) have been named following Perez, Libois, and Nieberding (2013).

3 | RESULTS

The mapDamage analysis (Figure S2), which shows the expected damage pattern of degraded ancient DNA, and negative PCR results on both extraction blank controls and other extracts from *Hypnomys* samples rule out the possibility of any introduction of contaminants or cross-contamination during laboratory work.

Overall, the results of our phylogenetic analyses are consistent with the published molecular phylogenies of Gliridae (e.g., Fabre et al., 2012; Montgelard et al., 2003; Nunome et al., 2007). While we did not find strong support for the previously established *Glis-Glirulus* clade, our results agree with Holden (2005)'s classification of glirid subfamilies—Graphiurinae (including *Graphiurus*), Glirinae (including *Glis* and *Glirulus*), and Leithiinae (including *Eliomys*, *Dryomys*, *Muscardinus*, and *Myomimus*)—which we find to be reciprocally monophyletic. Both maximum likelihood (ML) and MrBayes Bayesian inference (BI) analyses supported the monophyly of Graphiurinae (maximum likelihood bootstrap value [MLB] = 100, posterior probability [PP] = 1) and Leithiinae (sensu Holden, 2005; MLB = 79, PP = 0.99, Figure S3). The monophyly of the Leithiinae node has been previously well supported just using a 952-bp fragment of the *12S* by Montgelard et al. (2003). However, our results do not recapitulate support for Glirinae (*Glis-Glirulus* node) or the basal position of *Muscardinus* and *Myomimus* within Leithiinae, which were observed in published molecular phylogenies based on nuclear genes or a combination of nuclear and mitochondrial genes (Fabre et al., 2012; Montgelard et al., 2003; Nunome et al., 2007). Importantly, we obtained high support for a clade comprising *Hypnomys morpheus* and *Eliomys* (MLB = 100, PP = 1) and for the monophyly of *Eliomys* (MLB = 100, PP = 1) and *Dryomys* (MLB = 99, PP = 1). The clade formed by these three genera (*Dryomys*, *Eliomys*, and *Hypnomys*) received moderate support (MLB = 78, PP = 0.95).

The time-calibrated tree (Figure 2) displayed a similar topology to the uncalibrated Bayesian tree, that is, monophyly with similarly high posterior probability values of clades Gliridae (PP = 1), Graphiurinae (PP = 1), Leithiinae (PP = 1), *Dryomys* (PP = 1), and *Eliomys* (PP = 1), a *Hypnomys-Eliomys* clade (PP = 1), and a *Dryomys-Hypnomys-Eliomys* clade (PP = 0.97). The main difference between the trees was the unresolved relationship of Glirinae with Leithiinae (PP = 0.68, uncalibrated tree) or with Graphiurinae (PP = 0.49, calibrated tree). In general, the 95% highest posterior densities (HPD) of node ages were wide, though they overlapped with those observed in previously published glirid phylogenies (Table 4). The split between the fossil *Hypnomys* and its putative sister taxon *Eliomys* was 13.67 Mya (95% HPD = 7.39–20.07).

Our ML analysis using only the 370 bp *CYTB* sequences of *Eliomys*, *Hypnomys morpheus*, and the outgroup *Graphiurus kelleni* (Figure S5b) resulted in moderate support for the monophyly of *Eliomys* (MLB = 88) with *H. morpheus* as its sister taxon. Our haplotype network (Figure S5a) further illustrates the distinction between *H. morpheus* and extant *Eliomys* variation. Both analyses indicated that sequences from the fossil *H. morpheus* do not fall within the variability of the modern *E. quercinus* and *E. melanurus*. As expected, pairwise comparisons of sequence similarity displayed higher values when species from the same genus were analyzed (Figure S4).

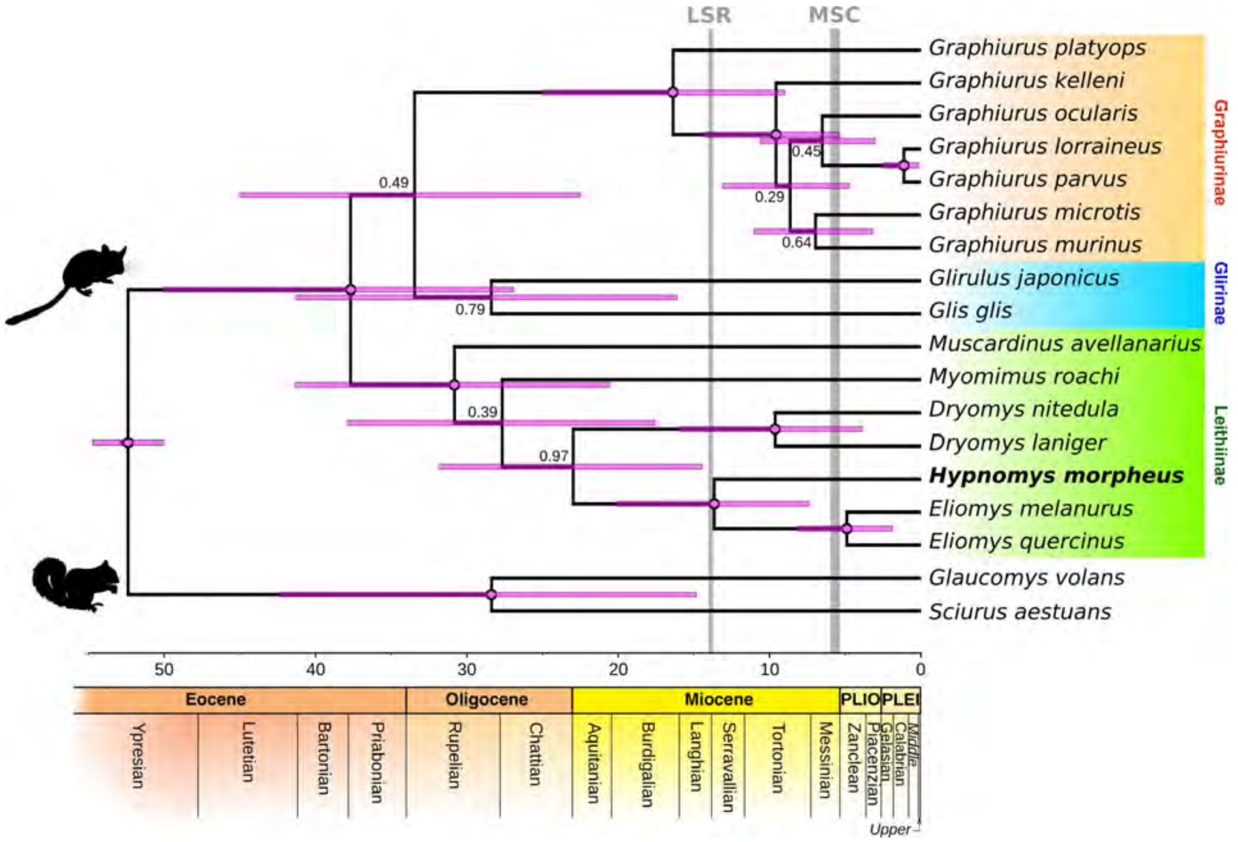

FIGURE 2 Phylogenetic position of *Hypnomys morpheus* within Gliridae based on mitochondrial sequences (1,330 bp) and using BEAST. Nodes are labeled with Bayesian posterior probabilities (PP), and circles in nodes indicate PP = 1. Purple bars represent 95% highest posterior density (HPD) intervals. Possible colonization events during the Langhian–Serravalian Regression (LSR) and Messinian Salinity Crisis (MSC) are indicated by gray shadings. See Table 2 for information about individual samples and accession numbers. PLIO: Pliocene; PLEI: Pleistocene. Time in million years before present (BP)

TABLE 4 Divergence ages of selected nodes reported in this and previous studies. All ages are in millions of years ago

Node	This paper	Montgelard et al. (2003)	Nunome et al. (2007)	Mouton et al. (2012)	Mouton et al. (2017)
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Our molecular data are fully consistent with a close relationship between *Hypnomys* and *Eliomys*, as suggested by past morphological analyses (e.g., Agustí, 1980, 1981; Bate, 1918; Mills, 1976; Zammit-Maempel & de Bruijn, 1982). The basal placement of *H. morpheus* outside the variability of the modern *Eliomys* species and the pairwise similarity (Figure S4) between the fossil and each of two *Eliomys* species studied here (which display equivalent levels of similarity as that between *Glis* and *Glirulus;* but see *Graphiurus platyops* Thomas, 1897 in comparison with other *Graphiurus* species using *12S* data) suggest that *Hypnomys* should not be considered as a subgenus of *Eliomys*, and the generic status established by Bate (1918) should be retained.

In general, the lowest values of the 95% HPD intervals for node ages (Table 4) are similar to the values obtained by Nunome et al. (2007), whereas the highest values of 95% HPD intervals are similar to those obtained by Montgelard et al. (2003). However, Freudenthal and Martín-Suárez (2013) suggested that the base age of Gliridae (50 Mya) used as a calibration age by Montgelard et al. (2003) was too old and should be replaced by 16 Mya, a view that has subsequently not been followed (e.g., Mouton et al., 2017). Despite the uncertainties of the node ages of our (and other published) calibrated trees, the available *Hypnomys-Eliomys* divergence estimate of 13.67 Mya (95% HPD = 7.39–20.07 Mya) allows us to identify three possible palaeobiogeographic scenarios for the origin of the *Hypnomys* lineage in the Balearic Islands.

The first possible origin for *Hypnomys*, which is the most commonly accepted hypothesis (e.g., Agustí, 1980; Alcover et al., 1981; Bover et al., 2014; Colom, 1978; Mas et al., 2018; Moyà-Solà & Pons-Moyà, 1980), involves a split from a continental ancestor during the Late Tortonian/Early Messinian (Figure 2) and its arrival into the Balearic Islands during the Messinian Salinity Crisis (MSC, 5.97–5.33 Mya; Krijgsman, Hilgen, Raffi, Sierro, & Wilson, 1999; Manzi et al., 2013). According to Agustí (1986) and Bover, Quintana, and Alcover (2008), the putative continental ancestor would be the fossil species *Eliomys intermedius* Priant, 1953 or *E. truci* Mein and Michaux, 1970, both representatives of the lineage *E. truci-E. yevesi-E. intermedius-E. quercinus* (Mansino, García-Álix, Ruiz-Sánchez, & Montoya, 2015). However, preliminary morphological analysis of the earliest known representative of the *Hypnomys* lineage (currently under analysis) obtained from the Early Pliocene Zanclean site of Na Burguesa-1 (NB-1) on Mallorca conflicts with this hypothesis. The NB-1 glirid shows an unexpectedly complex dental pattern (Figure 3), whereas proposals that *Hypnomys* descends from fossil *Eliomys* species (e.g., Agustí, 1980, 1981, 1986; Alcover & Agustí,

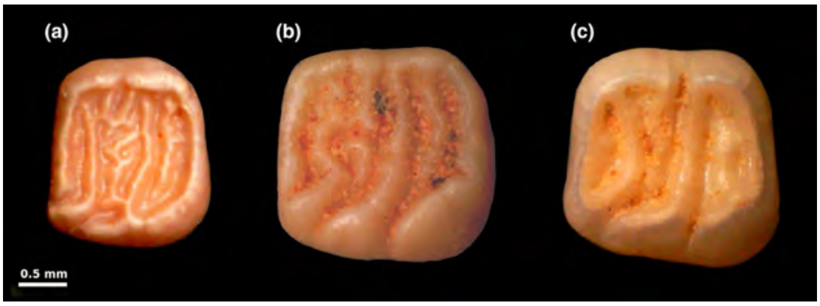

FIGURE 3 Decrease of complexity pattern in occlusal surface of teeth in the *Hypnomys* phylogenetic lineage depicted using lower molars (m1-2) from different Mallorcan fossil glirids. From least recent to more recent (a) Gliridae from Na Burguesa-1 (NB-1), Zanclean (Early Pliocene); (b) *H. onicensis* (Early Pleistocene); (c) *H. morpheus* (Middle Pleistocene to Holocene)

1985; Bate, 1918; Zammit-Maempel & de Bruijn, 1982) suggest that members of the *Hypnomys* lineage evolved increasing dental pattern complexity through time from a relatively dentally simple *Eliomys*-like ancestor. Reumer (1982) likewise observed a contrary trend toward a simplification of the dental pattern in the *Hypnomys* lineage (from *H. waldreni* to *H. morpheus*). Thus, while the results of our molecular dating analyses are consistent with this hypothesis, it conflicts with available morphological evidence.

An alternative and more morphologically plausible origin for *Hypnomys* is its descent from a Middle-Late Miocene glirid with a high dental complexity, such as *Vasseuromys* Baudelot and de Bonis, 1966, or some closely related genus. *Vasseuromys* spans the latest Oligocene to Late Miocene (Sinitsa & Nesin, 2018) while the older *Microdyromys* de Bruijn, 1966 and *Bransatoglis* Hugueney, 1967, which also possess high dental complexity, span the Early Oligocene to the Middle Miocene and the Late Oligocene to the Middle Miocene, respectively (Freudenthal & Martín-Suárez, 2013). Under this scenario, the simplified dental pattern displayed by more recent *Hypnomys* species (Figure 3) would be an effect of insular evolution (Reumer, 1982).

A final possibility for the origin of *Hypnomys*, consistent with the upper bounds of our node age 95% HPDs, is an early split from mainland ancestors and pre-MSC arrival to the Balearic Islands during the Langhian–Serravalian regression (Moyà-Solà, Quintana, Alcover, & Köhler, 1999; Riba, 1981). However, the fossil record of mammals of this age from Mallorca and Menorca is restricted to the ochotonid *Gymnesicolagus gelaberti* Mein & Adrover, 1982, and the glirids *Carbomys sacaresi* Mein & Adrover, 1982, *Margaritamys llulli* Mein & Adrover, 1982 and *Peridyromys ordinasi* Mein & Adrover, 1982 in Mallorca (Adrover, Agustí, Moyà-Solà, & Pons-Moyà, 1985; Mein & Adrover, 1982), and *Margaritamys adroveri* Quintana & Agustí, 2007 in Menorca (Quintana & Agustí, 2007). All of the glirids from this faunal episode have lower dental complexity than NB-1 glirid, making them unlikely ancestors (as for *Eliomys*).

Although the resolving of phylogenetic relationships of all extinct and extant Gliridae subfamilies is beyond the scope of this paper, the dental morphology and the genetics of *Hypnomys* clearly support its inclusion within Leithiinae. Our node age estimates, the chronological range of *Vasseuromys*, and the original complex dental pattern of *Hypnomys* (see Figure 3a in this paper, and *Vasseuromys tectus* Sinista and Nesin, 2018 depicted in Figure 6 in Sinista & Nesin, 2018) suggest that *Vasseuromys*, or some close relative, could be considered as the potential ancestor of *Hypnomys*.

Ultimately, obtaining additional genetic data from extinct and extant dormouse species as well as a systematic review of extinct genera could contribute to further illuminating the evolution, taxonomy, and palaeobiogeography of Gliridae.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. *Hypnomys morpheus* bones showing the characters shared by Leithiinae according to Wahlert et al. (1993).

Figure S2. Results of mapDamage analyses of reads from *Hypnomys morpheus* mapped to *Eliomys CYTB* and *12S* genes and to *Glis glis* complete mitogenome (Accession numbers provided in the figure).

Figure S3. Maximum-Likelihood and Bayesian phylogenetic relationships of Gliridae (see Table 2 for extant individuals and accession numbers) including the extinct *Hypnomys morpheus* (ACAD 14874), and *Glaucomys volans* and *Sciurus vulgaris* as outgroups.

Figure S4. Heatmap of pairwise similarity between the Gliridae sequences used in this paper.

Figure S5. Haplotype network analysis (a) and ML tree (b) of 370-bp fragment of *CYTB* from 56 *Eliomys* individuals and *Hypnomys morpheus*.

Alignment S1. Alignment of 1,330 bp of *CYTB* and *12S* mitochondrial genes in Phylip format used for the Gliridae phylogenetic analyses.

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Annex 2. Articles relacionats amb els objectius de la present Tesi, fora del Programa de Doctorat de Ciències de la Terra de la UB

5. Torres, E., Bailon, S., Bover, P. & Alcover, J.A. 2014. Sobre la presencia de un vipérido de gran talla perteneciente al Complejo de Víboras Orientales en el yacimiento de Na Burguesa-1 (Mioceno Superior/Plioceno Inferior, Mallorca). *Fundamental*, 24: 237-240.

Sobre la presencia de un vipérido de gran talla perteneciente al Complejo de Víboras Orientales en el yacimiento de Na Burguesa-1 (Mioceno Superior/Plioceno Inferior, Mallorca)

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Introducción

Los primeros restos fósiles atribuidos a serpientes procedentes de Baleares se obtuvieron en Menorca, donde Bailon *et al.* (2002) describieron la especie fósil *Vipera natiensis*. Posteriormente Bailon *et al.* (2005) documentaron la presencia de colúbridos en esta misma isla. Ese mismo año se descubrió en Mallorca el yacimiento del Caló den Rafelino (CdR, Plioceno inferior), que fue dado a conocer por Bover *et al.* (2007). Este depósito consiste en una brecha fosilífera muy pobre con una matriz de limos rojos endurecidos que rellenan una antigua cavidad emplazada dentro del Complejo de Arrecifes del Mioceno superior (Fornós, 1998; Pomar *et al.*, 1990). En este depósito se obtuvieron las dos únicas vértebras de un vipérido que se ha podido atribuir al Complejo de Víboras Orientales (OVC) (Bailon *et al.*, 2010). Se trata de una especie de grandes dimensiones, con una longitud corporal cercana o superior a los 2 m, lo que la convierte en la víbora fósil que alcanza mayores dimensiones de Europa. Asociados a estos restos han aparecido otros reptiles [*Maioricalacerta rafelinensis* (Bailon *et al.*, 2014); cf. *V. natiensis*, *Dopasia* sp. y Colubrinae indet. (Bover *et al.*, 2014)] y de mamíferos [*Myotragus palomboi* (Bover *et al.*, 2010); *Nesiotites rafelinensis* (Rofes *et al.*, 2012); *Hypolagus balearicus* (Quintana *et al.*, 2010) y *Tragomys macpheei* (Agustí *et al.*, 2012)]. Esta fauna ha permitido ampliar el conocimiento de la colonización de las Baleares durante el Messiniense, y de la fase inicial de su evolución en condiciones de aislamiento, iniciada hace 5,33 Ma (final de la crisis salina del Messiniense).

En el 2012 miembros del Speleo Club Mallorca descubrieron el yacimiento de Na Burguesa-1. Este depósito cárstico se halla localizado en las proximidades del Mirador de Na Burguesa (Palma). Está formado por brechas fosilíferas muy ricas, con una matriz de limos rojos cimentados, que rellenan una cueva o fisura, excavada en sedimentos carbonatados del Lías inferior. Los bloques de brechas estudiados fueron extraídos de su emplazamiento original y desplazados unos pocos metros debido a la construcción de una pequeña edificación del servicio Municipal de Aguas de Palma. Estos bloques están proporcionando una gran cantidad de restos de vertebrados pertenecientes a taxones próximos, pero ligeramente más antiguos, a los procedentes del yacimiento del CdR.

De acuerdo con Bover *et al.* (2014) la fauna herpetológica de Na Burguesa-1 incluye un quelonio (indet.), un gecónido (indet.), un lacértido (indet.), un escíncido (cf. *Chalcides*), un ánguido (*Dopasia*), un escolecofidio (indet.), un colúbrido (indet.) y un vipérido, que, tentativamente, se atribuyó a una *Vipera* sp. del OVC.

El objetivo de este trabajo es confirmar la presencia de una especie de *Vipera* perteneciente al OVC en el yacimiento de Na Burguesa-1 a partir de una nueva vértebra, de gran tamaño, recientemente exhumada.

Extracción y preparación de los restos fósiles

Los bloques obtenidos del yacimiento de Na Burguesa-1 han sido tratados mediante baños sucesivos en ácido acético. El proceso se inicia con la reducción del tamaño de los bloques mediante la realización de perforaciones en la roca y la inyección de cemento expansivo, fracturando la roca al cabo de unas 24h. Posteriormente se consolidan los elementos óseos visibles con Paraloid-B72 al 5%, se sumergen las rocas en ácido acético al 10% durante 48h y se dejan en agua durante 48h. Finalmente se ponen a secar y se repite el ciclo hasta retirar los elementos óseos existentes en la roca.

Una vez aislados los huesos de la roca que lo contenían, se eliminan los restos de matriz mezclada con consolidante mediante un pincel fino impregnado en acetona. Finalizada la limpieza, el hueso se consolida por inmersión en Paraloid-B72 al 5%.

Material: IMEDEA 104072: vértebra dorsal de ofidio de tamaño grande (Fig. 1 A-E). Depositado en el Institut Mediterrani d'Estudis Avançats (IMEDEA, CSIC-UIB), Esporles, Mallorca.

Medidas: Anchura mínima interzigapofisaria*: 12,6 mm; Longitud máxima de la vértebra, entre la cresta anterior de la faceta prezigapofisaria y la cresta posterior de la faceta postzigapofisaria: 15,1 mm; Anchura máxima anterior, entre las crestas laterales de las facetas de las prezigapófisis*: 22,5 mm; Anchura máxima posterior, entre las crestas laterales de las facetas de las postzigapófisis*: 19,0 mm; Anchura del zigosfeno: 8,2 mm; Anchura del cótilo: 6,85 mm; Altura del cótilo: 6,7 mm.

* Medidas realizadas desde el punto correspondiente disponible en la vértebra IMEDEA 104072 hasta el plano de simetría y posteriormente duplicadas.

Descripción

La vértebra conserva en condiciones óptimas el lateral izquierdo, mientras que parte del lateral derecho se encuentra seccionado oblicuamente al plano de simetría de la vértebra, dejando únicamente conservada la parte dorsal más próxima a la espina neural y la región anterior.

En vista dorsal (Fig. 1A), la vértebra es más ancha que larga (ratio Longitud máxima/Anchura máxima anterior = 0,67). La faceta articular de la prezigapófisis conservada presenta una morfología subrectangular y está inclinada en dirección antero-lateral. El proceso prezigapofisario es cónico y relativamente corto, su longitud corresponde aproximativamente a ¼ de la longitud de la faceta prezigapofisaria. La parte distal de la postzigapófisis presenta una morfología angulosa como consecuencia de la presencia de una espina epizigapofisaria y el arco neural termina con una muesca central relativamente profunda bajo la parte posterior de la espina neural. La cresta anterior del zigosfeno se encuentra ligeramente erosionada pero se puede observar que es trilobulada, con un lóbulo central poco marcado. La espina neural es larga, relativamente fina, y anteriormente se prolonga hacia el dorso del zigosfeno. Sobre el arco neural se aprecian las impresiones de los músculos dorsales y sobre el lado izquierdo, justo detrás de la faceta prezigapofisaria el arco neural presenta una excrecencia ósea probablemente patológica.

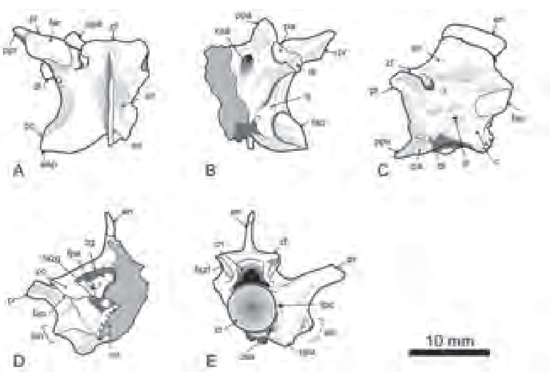

Figura 1. Vértebra dorsal IMEDEA 104072. (A) vista dorsal; (B) vista ventral; (C) vista lateral izquierda; (D) vista posterior; (E) vista anterior. Abreviaciones: an, arco neural; c, centrum; cn, canal neural; co, cóndilo; csa, canal subcentral anterior; ct, cótilo; di, diapófisis; eep, espina epizigapofisaria; en, espina neural; fao, faceta articular postzigapo-fisaria; fap, foramen parazigantral; far, faceta articular prezigapofisaria; fazf, faceta articular del zigosfeno; fazg, faceta articular del zigantro; fl, foramen lateral; fpc, foramen paracotilar; pa, parapófisis; po, postzigapófisis; ppa, proceso parapofisario; ppr, proceso prezigapofisario; pr, prezigapófisis; sin, sinapófisis; zf, zigosfeno; zg, zigantro.

En vista ventral (Fig. 1B), el *centrum* es robusto con márgenes laterales bien definidos. La base del proceso parapofisario se proyecta medialmente hasta conectar con el cótilo cerrando ventralmente la parte anterior del sillón subcentral y formando un corto canal subcentral anterior para el paso de la arteria vertebral. La parapófisis presenta un margen bien marcado que delimita una morfología subcircular y una superficie articular lisa. La diapófisis es protuberante y muestra una morfología y superficie irregular, posiblemente debido a un estado de conservación no tan bueno. La faceta articular de la postzigapófisis presenta una morfología suboval. La presencia de hipapófisis no puede ser asegurada debido a la fragmentación del *centrum*.

En vista lateral (Fig. 1C), la vértebra es ligeramente más alta que larga. El arco neural presenta una morfología deprimida. La espina neural es ligeramente más alta que larga y posee límites anterior y posterior inclinados posteriormente. El foramen lateral se localiza en una amplia depresión circular de la pared lateral de la vértebra. Los procesos parapofisarios están dirigidos antero-ventralmente.

En vista posterior (Fig. 1D), se observa la faceta articular de la postzigapófisis inclinada dorsalmente. El zigantro es profundo y muestra una faceta articular bien desarrollada. Únicamente se conserva un margen residual de cuello del cóndilo. El arco neural es claramente deprimido.

En vista anterior (Fig. 1E), la prezigapófisis presenta una superficie inclinada dorsalmente. El zigosfeno tiene un aspecto robusto y es ligeramente más ancho que el cótilo, y con un límite dorsal casi horizontal. El foramen paracotilar es claramente visible, situado ligeramente por encima de la línea media del cótilo y el canal neural es reducido. El sillón subcentral izquierdo está cerrado ventralmente y constituye un foramen debido a la expansión ósea existente entre la base del proceso paradiafisario y la base del cótilo mencionada anteriormente.

La morfología de esta vértebra, ligeramente más corta que alta y con una espina neural relativamente alta, sugiere que puede tratarse de una vértebra dorsal media.

Discusión

La atribución de la vértebra dorsal IMEDEA 104072 a la familia Viperidae se basa en la siguiente combinación de caracteres: (1) arco neural deprimido en norma posterior, (2) facetas articulares zigapofisarias inclinadas dorsalmente, (3) proceso parapofisario orientado antero-ventralmente y (4) cótilo y cóndilo desarrollados (Bailon *et al.*, 2010).

Según la agrupación propuesta por Szyndlar y Rage (1999), basada en la morfología de las vértebras precloacales de las víboras, este ejemplar pertenecería al grupo OVC por las siguientes razones: presentar un gran tamaño y robustez, un centrum corto y con márgenes laterales bien definidos y exhibir una espina neural desarrollada.

Estas características confirman la presencia de una especie de este grupo de víboras en el yacimiento de NB-1. Su tamaño es inferior al de la vértebra de CdR. Esta diferencia de talla es difícil de interpretar. Con el material disponible no se puede determinar si se relaciona con la mayor antigüedad de los materiales del CdR o con la heterogeneidad de las vértebras en función de su posición en la columna vertebral, un rasgo que se agudiza con la edad (Sarris, 2013).

Se han detectado algunas diferencias entre la vértebra de NB-1 y las del depósito de CdR. La morfología del proceso postzigapofisario de la vértebra de NB-1 presenta un extremo anguloso, debido a la presencia de la espina epizigapofisaria, mientras que la de CdR, que no presenta esta estructura, muestra un perfil más redondeado y ligeramente curvado hacia la parte anterior de la vértebra. La faceta articular de la postzigapofisis del ejemplar de NB-1, tiene una morfología suboval con una región de la superficie que tiene una inclinación distinta a la del conjunto, en cambio la de CdR es rectangular, plana y subhorizontal. El foramen lateral de la vértebra de NB-1 se sitúa en torno a una depresión circular, mientras que la del depósito de CdR se localiza en una depresión longitudinal profunda. La cresta dorsal del zigosfeno es bastante horizontal en el caso del ejemplar de NB-1, a diferencia de la vértebra de CdR, la cual muestra una superficie ligeramente cóncava.

La presencia de un canal subcentral anterior cerrado ventralmente por una expansión ósea de la base del proceso parapofisario y la excrecencia ósea observada sobre la parte antero-lateral izquierda del arco neural, son dos caracteres hasta ahora inéditos en la literatura sobre morfología vertebral de serpientes y parecen corresponder a una anomalía ósea individual por lo que consideramos que carecen de valor sistemático.

La vértebra IMEDEA 104072 documenta la presencia de una *Vipera* del OVC en el yacimiento de NB-1. El establecimiento de la identidad específica de esta víbora y de su relación con la víbora del CdR requiere la obtención de nuevos materiales.

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Integrative Zoology 2014; 9: 183–196 doi: 10.1111/1749-4877.12049

REVIEW

Late Miocene/Early Pliocene vertebrate fauna from Mallorca (Balearic Islands, Western Mediterranean): an update

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Abstract

The vertebrate fossil record from the Balearic Islands (western Mediterranean) has improved considerably over the past decade, especially in Mallorca and Menorca. In Menorca, the Pliocene terrestrial fauna was updated by the discovery and description of the large-sized leporid *Nuralagus*, several reptiles and an amphibian. In Mallorca, paleontological exploration yielded 2 deposits with a Late Miocene/Early Pliocene chronology, Caló den Rafelino (CdR) and Na Burguesa-1 (NB-1). So far, 4 new mammalian taxa and 2 new reptiles have been identified for the CdR deposit, whereas the faunal assemblage from the recently discovered deposit (Apr 2012) of NB-1 is currently composed of, at least, 6 terrestrial mammals, 8 reptiles and an amphibian. Its faunal composition and some primitive characteristics of the obtained taxa suggest that the chronology of this deposit is slightly earlier than the CdR. The terrestrial vertebrates recorded in these 2 Mallorcan deposits are changing the view of the paleofaunal assemblage previously known for the Plio–Pleistocene of the island. Morphological characteristics displayed by some of the taxa suggest that these faunas would be at the beginning of an isolated evolution. In this paper we present a preliminary report on the fossils recovered from the NB-1 deposit, as well as some unpublished data from CdR, and we analyze the whole fauna from both Mallorcan deposits, focusing on taxonomical and paleobiogeographical aspects.

Key words: Early Pliocene, Late Miocene, Mallorca, new fauna, paleobiogeography

INTRODUCTION

The Balearic Islands are an archipelago located at the Western Mediterranean Sea. It is comprised of 2 sub-archipelagos, the Gymnesic islands (Mallorca, Menorca and surrounding islets) and the Pityusic islands (Eivissa, Formentera and surrounding islets) (Fig. 1). Although these islands are geographically close to each other, remarkable differences in their Pliocene and Pleistocene fossil records exist.

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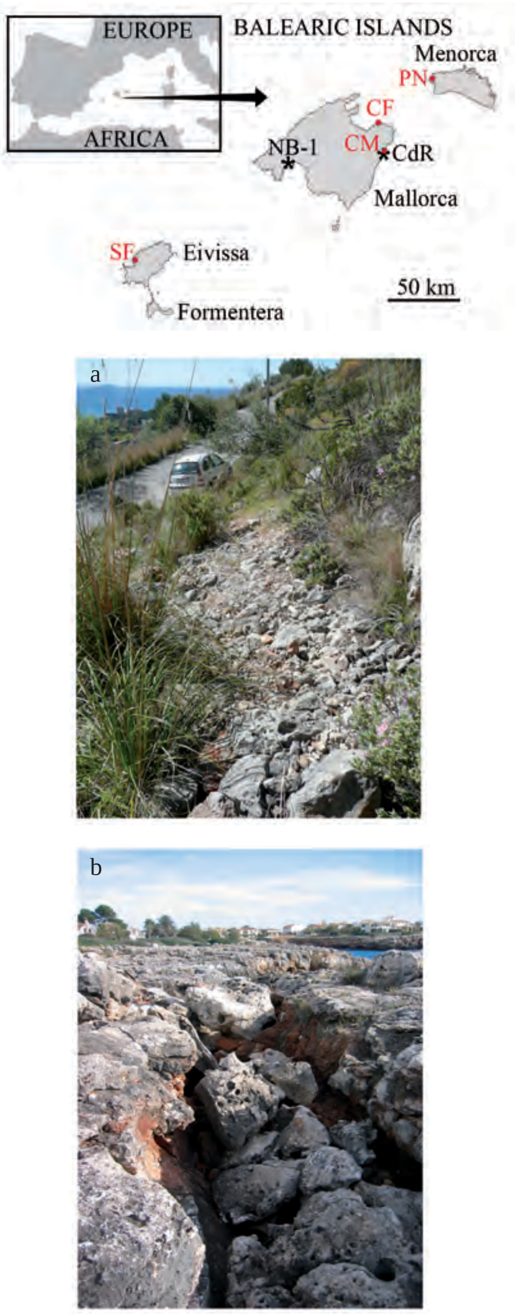

Figure 1 Map and location (top) of the Late Miocene/Early Pliocene interval deposits presented in this paper and Pliocene Balearic deposits mentioned in the text. CdR, Caló den Rafelino; CF, Crull de Cap Farrutx; CM, Cala Morlanda; NB-1, Na Burguesa-1; PN, Punta Nati; SF, Ses Fontanelles. (a) View of the NB-1 deposit. (b) View of the CdR deposit.

Two different insular episodes can be identified in the Miocene to Holocene fossil record of the Balearic Islands (e.g. Alcover *et al.* 1981; Moyà-Solà *et al.* 1999; Bover *et al.* 2008). A first episode has been related to the Langhian–Serravalian regression (Middle Miocene). It has only been recorded in Mallorca and Menorca. The 2 main Mallorcan sites representatives of this episode (Santa Margalida and Sant Llorenç) have yielded remains of a lagomorph (*Gymnesicolagus gelaberti* Mein & Adrover, 1982) and 3 glirids (*Carbomys sacaresi* Mein & Adrover, 1982, *Margaritamys llulli* Mein & Adrover, 1982 and *Peridyromys ordinasi* Mein & Adrover, 1982) (Mein & Adrover 1982; Adrover *et al.* 1985). Other taxa found in pre-Messinian deposits (Cova des Coll and Cova de Cala Varques B; Gràcia *et al.* 1997, 2000) are a large terrestrial tortoise (Testudinidae) and a brackish soft-shell turtle (*Trionyx* sp.) (Bover *et al.* 2008). A related fauna, also belonging to this episode, was recovered from the Menorcan deposits of Punta Nati-2 and Es Cul de sa Ferrada, with *G.* aff. *gelaberti*, *Margaritamys adroveri* Quintana & Agustí, 2007, an undetermined viperid, an undetermined great-sized tortoise, 1 or more small-sized reptiles and a bird (Bailon *et al.* 2002; Quintana & Agustí 2007).

The second episode started at the Messinian Salinity Crisis (MSC) and spreads over all the Plio–Pleistocene. Until the end of the 1990s, the record of terrestrial vertebrates from this episode was mainly represented in Mallorca and Menorca by 3 mammalian evolutionary lineages: a bovid (*Myotragus*), a glirid (*Hypnomys*) and a soricid (*Nesiotites*), together with a lacertid of the genus *Podarcis* (Early Pleistocene to Holocene), and the amphibians *Alytes* (Early Pleistocene to Holocene) and *Discoglossus* (Early Pleistocene) (Alcover *et al.* 1981; Bover *et al.* 2008). The fossil record of the 3 mammalian lineages is remarkably complete throughout the Pliocene to Holocene on Mallorca and throughout the Early Pleistocene to Holocene on Menorca (see Alcover *et al.* 1981; Agustí & Moyà-Solà 1990; Moyà-Solà *et al.* 1999; Bover *et al.* 2008 for further detail on the fauna). In addition, a peculiar Pliocene fauna was known from Menorca, composed of the glirid *Muscardinus cyclopeus* Agustí, Moyà-Solà & Pons-Moyà, 1982, the bat *Rhinolophus* cf. *grivensis* Depéret, 1892 and the giant tortoise *Cheirogaster gymnesica* (Bate, 1914) (Bate 1914; Pons-Moyà *et al.* 1981; Agustí *et al.* 1982).

In Eivissa, a distinctive faunal succession has been observed. The earliest fauna recorded comes from the deposit of Ses Fontanelles. It includes 2 bovids (a caprine and an antilopine), 2 rodents (the gerbillid *Debruijnimys* sp. and the glirid *Eliomys* sp.), a leporid (identified as *Hypolagus* sp. by Quintana *et al.* 2010), an insectivore, a lizard and a tortoise (Moyà-Solà *et al.* 1984, 1999; Agustí & Moyà-Solà 1990). It was attributed to the Late Miocene (Messinian)/Early Pliocene (Moyà-Solà *et al.*

1999; Bover *et al.* 2008). A single deposit from the Late Pliocene/Early Pleistocene of Eivissa is known, Cova de Ca Na Reia, containing 2 glirids (*Eivissia canarreiensis* Alcover & Agustí, 1985 and *Hypnomys* sp.), a tortoise (*Cheirogaster* sp.), a lizard (*Podarcis* sp.), bats and birds (Kotsakis 1981; Alcover & Agustí 1985; Bour 1985; Alcover 1989). Remains of giant tortoises are also known from other Early–Middle Pleistocene deposits from Eivissa and Formentera (Bover *et al.* 2008). Finally, the Late Pleistocene–Holocene deposits from the Pityusic Islands have yielded birds, bats and a lizard (*Podarcis pityusensis* Boscá, 1883), but no other fossil terrestrial vertebrates have ever been recorded from them (Florit *et al.* 1989).

The discovery of Pliocene deposits in Mallorca and Menorca over the past 15 years has improved substantially the knowledge on the paleofauna of the second faunal episode, and it has shed light on the stock that arrived to the islands during MSC, an event that has been situated between 5.6 and 5.32 Ma (Gautier *et al.* 1994; Clauzon *et al.* 1996; Krijgsman *et al.* 1999). In Menorca, several deposits in the northwest coast of the island, in Punta Nati (municipality of Ciutadella, Quintana 1998), yielded a Pliocene fauna coeval to *M. cyclopeus*, *Rhinolophus* cf. *grivensis* and *Cheirogaster gymnesica*. It includes *Nuralagus rex* Quintana, Moyà-Solà, Köhler, 2011, *Vipera natiensis* Bailon, Garcia-Porta & Quintana, 2002, *Vipera* sp., *Coluber* sp., Gekkonidae indet., *Podarcis* aff. *lilfordi*, *Blanus* sp., *Latonia* sp. (Bailon 2004; Bailon *et al.* 2002, 2005; Garcia-Porta *et al.* 2002; Quintana *et al.* 2005, 2011) and several bird species (such as *Pterodromoides minoricensis* Seguí, Quintana, Fornós & Alcover, 2001, *Scolopax carmesinae* Seguí, 1999, *Camusia quintanai* Seguí, 2002, *Tyto balearica* Mourer-Chauviré, Alcover, Moyà-Solà, Pons-Moyà, 1980, *Athene* sp., *Corvus* sp. and an unidentified passeriform [Seguí 1998, 1999, 2002; Seguí *et al.* 2001]).

Early Pliocene fauna from Mallorca have started to be identified over the past decade (Bover *et al.* 2007). In this paper we present an overview of the Mallorcan vertebrate fauna from the Late Miocene/Early Pliocene interval based on the findings from 2 sites, Caló den Rafelino (CdR) (Manacor) and Na Burguesa-1 (NB-1) (Palma). As the work on the NB-1 breccia is now in progress, we only can present here preliminary data on this site, based on the first extracted and identified bones.

MATERIALS AND METHODS

Deposits

Caló den Rafelino

This deposit (Fig. 1b) is located at the eastern coast of Mallorca, at the north of CdR (from where it takes its name) and at the south of Cala Morlanda, in the municipality of Manacor. It was discovered by Josep Quintana and Pere Bover in the spring of 2004 and it was excavated the same year.

The deposit, located 5 m asl, consists of consolidated red silt of karstic origin which are the floor sediment of a collapsed cave in the Upper Miocene limestone of the so-called Reef Complex (Pomar *et al.* 1990; Gómez-Pujol *et al.* 2007) of Late Tortonian–Messinian chronology (Bizon *et al.* 1973). Just a small portion of the sediments (around 1 m^2 at the northeast extreme of the cave sediments) has yielded fossil remains while the rest of the sediment seems to be sterile. The thickness of this red silt is unknown but the structure of the fossil cave and its proximity to the sea (approximately 6 m, and 5 m asl) suggest that it is not very large.

The chronology of the deposit has been indirectly estimated. It postdates the Upper Miocene limestone and characters of some of the taxa, more primitive than those of the fauna present in the later Early Pliocene deposit of Cala Morlanda (Moyà-Solà & Pons-Moyà 1982; Pons-Moyà 1990), suggest that it should be considered as an Early Pliocene deposit, but a Messinian chronology cannot be completely discarded.

The bones obtained from this breccia were mainly broken, worn and eroded.

Na Burguesa-1

It was discovered in Apr 2012 by the Mallorcan speleologists Damià Vicens, Damià Crespí and Antelm Ginard from the Speleo Club Mallorca. The deposit (Fig. 1a) is located at 160 m asl and close to the road from the neighborhood of Génova to the Mirador de Na Burguesa, at the municipality of Palma. The original location of the breccia has not been found, as the findings are blocks extracted from the original site and used to facilitate the access to a small house, but it is probably close to or under a small construction of the Mallorcan water company EMAYA built in the slope of the mountain.

The breccia is constituted by brown–red silts and, geologically, it was in a cave or fissure excavated in the Lower Lias sediments present in the area. The obtained fauna is related to that from CdR and both can be considered as chronologically close, with CdR being slightly more recent than NB-1. Further study of the fauna will shed more light on the NB-1 deposit chronology. After obtaining the relevant permits from the Mallorcan Government, several large blocks were recovered and the bones extracted. The obtained bones are in better condition than those from CdR.

Bone extraction

The obtained breccias from CdR and NB-1 were treated or are currently being treated (NB-1) with acetic acid to extract the bones. Cycles of consolidation of the bones with Paraloid-B67 (5%), treatment with acetic acid (10%, 48 h) and fresh water immersion (7 days) have been used. The breccia from NB-1 is much richer than that from the CdR.

Geological nomenclature

In this paper we use the nomenclature for the Pliocene and Pleistocene presented by Gibbard *et al.* (2010), following the International Union of Geological Sciences (IUGS) updated chronology of the base of the Quaternary.

Measurements/nomenclature

Teeth nomenclature: lowercase letters are used ('m' for molar and 'p' for premolar) for lower teeth and uppercase letters for upper teeth. Measurements of reptile bones were taken with an electronic digital calliper (accuracy 0.01 mm) on bone projections using a camera lucida.

SYSTEMATIC PALEONTOLOGY

In this section, a complete list of the fauna so far obtained from CdR is presented. For NB-1, just some preliminary remarks on the fauna of the deposit will be furnished because it is currently being processed, and additional taxa could be obtained. Furthermore, as yet, only a small sample of amphibians/reptiles from NB-1 has been analyzed.

Fishes

Several fish teeth have been recovered from the CdR deposit. The taxonomical composition of this fish fauna is currently being studied (D. Vicens & P. Bover, unpubl. data). The presence of fish teeth in a mainly terrestrial faunal deposit is intriguing. Their incorporation at the site deposition may be related to some bioaccumulator agent (such as a seabird).

Birds

A single bird bone (proximal fragment of a humerus) has been obtained from the CdR (unidentified bird). Bird bones are also present in NB-1.

Amphibians

Order Anura Fischer von Waldheim, 1813

Family Bufonidae (?) Gray, 1825

Material: 1 sacral vertebra (NB-1).

The vertebra is procoelous and it bears an anterior cotyle and 2 clearly separated posterior condyles. The sacral processes are only moderately widened anteroporteriorly. The centrum is relatively short and, in dorsal view, a small pit occurs at the base of each sacral process. This combination of characters suggests referral to the Bufonidae (e.g. Sanchiz 1977; Bailon & Hossini 1990; Bailon 1999), but such an attribution cannot be made without reservation. If recovery of further material shows that assignment to the Bufonidae is accurate, then this anuran would be the first fossil record of the family in the Balearic Islands, as the presence of the extant species *Bufo balearicus* (Boettger, 1880) in these islands is the consequence of a recent human introduction (Hemmer *et al.* 1981; Pinya & Carretero 2011).

Reptiles

Order Chelonii Linnaeus, 1758

Material: 2 terminal phalanges (IMEDEA 90102, 90103) (CdR), 1 phalange and shell plates (NB-1).

Two terminal phalanges probably belonging to a large-sized terrestrial tortoise (Testudinidae) have been recovered from CdR. A phalange and shell fragments of a tortoise have been obtained from NB-1.

Order Squamata Opell, 1811

Family Gekkonidae Gray, 1825

Material: 1 fragment of right dentary (NB-1).

The presence of a Meckel's groove entirely surrounded by the dentary and of numerous pleurodont, cylindrical and monocuspid teeth allows the attribution of this dentary to the Gekkonidae. However, a more precise identification is not possible. Bailon *et al.* (2005) described remains of gekkonids from the Pliocene of Menorca.

Family Lacertidae Batsch, 1788

Maioricalacerta rafelinensis Bailon, Boistel, Bover & Alcover, 2014

Material: 1 left fragmented dentary (IMEDEA 90107), 1 right dentary fragment (IMEDEA 90109), 2 left maxilla fragments (IMEDEA 90105, 90106), 1 caudal vertebra (IMEDEA 90260) (CdR).

Remains of a large-sized lacertid were recovered from the CdR deposit. This lizard displays short and robust dentaries having a thick lateral wall, a reduced number of tooth positions (13) and amblyodont teeth. It has been described as a new genus and species, *Maioricalacerta rafelinensis* (Bailon *et al.* 2014).

Lacertidae, unidentified genus and species

Material: 1 left fragmentary maxillary (NB-1).

The presence of cylindrical, pleurodont and bicuspid teeth, with a well developed central cusp and a small anterior cusp, permits attribution of this maxilla to the Lacertidae (Barahona & Barbadillo 1997). This family is known in the Balearic Islands since the Middle Miocene of Menorca (Bailon 2004).

Family Scincidae Gray, 1825

cf. *Chalcides* Laurenti, 1768

Material: 1 right dentary (NB-1) (Fig. 2g).

The dentary, comprised of 2 fragments, has an approximate length of 4.7 mm, thus belonging to a small-sized individual. In medial view, Meckel's canal is open throughout the dentary, but in its anterior half it narrows and it is located medioventrally. The mandibular symphysis is reduced. The subdental table, the ventral margin of the bone and the dental crest are slighltly curved and they give an elongated appearance to the dentary. In lateral view, 6 dental foramina can be observed and, posterodorsally, there is no coronoid impression on the lateral wall of the dentary. Teeth are pleurodont, monocuspid, cylindrical and they have blunt apexes. Medially, each apex displays a series of small vertical ridges. The dentary has 19 teeth. The morphology of this dentary fits into the general morphological pattern observed in the small-sized individuals of *Chalcides* (Barbadillo 1989; Bailon 2000; Blain *et al.* 2007, 2008; Blain 2009).

In the fossil record of the Balearic Islands, Boulenger (in Bate 1918) mentioned *Chalcides* sp. from a currently unknown deposit from Menorca. Thus, the identification of *Chalcides* in NB-1 deposit could confirm the presence of skinks on these islands during the Late Miocene/Early Pliocene interval.

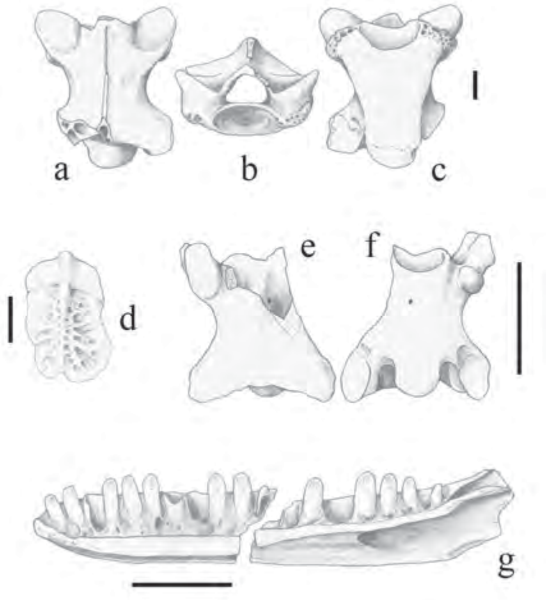

Figure 2 Several reptiles from the Mallorcan Late Miocene/Early Pliocene deposits: (a–c) dorsal vertebra of *Dopasia* sp. from CdR (IMEDEA 90115) in dorsal (a), anterior (b) and ventral (c) views; (d) osteoderm in dorsal view *Dopasia* sp. from NB-1; (e,f) dorsal vertebra of Scolecophidia from NB-1 in dorsal (e) and ventral (f) views; and (g) right dentary of Scindidae cf. *Chalcides* from NB-1 in medial view. Scale bars equal 1 mm.

Family Anguidae Gray, 1825

Dopasia Gray, 1853

Material: 1 trunk vertebra, IMEDEA 90115 (CdR, Fig. 2a–c); 1 fragment of dentary, 1 trunk vertebra, 3 caudal vertebrae and 2 osteoderms (NB-1, Fig. 2d).

A medium-sized vertebra (centrum length = 4.3 mm) from CdR displays a characteristic anguid morphology and it is tentatively attributed to *Dopasia*. It is procoelous, depressed, moderately elongated and its cotyle and condyle are dorsoventrally flattened. The ventral surface of the centrum is sub-triangular and slightly convex in transverse section; the lateral margins of the centrum diverge anteriorly and are slightly concave laterally. The neural spine, partially broken, is moderately robust in its posterior half. No zygosphene–zygantrum, precondylar constriction and hemal keel can be observed on the vertebra.

When compared with the different anguids known from the Neogene of mainland Europe, the CdR vertebra displays size and morphological characteristics observed in *Dopasia* (*sensu* Augé 2005; i.e. European species formerly included in *Ophisaurus* s.l. and *Pseudopus* excluded), but a more precise attribution is not possible. In *Anguis*, the lateral margins of the centrum are mainly parallel and the vertebrae are slightly smaller, whereas in *Pseudopus* the vertebrae size is greater and the lateral margins of the centrum are markedly more divergent than in the CdR vertebra (Estes 1983; Roček 1984; Bailon 1989, 1991; Augé 2005; Blain 2009; Delfino *et al.* 2011).

To our knowledge, this is the first record of a member of the Anguidae in the Balearic Islands. On islands, *Dopasia* is only known from the Late Pliocene (MN16) of Sardinia (Delfino *et al.* 2011), whereas on the European continent, the genus has been recorded from the Oligocene to the Early Pleistocene (Augé 2005; Blain 2009; Blain & Bailon 2010). Today, the genus is restricted to Asia. No extant anguids currently live in the Balearic Islands.

The material obtained from NB-1 deposit confirms the presence of *Dopasia* (*sensu* Augé 2005) in the Mallorcan Pliocene. The studied dentary fragment displays a tooth that is subpleurodont, slightly hook-shaped and unicuspid; the apex lacks ridges and it is directed postero-medially. The trunk vertebra is procoelous, with dorsoventrally depressed cotyle and condyle. Its centrum is subtriangular, with a smooth ventral surface that is slightly convex in transverse section, and with slightly concave and anteriorly divergent lateral margins. The caudal vertebrae display 2 pairs of transverse processes, each being partly subdivided longitudinally by an autotomic septum and, in the posterior third of the vertebra, haemapophyses fused to the centrum. The osteoderms are simple, with a smooth basal area and with an external area displaying vermicular ornamentation. One of the osteoderms has lateral margins that are slightly beveled and a longitudinal keel typical of the mediodorsal osteoderms. All these characteristics allow the attribution of this fossil material to *Dopasia* and also differentiate it from the other anguids known for the European fossil record (Estes 1983; Roček 1984; Bailon 1989, 1991; Augé 2005; Blain 2009).

Infraorder Scolecophidia Dumeril & Bibron, 1844

Material: 1 vertebral trunk (NB-1) (Fig. 2e–f).

The vertebra is very small with a centrum length slightly longer than 1 mm. It is dorso-ventrally compressed, with a simple morphology typical of this group of snakes (flattened neural arch, without neural spine and posterior medial notch; narrow centrum without hemal keel; dorsoventrally flattened cotyle and condyle; well developed subcentral foramina, but paracotylar foramina absent; and prezygapophyseal processes present and synapophyses not divided) (Rage 1984; McDowell 1987).

Within this group of snakes, the morphology of the vertebrae is highly homogeneous and the taxonomical identification, even at family level, is particularly difficult. Scolecophidia have been recorded in the Early Paleocene from Hainin (Belgium) (Vidal *et al.* 2009), and in the Early Pleistocene of the Illes Medes (Spain) (Bailon 1991). The vertebra from NB-1 deposit is the first and sole record of this group in the Balearic Islands. *Typhlops vermicularis* Merrem, 1820 is the only known extant Scolecophidia in Europe (Montenegro, Greece, Albania, Macedonia and Bulgaria) (Gasc *et al.* 1997).

Family Colubridae Opell, 1811

'Colubrinae' type

Material: 2 vertebral trunks (IMEDEA 90114 and 90261), 3 fragments of centra (IMEDEA 90267, 90269 and 90270) (CdR); 1 vertebral trunk (NB-1).

The vertebrae from CdR belong to small-sized individuals, with a centrum length less than 4 mm. The vertebrae are slightly longer than wide; their neural spine and posterior notch are well developed. They display rounded cotyle and condyle; paracotylar foramina are present and the centrum is subtriangular and bears a well marked off hemal keel. These characteristics allow the attribution of these vertebrae to a Colubridae of 'colubrinae' type (*sensu* Szyndlar 1991). The preservation of the vertebrae (partly fragmented and eroded) does not allow further identification.

The sole vertebra from NB-1 studied here is from a medium-sized individual (centrum length = 4.5 mm). It is slightly longer than wide (ratio centrum length/interzygapophyseal width = 1.3) and it does not display a hypapophysis. These 2 characters allow us to refer to this vertebra as a colubrid of 'Colubrinae' type (*sensu* Szyndlar 1991). The centrum is narrow, with well-defined subcentral ridges and a well developed hemal keel. The zygapophyses are rectangular and arranged on the horizontal plane. The prezygapophyseal processes are cylindrical, blunt and shorter than the prezygapophyses. The cotyle and condyle are small and rounded. The diapophyses are located more posteriorly than the parapophyses. In posterior view, the neural arch is vaulted, its dorsal edges being slightly convex. Together with the vertebrae from CdR, the colubrid from the NB-1 deposit displays a vertebral morphology similar to that of the material described from the Menorcan Pliocene, and attributed to '*Coluber*' sp. [*Coluber dolnicensis* Szyndlar, 1987: *Coluber pouchetii* (Rochebrune, 1880) group] (Bailon *et al.* 2005); therefore, they probably represent the same taxon.

Family Viperidae Laurenti, 1768

Vipera Laurenti, 1768 **(Oriental Vipers Complex)**

Material: 1 middle trunk vertebra (IMEDEA 90113), 1 cervical vertebra (IMEDEA 90116) (CdR). Tentatively, 2 vertebrae from NB-1.

Bailon *et al.* (2010) study 2 vertebrae of a large snake obtained from the CdR deposit. The combination of characters, such as straight hypapophysis, posteriorly depressed neural arches, zygapophyseal articular facets inclined dorsally, parapophyseal processes directed anteroventrally, large condyles and cotyles, relatively short centrum and condyle ventrally attached to the hypapophysis basis, allowed these authors to assign these vertebrae to a member of the Viperidae: more specifically, to the 'Oriental Vipers Complex' (according to the classification suggested by Szyndlar & Rage 1999). Based on the size of the centrum, a body length close or even greater than 200 cm was estimated for this viper; it may be considered the largest European viper belonging to this complex. Two viperid vertebrae obtained in NB-1 could belong to the same or to a related taxon.

cf. *Vipera natiensis* Bailon, Garcia Porta & Quintana, 2002

Material: 1 anterior trunkal vertebra or cervical vertebra (IMEDEA 90264) (CdR).

The vertebra belongs to a small-sized individual, with a centrum slightly longer than 2 mm. In posterior view, the neural arch is dorsoventrally flattened. The articular surfaces of the zygapophyses are inclined laterodorsally, and the prezygapophyseal processes are short and blunt. The vertebral centrum is markedly convex ventrally in transverse section; it bears a hypapophysis and its subcentral ridges are somewhat indistinct. These characters suggest that this vertebra could belong to a viper close to *V. natiensis* that was described by Bailon *et al.* (2002) from the Pliocene of Menorca.

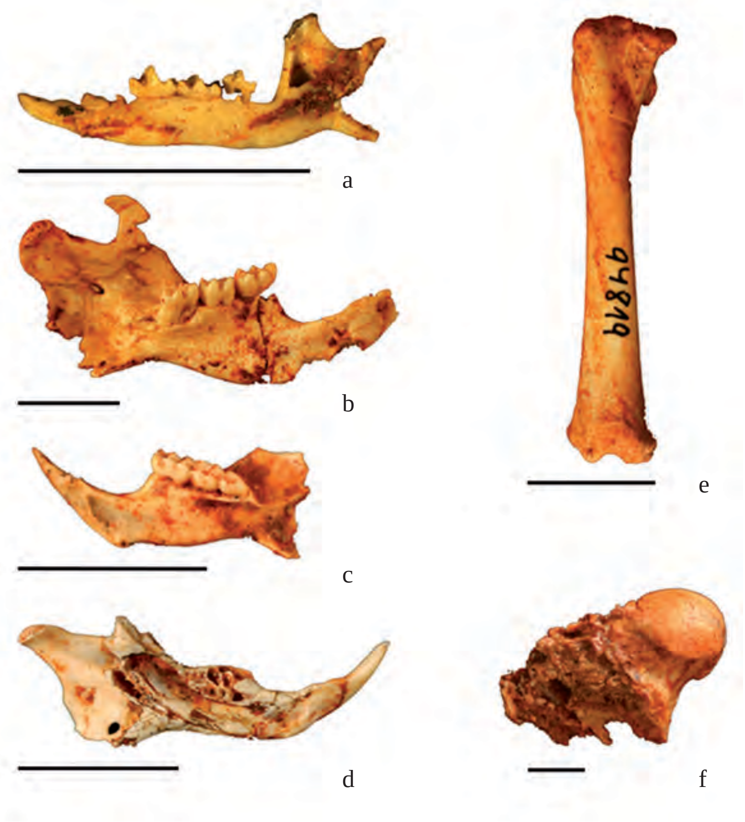

Figure 3 Mammalian species obtained in NB-1: (a) Soricinae indet., jaw, lingual view, (b) Cricetinae indet., jaw, lingual view, (c) Muridae indet., jaw, lingual view, (d) *Eliomys*/*Hypnomys*, jaw, lingual view, (e) cf. *Hypolagus*, femur, frontal view and (f) cf. *Myotragus*, proximal epiphysis of a right femur, frontal view. Scale bars equal 1 cm.

Mammals

Order Eulipotyphla Waddell, Okada & Hasegawa, 1999

Family Soricidae Fischer von Waldheim, 1817

Subfamily Soricinae Fischer von Waldheim, 1817

Nesiotites rafelinensis Rofes, Bover, Cuenca-Bescós & Alcover, 2012

Material: 1 incomplete left mandible with p4, m1, m2, and m3 (IMEDEA 91950) (CdR).

The material obtained from CdR was used by Rofes *et al.* (2012) to describe a new species of *Nesiotites*, *Nesiotites rafelinensis*. Although the species is based on a single mandible, it displays enough diagnostic features to be distinguished from the other remaining *Nesiotites* species. A combination of characteristics, including teeth size, mandible size, absence of accessory cusps on the oblique crest of the first and second lower molars, inconspicuous cuspule and lingual crest on the lingual basin of the p4, broad and pronounced buccal and lingual cingula of the lower teeth, slightly undulated buccal cingulum and slightly forward placement of the mental foramen, allowed the description of *N. rafelinensis* as a new species. Thus, this species combines primitive dental traits with a relatively large size.

Soricinae unidentified

Material: 2 fragmented skulls, 2 mandibles, and some postcranial bones (NB-1).

The insectivore remains are here provisionally attributed to *Nesiotites/Asoriculus* (Fig. 3a). The absence of accessory cusps in m1–m2, the almost straight buccal cingulum and the forward position of the mental foramen are typical of both groups (i.e. *N. rafelinensis* and *Asoriculus gibberodon* Petényi, 1864).

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer von Waldheim, 1817

Tragomys macpheei Agustí, Bover & Alcover, 2012

Material: 1 right m1 (IMEDEA 90614, holotype), 17 cheek teeth, 2 incisors, 3 mandible fragments, 2 maxillae fragments, 9 fragments of postcranial long bones, 1 calcaneum and 1 astragalus (see Agustí *et al.* [2012] for an extensive list of material) (CdR).

Agustí *et al.* (2012) describe a new genus and a new species of Cricetidae based on the material obtained from CdR, *Tragomys macpheei*. It displays a large size, and a distinctive selenodont pattern and hypsodont teeth.

Cricetinae unidentified

Material: Currently, approximately 200 bones, complete or fragmented, including 10 mandibles, 3 maxillae, complete femora, humerus, radius, tibia and a partial skull, representing most of the elements of the skeleton (NB-1).

Remains of a large-sized cricetine with slightly selenodont and hypsodont dentition have been recovered in the NB-1 (Fig. 3b). Most probably, it corresponds to the putative ancestor of *T. macpheei*.

Family Muridae Illiger, 1811

Muridae unidentified

Material: 3 mandibles, 1 maxillar, 1 humerus and 1 femur (NB-1).

Another slightly hypsodont small rodent has been recorded in the NB-1 deposit (Fig. 3c). The absence of the anterior accessory cusp (tma) and the poorly marked stephanodonty in the teeth studied allows the attribution of these remains to a derived species of *Occitanomys* or *Castillomys*, but additional analysis is needed to go further in the identification.

Family Gliridae Thomas, 1897

***Hypnomys* sp.**

Material: 1 m1 (IMEDEA 90622) and 1 M1 (IMEDEA 90623) (CdR).

In addition to *T. macpheei*, a second rodent species is present at CdR. This second species corresponds to a very early member of the dormice genus *Hypnomys*. Because the scanty material does not permit us to make inferences about its specific identity, we will refer to it as *Hypnomys* sp. (Fig. 4). In the upper first molar, a continuous endoloph connects the anteroloph, protoloph, metaloph and posteroloph (Fig. 4b). The anterior centroloph is labially fused to the protoloph. The paracone is not individualized as a cusp, nor is the metacone. An anterior extra ridge is present between the protoloph and the anterior centroloph. The posterior centroloph is fused to the metaloph. The lingual ends of the anterior and posterior centrolophs are fused. It presents 3 roots, 2 labials and 1 very wide lingual root. In this way, *Hypnomys* sp. from CdR looks very much to be the oldest species of the *Hypnomys* described from Mallorca and Menorca, such as *Hypnomys waldreni* Reumer, 1979, *Hypnomys onicensis* (Reumer, 1994) and *Hypnomys eliomyoides* Agustí, 1980 (Reumer 1979, 1981; Agustí 1980). However, it differs from these old *Hypnomys* species by the still *Eliomys*-like narrow M1 and m1. Its dimensions (first m1: 1.82 × 1.96 mm; first M1: 1.62 × 1.64 mm) are also lower than those of other *Hypnomys* species, and closer to those of the Late Miocene *Eliomys*, such as *Eliomys intermedius* Friant, 1953 and *Eliomys truci* Mein & Michaux, 1970. However, the dormouse from CdR differs significantly from *Eliomys* because the upper molar presents much less prominent labial cusps, as it is also the case in *Hypnomys*.

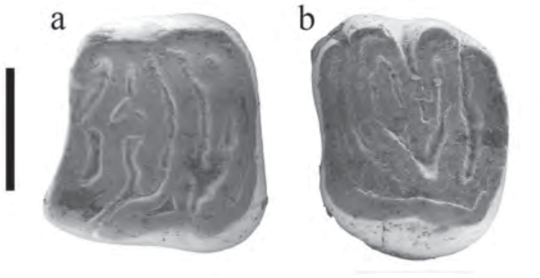

Figure 4 Occlusal view of the 2 teeth of *Hypnomys* sp. retrieved from the Caló den Rafelino deposit: (a) IMEDEA 90622, left m1 and (b) IMEDEA 90623, left M1. Scale bar equals 1 mm.

Eliomys*/*Hypnomys sp.

Material: Abundant material, including currently approximately 300 bones representing most of the elements of the skeleton (NB-1).

The glirid present in NB-1 (Fig. 3d) is small. It most probably represents the ancestor of, or an ancestral species inside, the *Hypnomys* lineage.

Order Lagomorpha Brandt, 1855

Family Leporidae Gray, 1821

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

Material: 1 left p3 (IMEDEA 90123, Holotype), 10 cheek teeth, 1 incisor, 5 postcranial bones (see Quintana *et al.* [2010] for an extensive list of material) (CdR). Here, 20 juvenile bones (NB-1) are tentatively attributed to *Hypolagus*, as cf. *Hypolagus*.

The first record of *Hypolagus* in the Balearic Islands is reported by Quintana *et al.* (2010). These authors describe a new species, *Hypolagus balearicus*, based on tooth characteristics and some postcranial features. The p3 of *H. balearicus* displays a small size, trapezoidal outline, with a shallow and well-marked anteroflexid, shallow protoflexid, deep hypoflexid and lack of paraflexid. All these characteristics allow the differentiation of the Mallorca species from the other species of *Hypolagus*. In addition, more robust postcranial bones are observed in this species. The presence of *Hypolagus* in the Balearic Islands represents one of the westernmost European records of the genus. The fossils obtained in

NB-1 (Fig. 3e) include complete bones of juveniles that are here tentatively attributed to *Hypolagus*.

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Myotragus palomboi Bover, Quintana & Alcover, 2010

Material: 1 right metatarsal (IMEDEA 90140, Holotype), 4 cheek teeth, 2 incisiforms, 12 postcranial bones (see Bover *et al.* [2010] for an extensive list of material) (CdR); 2 bones and 1 tooth of a juvenile bovid (NB-1) are here tentatively attributed to *Myotragus*, as cf. *Myotragus* (Fig. 3f).

The earliest representative of *Myotragus*, *Myotragus palomboi*, is described by Bover *et al.* (2010). It displays relevant similarities that allow its attribution to *Myotragus*, but there are remarkable differences between *M. palomboi* and the former earliest species of *Myotragus*, *Myotragus pepgonellae* Moyà-Solà & Pons-Moyà, 1982. The CdR *Myotragus* has a larger p2, with no hypsodont nor ever-growing incisors, with more rectangular wear surface and with enamel surrounding the whole crown (and not elongated incisors as in the other *Myotragus* species), and a lower robustness index of the studied postcranial bones than in *M. pepgonellae*. Specifically, the metatarsal bone is longer than the other representatives of the genus and its morphology seems to be intermediate between *M. pepgonellae* and the putative mainland ancestors *Aragoral* and *Norbertia*.

DISCUSSION

Insular environments are characterized by unbalanced faunas with a reduced number of endemic species displaying morphological traits that follow well-described patterns (the so-called 'insularity syndrome'). The faunal record of the 2 Mallorcan deposits presented here partially agrees with this insular pattern. So far, in none of these deposits have carnivores been obtained, and the number of recorded species is reduced (5 mammals and 6 reptiles in CdR, and 6 mammals, at least 8 reptiles and 1 amphibian in NB-1).

Morphological traits observed in some taxa suggest that the fauna from CdR and NB-1 would be in an early stage of its isolated evolution. The species of the fauna from CdR displays more derived characters than those from NB-1. In this sense, the large size of *Tragomys*, the reduction of the premolar size observed in *M. palomboi* (a progressive loss of teeth is considered an insular evolutionary effect in the *Myotragus* lineage [Alcover *et al.* 1981]) and the characteristic selenodont teeth pattern of *T. macpheei* suggest the beginning of an isolated evolution. The glirid, the soricid and the murid are only slightly modified, suggesting also a proximity to the isolation event. In contrast, although *H. balearicus* p3 has a relatively smaller size when compared to other species of *Hypolagus*, the scarce postcranial bones available do not allow determination of whether insular evolutionary effects occurred in the species.

According to Bailon *et al.* (2010), the large size of *Vipera* sp. ('Oriental Vipers Complex') from CdR cannot be explained in terms of insular evolution itself but as the result of a co-evolutionary process between this group of snakes and the size of the prey. In addition, as the mainland ancestor of this snake is unknown, no definitive inferences on dwarfism or gigantism can be made. The same accounts for the remaining reptiles and for the amphibian.

The faunal composition of NB-1 and CdR represents a faunal assemblage that could be related to the colonization pattern. It has been widely accepted that the arrival of the faunal stock recorded for the Plio–Pleistocene in the Balearic Islands occurred during the MSC (Agustí *et al.* 2006; van der Made *et al.* 2006; Bover *et al.* 2008 and references therein), around 5.6–5.32 Ma ago (Gautier *et al.* 1994; Clauzon *et al.* 1996; Krijgsman *et al.* 1999). While the founder stock of terrestrial vertebrates was initially thought to be composed in Mallorca of the ancestors of *Myotragus*, *Hypnomys* and *Nesiotites* lineages together with a reptile (*Podarcis*) and 2 amphibians (*Alytes* and *Discoglossus*), the discovery of the 2 deposits studied in this paper allows the reporting of a different scenario, and sheds light in the understanding of the Late Miocene/Early Pliocene faunal assemblage from the Eivissan deposit of Ses Fontanelles.

In Fig. 5, a schematic view of the faunal succession of terrestrial vertebrates from the Balearic Islands throughout Late Miocene/Early Pliocene to Holocene is presented. Although further analysis of the NB-1 fauna is necessary, if we roughly compare the taxonomical groups (rather than taxa at genus/species level) recorded in the several Pliocene deposits from these islands, the Mallorcan deposits of NB-1 and CdR share 5 species or close relatives of the 6 mammals and at least 4 reptiles (a tortoise, *Dopasia*, *Vipera* sp. OVC, and a colubrine), and, therefore, may be considered deeply related. In addition, 4 of the mammalian taxa and probably 2 reptiles are shared by the Mallorcan and Eivissan deposits, suggesting that the fauna from Ses Fontanelles is also related to the same colonizer stock. The differences in taxa composition may be related to an insufficient fossil record or/and to taphonomical reasons. Nevertheless, a more extensive study of the Mallorcan and Eivissan Pliocene fauna is required to confirm the relationship between these deposits.

A clear relationship cannot be established between the Late Miocene/Early Pliocene Mallorcan fauna and the Pliocene (*sensu lato*) Menorcan fauna. The mammals present in the Pliocene deposits from Menorca, *N. rex* and *M. cyclopeus*, can be clearly distinguished from the lagomorph and glirid, respectively, present in NB-1,

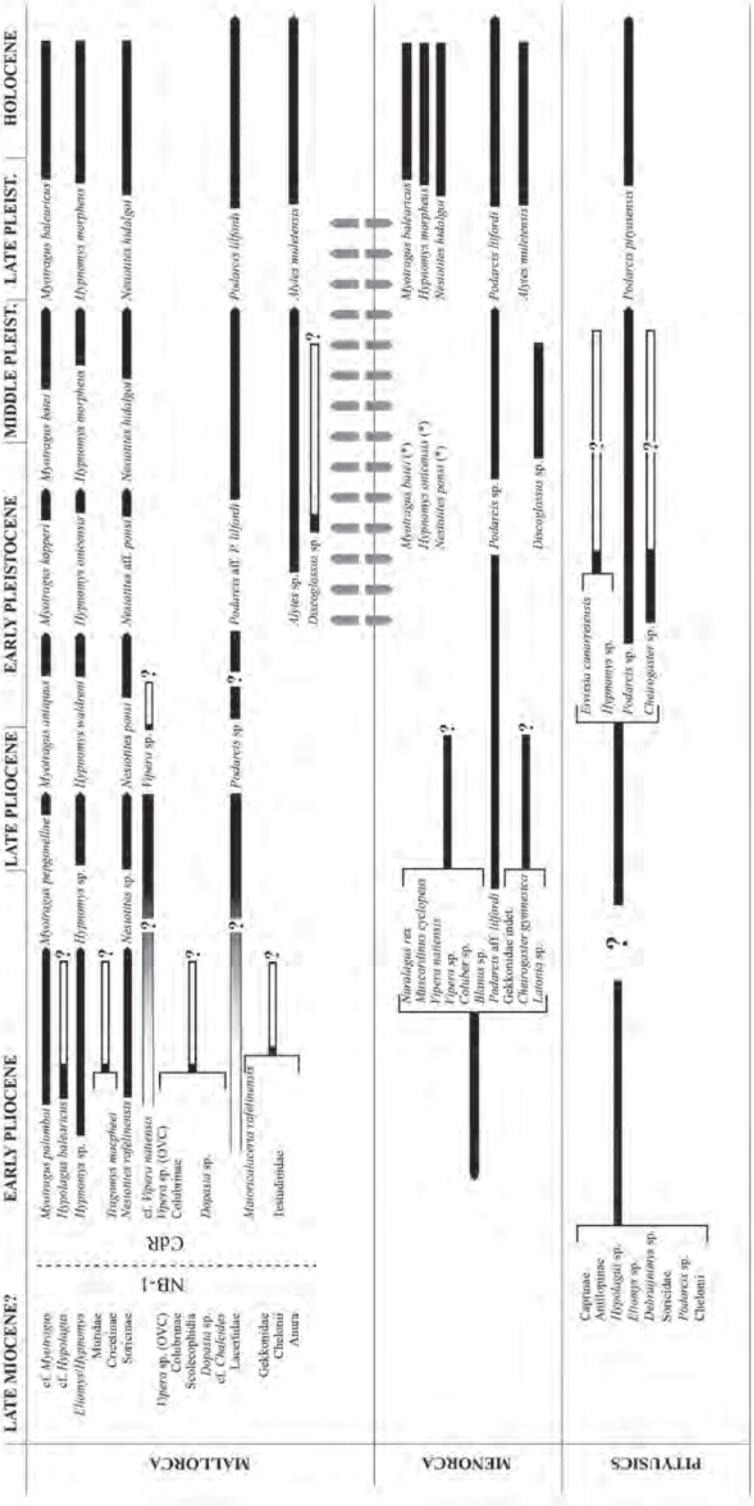

Figure 5 Diagram of the Late Miocene/Early Pliocene to Holocene vertebrate terrestrial fauna from the Balearic Islands. *The taxonomical identity of the described species from Menorca *Myotragus binigausensis* Moyà-Solà & Pons-Moyà, 1980, *Hypnomys eliomyoides* Agustí, 1980 and *Nesiotites meloussae* Pons-Moyà & Moyà-Solà, 1980 is unclear and is under discussion (Reumer 1982; Bover & Alcover 2000; Moyà-Solà *et al.* 2007; Pons-Monjo *et al.* 2012). Here we consider these species as being synonymous with the Mallorcan coetaneous taxa, following Bover *et al.* (2008). Gray arrows indicate contacts between Mallorca and Menorca during Quaternary glaciations.

CdR and Ses Fontanelles deposits, and although some of the reptiles could be similar (Gekkonidae, small Lacertidae) or may even be the same taxa (*V. natiensis*, Colubrinae), further discoveries and analyses are necessary to definitively establish or reject a relationship among these faunas.

The knowledge on the Pliocene vertebrate fauna from Mallorca has been improved thanks to the discovery of the deposits of NB-1 and CdR (Fig. 5). More species than previously thought arrived to the Balearic Islands during the MSC. At least 6 mammals and 8 reptiles colonized Mallorca during this period. Most of them became extinct during the Pliocene. In Mallorca, just 3 mammalian species have been recorded in the later Early Pliocene deposits (*M. pepgonellae*, *Hypnomys* sp. and *Nesiotites* sp., Moyà-Solà & Pons-Moyà 1982; Pons-Moyà 1990). Remains of a *Vipera* related to *V. natiensis* (S. Bailon & P. Bover, unpubl. data) and of *Podarcis* have been recovered in the Late Pliocene deposit of Crulls de Cap Farrutx (in addition to the 3 mammalian lineages with the species *Myotragus antiquus* Pons-Moyà, 1977, *H. waldreni*, and *Nesiotites ponsi* Reumer, 1979).

The presence of a remarkable number of reptiles in the Messinian–Early Pliocene fossil record of the Balearic Islands seems to agree with the subtropical climate conditions, as recorded over the Mediterranean area (see Fauquette *et al.* 1999; Jiménez-Moreno *et al.* 2010). Although an increase in hypsodonty has been recorded in insular species and it is considered as part of an 'island syndrome' (e.g. Jordana *et al.* 2012), the very hypsodont dentition of *M. palomboi* and the hypsodont and selenodont dentition of *T. macpheei* might indicate the consumption of sclerophyll plants. The amblyodont dentition of *M. rafelinensis* from CdR could have also been an important selective advantage for feeding on particularly hard shell molluscs in the warm and dry climate during the earlier Early Pliocene, as the shell of molluscs is known to be harder and wider in arid conditions (Sacchi & Testard 1971).

The absence of carnivores in this fauna leaves the large *Vipera* sp. ('Oriental Vipers Complex'), together with birds of prey, as a main predator for the Mallorcan Pliocene fauna.

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Closing the gap: New data on the last documented *Myotragus* and the first human evidence on Mallorca (Balearic Islands, Western Mediterranean Sea)

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Abstract

The chronology of the extinction of the Balearic fossil bovid *Myotragus balearicus* in Mallorca and Menorca has been under discussion since its discovery in 1909, and especially in the last decades, thanks to the radiocarbon dates that have been obtained from several deposits of the island of Mallorca. Here, we present new radiocarbon dates of *M. balearicus* bones (including the most recent date ever obtained for the species, 4035 ± 32 BP, 2830–2470 cal. BC) that together with a newly published radiocarbon date for the evidence of the first human presence in the island (introduced Caprinae bone, 3884 ± 36 BP; 2470–2210 cal. BC) allow us to reduce the uncertainty period for the *Myotragus* extinction (UPME) in Mallorca from 1660 to 620 years ($p > 95\%$) or even to 350 years ($p > 90\%$) and to reject the hypotheses suggesting a climate change–driven (i.e. non-human) extinction of the species. This new scenario points to the causal relationship between the first human arrival and the *M. balearicus* extinction. The chronological gap between the earliest documented *M. balearicus* and the first documented human presence represents one of the shortest time periods documented between endemic megafauna and humans on any Mediterranean island.

Keywords

extinction, first human, Holocene, last megafauna, Mediterranean islands, radiocarbon dates

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Introduction

The causes of the extinction of endemic island mammals are a widely debated topic. The first arrival of humans onto the islands is usually considered a key factor to understand island extinctions. On some islands (e.g. Madagascar, West Indies, Sardinia), archaeological evidence exists of the contact between the first human settlers and endemic mammals (e.g. Van der Geer et al., 2010), while on other islands the evidence remains elusive. On the Mediterranean Islands, all the endemic insular mammals found in the fossil record have become extinct, except *Crocidura zimmermanni* in Crete (Reumer, 1996), *Crocidura sicula* in Sicily (Hutterer, 1991) and *Mus cypriacus* in Cyprus (Cucchi et al., 2006). Although there is a solid archaeological record documenting the survival of different small mammals until historical times (e.g. *Prolagus sardus*, *Microtus henseli, Rhagamys orthodon* on Sardinia; Vigne, 1992, 1999; Vigne and Alcover, 1985), no evidence of the contact between humans and the large autochthonous endemic mammals exists on the Mediterranean Islands, although it has been repeatedly claimed (e.g. *Myotragus* in Mallorca (Waldren, 1982), *Phanourios* in Cyprus (Simmons, 1999, 2013) and *Megaloceros* in Sardinia (Sondaar et al., 1986; Sondaar and Van der Geer, 2000)).

The extinction of *Myotragus* has been analysed by Burleigh and Clutton-Brock (1980) and Bover and Alcover (2003). Ramis and Alcover (2004) critically reviewed the ^{14}C available data and applied ‘hygienic’ protocols (sensu Anderson, 1991; Spriggs, 1989; Spriggs and Anderson, 1993) to the chronology and documentation available and established that the existing gap between the last documented presence of the endemic large mammals and the first documented presence of humans was *c.* 2400 years in Cyprus, *c.* 7550 in Crete, at least 5250 in Sardinia and *c.* 1660 in Mallorca. The latter was derived from the ^{14}C ages BM-1408 (documenting the last known presence of *Myotragus* after 3700 cal. BC; Burleigh and Clutton-Brock, 1980) and KIA-17389 (documenting the earliest human presence, prior to 2040 cal. BC; Calvo and Guerrero, 2002). This gap (3700–2040 cal. BC) represented the so-called ‘uncertainty period for the *Myotragus* extinction (UPME)’ on this island (Bover and Alcover, 2003).

Recent research on the chronology of the extinction of large mammals on other Mediterranean islands reduced the gap presented

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by Ramis and Alcover (2004) between the last documented presence of the endemic large mammals (e.g. Benzi et al., 2007; Zazzo et al., 2015) and the first documented presence of humans (e.g. Dawson, 2013; Phoca-Cosmetatou, 2011; Phoca-Cosmetatou and Rabett, 2014; Vigne, 2015; Vigne et al., 2009; Zazzo et al., 2015). Excluding charcoal-based radiocarbon dates – as recommended by different authorities and as we are proceeding here – and using 2σ intervals for calibrate dates, the gap between first humans and last representatives of the Mediterranean insular megafauna exceeds currently one millennium in all cases.

With the gap between the last evidence of *Myotragus* presence and the first evidence for human presence established by Bover and Alcover (2003), the causes for the *Myotragus* extinction have been subject to debate. While some authors concluded that both events were causally related (e.g. Bover and Alcover, 2003), others considered that the extinction of *Myotragus* was related to some ecological changes of climatic – non-anthropic – origin that took place slightly after 3700 BC (e.g. Lull et al., 1999, 2008: 13, 2013; Micó, 2005: 550) or even after 3000 BC (Welker et al., 2014).

Based on new radiocarbon ages and cultural documentation, Alcover (2008) proposed that the first human arrival to Mallorca probably occurred within the time frame 2350–2150 cal. BC. Other proposals place the first human arrival between 2500 and 2250 cal. BC (Lull et al., 2004; Micó, 2005) or even previous to 2800 cal. BC, possibly in the fourth millennium BC (Guerrero, 2007; Guerrero et al., 2006).

During the last decade, several studies have tried to narrow the chronological gap between these two milestones (the last *Myotragus* and the first human documentation) through new ^{14}C dates. Nevertheless, the ages obtained until 2015 did not substantially change the scenario about *Myotragus* extinction. The goal of this paper is to present the updated chronological information currently available for both late *Myotragus* and early human evidence on Mallorca.

Material and methods

Up to 13 samples of *Myotragus balearicus* from different Mallorcan caves have been accelerator mass spectrometry (AMS) dated at the Koninklijk Instituut voor Het Kunstpatrimonium (Brussels). The samples were pre-treated in laboratory premises following a modified Longin (1971) method. They were then combusted to carbon dioxide (Vandeputte et al., 1996), graphitized (Slota et al., 1987) and measured by AMS (Xu et al., 2004). No difficulties in obtaining the ^{14}C dates were reported, except in samples RICH-21981 and RICH-21982 in which a second test was necessary to be performed avoiding the NaOH wash step in the collagen pretreatment (first test did not furnish enough collagen to be dated) (M Boudin, personal communication, 2014).

The AMS radiocarbon dates are presented in yr BP (i.e. before present) following the standard reporting procedures. Radiocarbon calibration of both new and previously published ages was processed using the software OxCal v. 4.2.4 (Bronk Ramsey, 2009) and the IntCal13 curve (Reimer et al., 2013). The calibrated dates are expressed as 2σ and 1σ intervals (95.4% and 68.2% of confidence, respectively) and given as 'cal. BC'. As the magnitude of the standard error determines the rounding off (Stuiver and Polach, 1977), we rounded the values of the 2σ intervals to the nearest multiple of 10 when the standard error was less than 100 and to the nearest multiple of 100 when it was greater than 100.

Results

The new radiocarbon dates more recent than 7000 yr BP from *Myotragus* samples are listed in Table 1, together with additional dates in this time frame published elsewhere (Burleigh et al., 1982; Encinas and Alcover, 1997; Ramis and Alcover, 2001; Rivera et al., 2014; Waldren, 1982; Welker et al., 2014). The available C:N ratios (2.9–3.6) of the samples suggest that bone preservation was good enough to lend confidence to the radiocarbon determinations (DeNiro, 1985; Masters, 1987; Tuross et al., 1988).

The chronological evidence of human arrival to Mallorca derived from the radiocarbon age of a bone from an introduced caprine obtained by Aramburu-Zabala and Martínez-Sánchez (2015) has been included in Table 1. This sample came from a cave that did not furnish remains of the extinct Mallorcan fossil vertebrates, an exclusive archaeological site (for more information, see http://www.arqueobalear.net/static/pdf/INFERIOR.pdf). It was submitted to the same ^{14}C laboratory (Koninklijk Instituut voor Het Kunstpatrimonium in Brussels). All the analytical procedures were the same as previously indicated for the *Myotragus* samples, and no difficulties in obtaining the ^{14}C dates were reported. The C:N ratio (3.2) is consistent with good preservation.

Some of the new dates of *Myotragus* bones presented in Table 1 fall close to previous dates documenting the last presence of the species in Mallorca (i.e. UtC-6517). Two of the new dates, RICH-21771 and RICH 21772, furnished values that are the most recent obtained so far. Using the value of RICH-21772 (4035 ± 32 BP, 2830–2470 cal. BC), we can establish that the survival of *Myotragus* in Mallorca post-dated to 2830 cal. BC with a $p > 95.4\%$.

On the other hand, the date obtained by Aramburu-Zabala and Martínez-Sánchez (2015) on collagen from a domesticated caprine bone excavated in Cova de Son Pellisser (RICH-21853, 3884 ± 36 BP; 2470–2210 cal. BC) can be considered as the earliest evidence of human presence in Mallorca. It came from the lowermost archaeological level found at the cave and it documents human presence prior to 2210 cal. BC with a $p > 95.4\%$. No remains of *Myotragus balearicus* were obtained at Cova de Son Pellisser (Aramburu-Zabala and Martínez-Sánchez, 2015), and it can be reasonably assumed that *Myotragus* was already extinct – or at least it was very close to the extinction – during the deposition of the human-related remains at this cave.

On the basis of these new dates, the UPME has been reduced to 620 years (i.e. between 2830 and 2210 cal. BC).

Discussion

The conservative figure of 620 years for the UPME represents a considerable improvement for the chronology of the extinction of *Myotragus*, reducing the previous available UPME from 1660 to 620 years (i.e. over 60%). It should be noted that this is a conservative interpretation of the obtained ages, based on the 2σ extremes of the calibrated radiocarbon dates (see Figure 1).

A slightly less conservative UPME can be obtained using the RICH-21772 and RICH-21853 age probabilities (see Figure 1). The probability of human presence in Mallorca before 2280 cal. BC is >91.6, and before 2310 cal. BC is >68.2%. The probability of *Myotragus* presence in Mallorca after 2630 cal. BC is >93.8% and after 2580 cal. BC is >65.6%. Using 2630 cal. BC as *terminus post quem* for the last *Myotragus* presence (i.e. the *Myotragus* presence post-dates this age) and 2280 cal. BC as *terminus ante quem* for the first human presence (i.e. the human presence pre-dates this age), both supported by $p > 90\%$, an UPME of 350 years is obtained.

These new dates allow us to reject the hypotheses that the extinction of *Myotragus* occurred 1000 years before the human arrival to Mallorca (Lull et al., 1999, 2008, 2013; Micó, 2005). The current gap between the last *Myotragus* and the first human evidence is less than 620 years and highly probably less than 350 years. This chronological gap can be considered as one of the shortest time periods documented between the first human and the last endemic megafaunal presence on any Mediterranean island. Although currently no evidence of the direct contact between humans and *Myotragus* has been recorded, this lack of

Table 1. New and published radiocarbon datings of *Myotragus* bones posterior to 7000 yr BP and the radiocarbon dating of the evidence of the first human presence in Mallorca (introduced Caprinae bone). All *Myotragus* samples come from paleontological levels in speleological sites ('Cova' and 'Avenc') and rocksheleters ('Balma'), whereas the introduced caprine sample comes from a deposit (Cova de Son Pellisser) that is purely archaeological. Cova de Moleta and Balma de son Matge are sites where archaeological remains postdating 2300 cal BC have been also obtained (see Alcover, 2008).

Lab no.	Deposit	BP	2σ cal. BC	C/N	δ^{13}C (‰)	δ^{15}N (‰)	Source
Radiocarbon datings of Myotragus bones							
RICH-21772	Cova des Màrmol	4035 ± 32	2830–2820 (1.6%) 2630–2470 (93.8%)	3.1	−19.5	+5.9	1
BM-1408	Balma de Son Matge	4090 ± 400	3700–1600	na	−20.2	na	2, 3
RICH-21771	Coveta des Gorgs	4456 ± 33	3340–3010	na	na	na	1
GrA-49936	Cova de Moleta (coprolite)	4905 ± 40	3770–3640	na	na	na	4
Wk-33010	Cova Estreta (coprolite)	4950 ± 38	3800–3650	na	na	na	5
RICH-21981	Avenc des Gorg Blau	5165 ± 36	4050–3940 (88.0%) 3860–3810 (7.4%)	3.6	−21.0	+2.1	1
RICH-21776	Coveta des Gorgs	5438 ± 35	4350–4240	3.2	−19.8	+2.9	1
UtC-5171	Cova Estreta	5720 ± 60	4720–4450	na	na	na	6
CSIC-176	Balma de Son Matge	5820 ± 60	4830–4530	na	na	na	2
RICH-21975	Coveta des Gorgs	6313 ± 37	5360–5220	3.1	−19.8	+3.6	1
RICH_21769	Coveta des Gorgs	6588 ± 35	5620–5580 (17.0%) 5570–5480 (78.4%)	3.2	−20.8	+3.3	1
RICH-21768	Coveta des Gorgs	6594 ± 35	5620–5480	3.1	−20.2	+2.2	1
QL-29	Balma de Son Matge	6680 ± 120	5800–5400	na	na	na	2
RICH-21982	Cova de s'Olla	6909 ± 40	5880–5720	3.6	−20.7	+6.3	1
Radiocarbon datings of introduced Caprinae							
RICH-21853	Cova de Son Pellisser	3884 ± 36	2470–2280 (91.6%) 2250–2210 (3.8%)	3.2	−20.2	+5.4	7

Source: 1 = This paper; 2 = Waldren, 1982; 3 = Burleigh et al., 1982; 4 = Welker et al., 2014; 5 = Rivera et al., 2014; 6 = Encinas and Alcover, 1997; 7 = Aramburu-Zabala and Martínez-Sánchez, 2015.
na: not available.

evidence does not imply that it did not occur, and it probably reflects the short duration of their coexistence in Mallorca (Bover and Alcover, 2003). We can expect that future radiocarbon dates will further close the gap as it is unlikely that the dated material belongs to the last living specimen of *Myotragus* and to the first goat/sheep introduced by humans to the island. The available dates for both late *Myotragus* and early human presence are so close that few doubts remain about a causal relationship between human arrival and *Myotragus* extinction. In fact, the upper value of the 2σ interval of RICH-21772 and the lower value of the 2σ interval of RICH-21853 are the same (2470 cal. BC). The new dates definitively exclude a *Myotragus* extinction close to 3600 cal. BC, as suggested in several papers (Guerrero, 2000; Lull et al., 2008, 2013; for criticism, see Alcover, 2004).

Some authors (e.g. Lull et al., 1999; Micó, 2005; Welker et al., 2014; Yll et al., 2001) have suggested that the extinction of *Myotragus* could be related to climatic change (specifically to a drying process) affecting the Balearic Islands. These authors suggest that a climate crisis could have produced the extinction of the Balearic box (*Buxus balearica*) in Menorca and its decrease in Mallorca. These authors consider *Myotragus* as a box-eating specialist, an assumption coming from a misreading of Alcover et al. (1999) (see Alcover, 2004). Lull et al. (2008: 13, 2013: 619–620) exclude a human-related extinction of *Myotragus* and propose '[the *Myotragus*] extinction was caused by purely ecological factors and a thousand years before the first stable human settlements'. Similarly, Welker et al. (2014) consider that 'the extinction of *M. balearicus* can be related to the decline and regional extinction of a plant species (the Balearic box) that formed a major component of its diet', although they situated the extinction between 3000 and 2000 BC. The analysis of the content of Holocene coprolites of *Myotragus* from Cova des Moro (Yll et al., 2001) documents a population of *Myotragus* feeding on a plant assemblage that did not include the Balearic box. Consequently, the hypotheses of a box depending diet of *Myotragus* should be discarded. The palynological analyses of Burjachs (2006) suggest that the only putative aridification event during this period (that could have been involved in driving *Myotragus* to extinction) occurred on Menorca between 4770 ± 60 BP (3650–3380 cal. BC) and 4440 ± 70 BP (3340–2920 cal. BC), thus previous to 2920 cal. BC. Therefore, the new RICH-21772 date is posterior to this assumed Holocene climatic drying and it allows us to reasonably exclude a climatic cause for the *Myotragus* extinction.

Further evidence argues against the relevance of this putative climatic change in the Balearics. As mentioned, the event has been inferred from a vegetation change that apparently affected Menorca (Burjachs, 2006) and the nearby Mallorca. Nevertheless, it did not strongly affect the close and drier island of Eivissa, where the mesophytic vegetation persisted well into the first millennium BP (Yll et al., 2009). If the vegetation change on Menorca and Mallorca was derived from a climatic event, Eivissa should have been also affected, and this was not the case. The Balearic box currently also lives on Cabrera, a very dry island south of Mallorca (Lázaro and Traveset, 2009; Palau Ferrer, 1976). Additionally, it should be remarked that although currently the Balearic box is a relict plant in Mallorca, in 1850 there were important box forests containing very large specimens (Marès and Vigineux, 1880). Thus, the presumed extinction of *Myotragus* as derived from the box disappearance in Menorca and its decline in Mallorca as a result of an aridification process can be also questioned by the persistence of important box forests until the 19th century.

The information presented here brings closer the last evidence of the *Myotragus* presence and the first evidence of human presence on Mallorca, improving the knowledge on the timing and process of the *Myotragus* extinction. The new dates strongly reinforce the exclusion of a climatic deterioration as the cause for the *Myotragus* extinction. The footprint of humans as causing this extinction is now more evident.

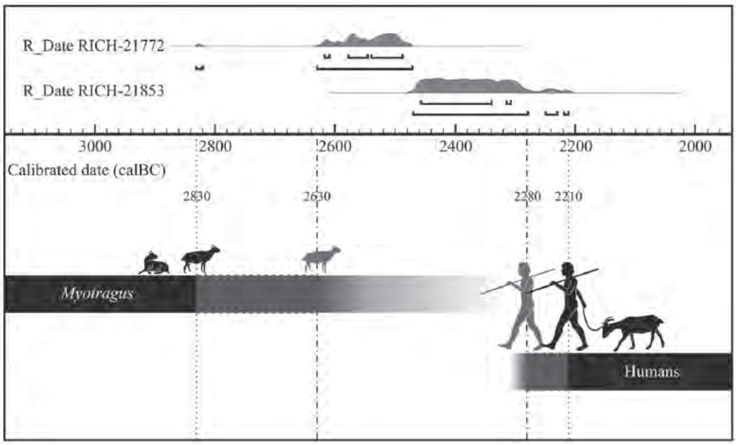

Figure 1. Graphical representation of the UPME limits using radiocarbon dates RICH-21772 (*Myotragus* bone) and RICH-21853 (introduced Caprinae bone as evidence of first human presence) in the island of Mallorca. Dotted lines represent the UPME limits at $p > 95\%$ (i.e. 630 years), whereas dash-dotted lines indicate UPME limits at $p > 90\%$ (i.e. 360 years). Calibration using OxCal v4.2.4 (Bronk Ramsey, 2009); r:5 IntCal13 atmospheric curve (Reimer et al., 2013). See text for further information.

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ORIGINAL PAPER

An early Pliocene anuran assemblage from Mallorca (Balearic Islands, Western Mediterranean): palaeobiogeographic and palaeoenvironmental implications

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Abstract A new anuran assemblage from the early Zanclean of Mallorca (Balearic Islands) is described using a set of 47 fossil bones obtained at the deposit of Na Burguesa-1, Mallorca. The assemblage includes four different anuran taxa: *Alytes* (*Baleaphryne*) aff. *muletensis*, *Discoglossus* sp., an indeterminate Bufonidae, and an indeterminate Ranidae. The record of *Alytes* and *Discoglossus* in this site represents the earliest evidence for the presence of their lineages on the Balearic Islands. The remains of the bufonid and the ranid constitute the first fossil record of these families in the Balearics. The discovery of this anuran assemblage has a relevant significance for the knowledge of the vertebrate colonisation of the Balearic Islands during the Messinian Salinity Crisis, especially due to the presence of a ranid and *Discoglossus*. These two taxa suggest that dispersal via a riparian corridor could have played a significant role in the Messinian colonisation of Mallorca, together with the corridor formed by the subaerial exposition of the Balearic Promontory. The Na Burguesa-1 site furnished one of the most diverse early Pliocene fossil anuran assemblages known so far in the Mediterranean islands.

Keywords Amphibia · Anura · Messinian Salinity Crisis · Palaeobiogeography · Na Burguesa-1 · Balearic Islands

Introduction

The amphibian fossil record of the Balearic Islands dates back to the early Pleistocene, except for a few remains attributed to cf. *Eopelobates* recovered at a late Oligocene site (Peguera, Mallorca; Sanchiz 1977a). The first fossil anurans discovered in the Balearic Islands were obtained from Cova de Moleta (Mallorca, late Pleistocene and Holocene) and were initially attributed to *Rana* sp. (Adrover 1966). Later on, Gasull and Adrover (1966) attributed two urostyles from Es Bufador de Son Berenguer (Mallorca, Quaternary) to an indeterminate anuran, whereas Ballman and Adrover (1970) recorded an anuran at Cova de Son Bauçà (Mallorca, middle/late Pleistocene). All these Mallorcan materials were studied by Sanchiz and Adrover (1979) who described the new genus and species *Baleaphryne muletensis* and they also attributed a few bones to *Bufo viridis* [currently *Alytes* (*Baleaphryne*) *muletensis* and *Bufotes balearicus*, respectively]. The latter species was actually introduced by humans, presumably during the Bronze Age (Hemmer et al. 1981) or even more recently. *A.* (*B.*) *muletensis* was posteriorly recorded in other Mallorcan caves (e.g. upper Pleistocene levels of Cova de na Barxa and Cova de Son Maiol; Holocene levels of Cova de

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Canet and Cova de la Mort; Alcover et al. 1984). The oldest fossils of *Alytes* known in the Balearic Islands were found at Pedrera de s'Ònix (Mallorca, early Pleistocene; Moyà-Solà and Pons-Moyà 1979; Alcover et al. 1984). Mayol et al. (1980) documented the survival of *A. muletensis* in several torrents of the Mallorcan Serra de Tramuntana mountain range. Shortly afterwards, Sanchiz and Alcover (1982) described *Alytes talaioticus* from two archaeological sites of Menorca: Rafal Rubí (XIVth-XIIIth century B.C.) and Torralba den Salort (IIIrd-IIth century B.C.). Nevertheless, this taxon was synonymized with *A. muletensis* by Sanchiz (1998).

In addition to the *Alytes* remains, a great number of bones from a large undescribed *Discoglossus* was recovered from early Pleistocene sites (Pedrera de s'Ònix, Alcover et al. 1981; Alcover et al. 1984; and Cova des Pas de Vallgornera, Bover et al. 2014a). This genus was also recorded in several Menorcan sites (Binigaus, probably early Pleistocene, and three different sites at Punta Nati, early or middle Pleistocene; Moyà-Solà and Pons-Moyà 1980; Quintana 1999). No *Discoglossus* remains have ever been recovered from more recent deposits, suggesting that the extinction of this taxon in the Balearics probably occurred at the end of the early Pleistocene or during the middle Pleistocene.

The most recently discovered anuran on the Balearics is a large Alytidae recovered from two Menorcan Pliocene deposits (Punta Nati 6 and 12), probably a new species attributed to *Latonia* by Quintana et al. (2005). Nevertheless, the few cranial elements recovered did not enable to go further in the taxonomic assignment of this material. Regarding the Pityusic Islands (Eivissa and Formentera), no anurans have been recorded in any of the known deposits.

The aim of this paper is to describe the anuran assemblage recovered from the palaeokarstic deposit of Na Burguesa-1 (Mallorca; Bover et al. 2014a, b) and to analyse its palaeobiogeographic and palaeoenvironmental significance. This site is currently furnishing unique information on the vertebrate stock that colonised Mallorca during the Messinian Salinity Crisis (hereafter MSC).

Location and geological setting

The deposit of Na Burguesa-1 (hereafter NB-1) is located on the South-Western part of the Serra de Tramuntana of Mallorca (Fig. 1), near Palma. The site is located in the mountain range of Na Burguesa, at 160 m a.s.l., and close to the road heading to the monument placed on top of Puig des Caragol. It has been attributed to the latest Messinian/earliest Pliocene (Bover et al. 2014b), although the presence of a mammal (Cricetinae) exhibiting gigantism, a size change relatable to insular evolution, suggests a very early Pliocene chronology as its most probable age. The deposit consists of a fossil-rich breccia infilling a palaeocave or fissure excavated in lower Lias grey limestone. Nowadays, the main cave is completely eroded and only the infilling sediments are preserved. The breccia is constituted by sharp pebbles of limestone embedded in a matrix of red-brown silts strongly cemented by calcite, and contains layers with abundant remains of small vertebrates, mainly bio-accumulated by raptorial birds.

NB-1 yielded thousands of bones, mainly of mammals (Soricinae, Cricetinae, Muridae, Gliridae, Leporidae and Bovidae). Four anurans and 12 reptiles, mainly identifiable to a family level, have been also recorded. Birds are less abundant. This faunal assemblage includes some of the ancestors of the species described from the early Pliocene deposit of Caló den Rafelino (Manacor, Mallorca; Bover et al. 2007, 2010, 2014b; Bailon et al. 2010, 2014; Quintana et al. 2010; Agustí et al. 2012; Rofes et al. 2012) and of the Plio-Pleistocene Mallorcan fauna (the so-called *Myotragus*-fauna; Bover et al. 2008). The late Miocene mainland relatives of some of the NB-1 taxa can be clearly tracked, supporting the hypothesis that a colonisation event of the island took place during the MSC (Bover et al. 2014b).

Materials and methods

The sample of anurans studied herein consists of disarticulated bones obtained from the NB-1 karstic breccia treated with acetic acid. The extraction procedure consisted on cycles of consolidation of the exposed bones with Paraloid B-72 (5%), immersion of the rocks in a solution of acetic acid (10%) during 48 h, followed by immersion in fresh water during 24 h and, finally, slow air drying. The process was iterated until the bones were released from the matrix. The extracted fossils were finally cleaned with acetone and consolidated with Paraloid B-72 (10%). This method allowed the recovery of 47 anuran bones, currently curated at the Institut Mediterrani d'Estudis Avançats (IMEDEA; Esporles, Mallorca).

Skeletons of specimens used for comparative purposes come from Muséum National d'Histoire Naturelle (MNHN; Paris, France), Museo Nacional de Ciencias Naturales (MNCN; Madrid, Spain), IMEDEA (Mallorca, Balearic Islands) and the database of Lisanfos KMS platform (Martín and Sanchiz 2013). The taxonomic nomenclature used follows Sanchiz (1998), whereas the anatomical nomenclature follows Bailon (1999) and Sanchiz (1977c, 1998). Specimens were examined under a Leica S8 APO stereomicroscope and images were obtained with a digital camera Leica DFC420. The most representative specimens were figured using Photoshop CS5.

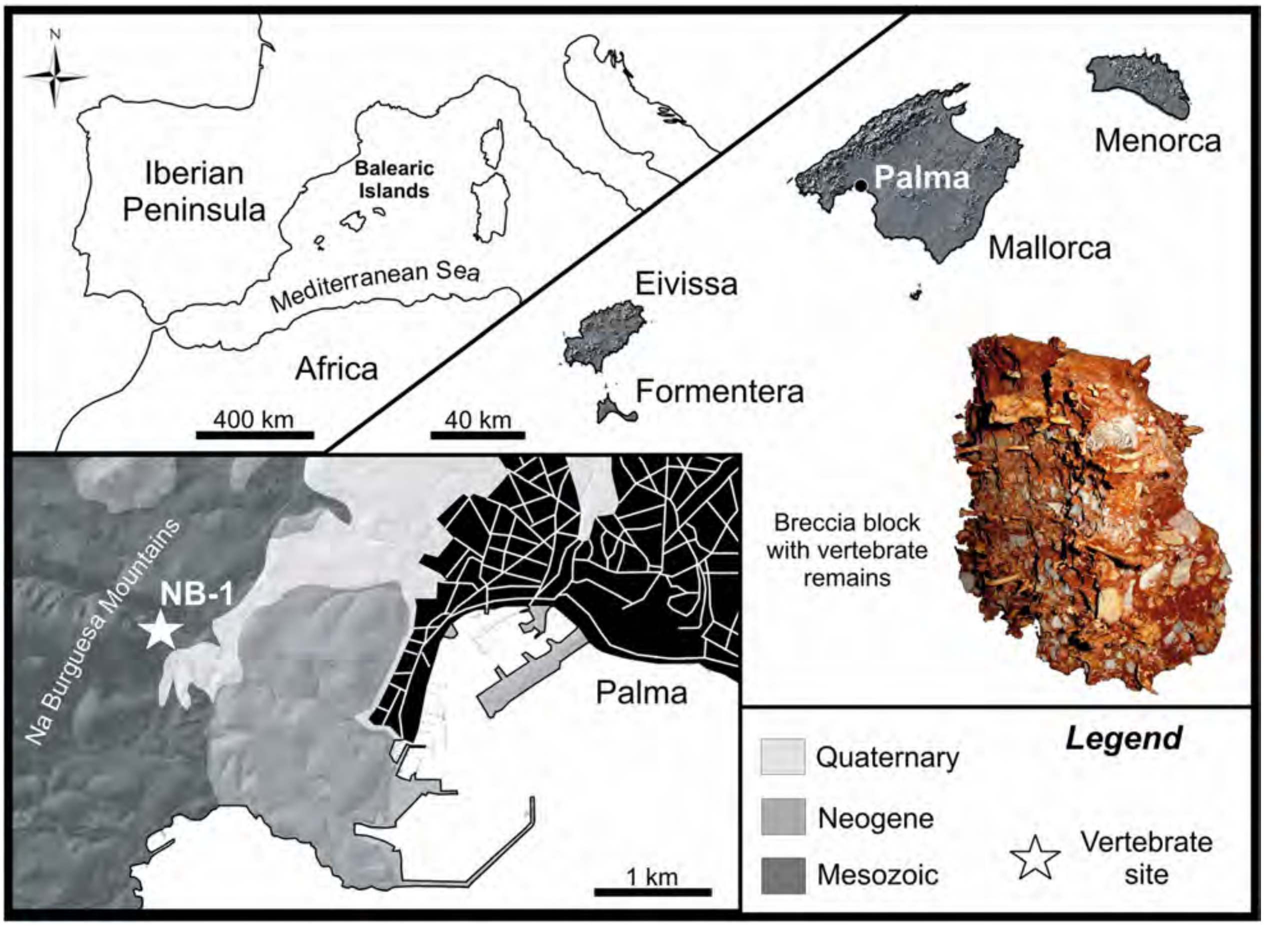

Fig. 1 Geographic and geological location of the early Pliocene palaeontological deposit of Na Burguesa-1 (NB-1, Mallorca, Balearic Islands)

Systematic palaeontology

Order Anura Fischer von Waldheim, 1813
Family Alytidae Fitzinger, 1843
Subfamily Alytinae Fitzinger, 1843
Genus *Alytes* Wagler, 1830
Subgenus *Baleaphryne* Sanchiz and Adrover 1979

Alytes (*Baleaphryne*) aff. *muletensis* (Sanchiz and Adrover 1979)
(Fig. 2)

Material examined: Right ilium (IMEDEA 103283; Fig. 2). Tentatively attributed to *A.* (*B.*) aff. *muletensis*: fragment of tibiofibula (IMEDEA 103543); distal fragment of radioulna (IMEDEA 103549); proximal fragment of radioulna (IMEDEA 103552).

Description

IMEDEA 103283: Right ilium without a developed crista dorsalis. It displays a low but conspicuous tuber superior with a rounded dorsal margin that is anteroventrally limited by a shallow groove. The tuber superior is located partially above the acetabulum and partially anterior to it. There are no supraacetabular and preacetabular fossae. The pars ascendens, although partially broken, is well developed, with a dorsal edge quite straight. The pars descendens is narrow, non-enlarged anteroventrally, and forms an angle of 120° with the pars cylindriformis. In medial view, the surface of the interiliac symphysis is broken. For this reason, the presence and morphology of tuber interiliacum cannot be evaluated.

The remaining fossils, here tentativelly attributed to *Alytes*, display few and not very informative diagnostic characters. Radioulnae and tibiofibulae bones are generally abundant in fossil sites, but they are found usually fragmented. In the best scenario, when complete, robustness, length and morphology of their terminal parts allow just a generic attribution. The proximal fragment of the radioulna IMEDEA 103552 displays a broken olecranon and a well-developed capitulum with rounded profile and a subcircular articular surface. In the anterior margin of the radius, there is a small fossa radii. The tibiofibula IMEDEA 103543 displays a quite rectilinear axis in anterior view, and it is only slightly curved in lateral

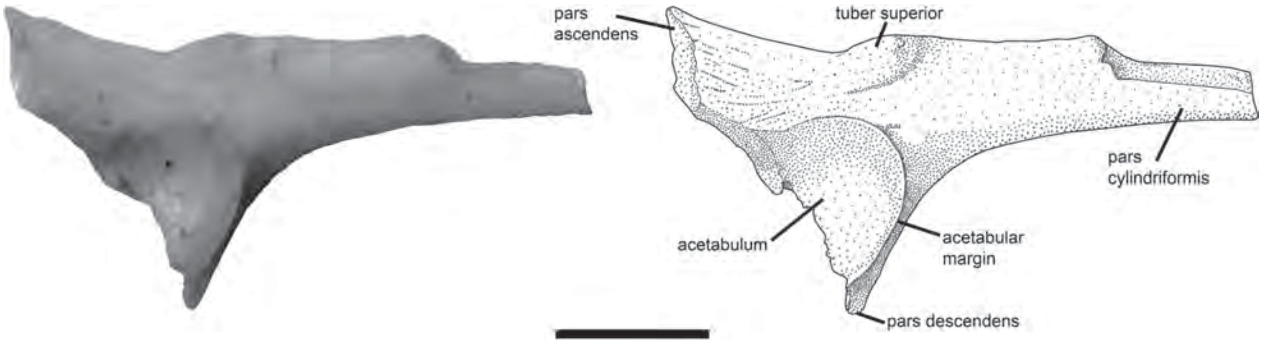

Fig. 2 Photograph (*left*) and interpretative sketch (*right*) of a right ilium of *Alytes* aff. *muletensis* in lateral view (IMEDEA 103283). *Scale bar*, 1 mm

view. The proximal and distal ends of the tibiofibula are twice as broad as the diaphysis at the level of the foramen nutritium.
Comparison: In the ilium, the absence of crista dorsalis on pars cylindriformis, the length of the pars ascendens, the presence of tuber superior partially above the acetabulum and partially anterior to it, and the presence of a non-ventrally enlarged pars descendens, among others, are diagnostic characters of the genus *Alytes* (Böhme 1977; Bailon 1999; Blain 2009; Bastir et al. 2014). The IMEDEA 103283 ilium shows a rectilinear pars ascendens as in the modern relative *A. muletensis*, while in the ilia of the other extant *Alytes* species the pars ascendens is dorsally curved. Despite the small size, this bone displays a tuber superior proportionally similar to those of *A. muletensis* and *Alytes maurus*, and smaller than in *Alytes dickhilleni*, *Alytes cisternasii* and *Alytes obstetricans*, although it is slightly displaced anteriorly. On the other hand, *A. muletensis* displays a marked supraacetabular fossa, whereas it is inconspicuous in IMEDEA 103283. An angle of approximately 90° can be observed between pars descendens and pars cylindriformis in *A. muletensis*, whereas in *A. cisternasii*, *A. obstetricans*, *A. dickhilleni* and *A. maurus* this angle is greater than 90°, and around 120° in IMEDEA 103283. The bones tentatively attributed to *A.* (*B.*) aff. *muletensis* display morphology and size that fit well with this species.

Subfamily Discoglossinae Günther, 1858
Genus *Discoglossus* Otth, 1837

Discoglossus sp.
(Fig. 3a–g)

Material examined: Fragments of maxillae (IMEDEA 103310, 105361; Fig. 3a, b); praesacral vertebrae (IMEDEA 103156, 103363, 105595, 105596, 105598; Fig. 3c); sacral vertebra (IMEDEA 105688; Fig. 3d); left radioulnae (IMEDEA 105967, 106492; Fig. 3e); distal fragment of left tibiofibula (IMEDEA 103542; Fig. 3f); almost complete tibiale-fibulare (IMEDEA 103196; Fig. 3g); fragments of tibiale-fibulare (IMEDEA 105703, 105966).

Description

IMEDEA 103310: Fragment of a right maxilla with pleurodont and pedicellate teeth. It has a developed and anteriorly inclined processus palatinus and a relatively thick lamina horizontalis. The tip of the processus palatinus is broken. In lingual view, a medial edge running down the processus palatinus can be observed. This processus surrounds partially the sulcus nasolacrimalis and it is ventrally separated from the lamina horizontalis by a groove. Anteriorly, the fossa maxillaris is shallow. The lateral surface of the bone does not show any dermal ornamentation.
IMEDEA 105361: Posterior fragment of a left maxilla. This maxilla preserves part of the processus zygomatico-maxillaris, but a great portion of it is broken, and thus its morphology cannot be fully described. The distal portion of the processus posterior is slightly broken. The margo orbitalis is wide, regularly concave and with a smooth lateral surface. In lingual view, the teeth row does not extend posteriorly beyond the posterior limit of the lamina horizontalis, which ends in a moderately developed and dorsally curved processus pterygoideus. There is not a posterior depression (sensu Roček 1994).

Five opisthocoelous praesacral vertebrae corresponding to the 2nd–5th position have been obtained. The most complete specimen, IMEDEA 103156, corresponds to a 4th praesacral vertebra. The condyle and the cotyle have a circular section, and a low neural spine prolonged in a long posterior processus spinosus characterises the vertebra. The neural arch is wide. The processus transversus is wider distally than proximally.
IMEDEA 105688: Small sacral vertebra with an anterior condyle dorsoventrally compressed and two well separated posterior oval condyles. The neural arch is short and it displays a slightly developed neural spine. The sacral diapophyses have a relatively wide basis and their distal expansions are broken, but a distal widening can be observed.
IMEDEA 105967: Near complete medium-size left radioulna. This bone is long and relatively robust. The distal part of the radius is broken, but the ulna is complete.

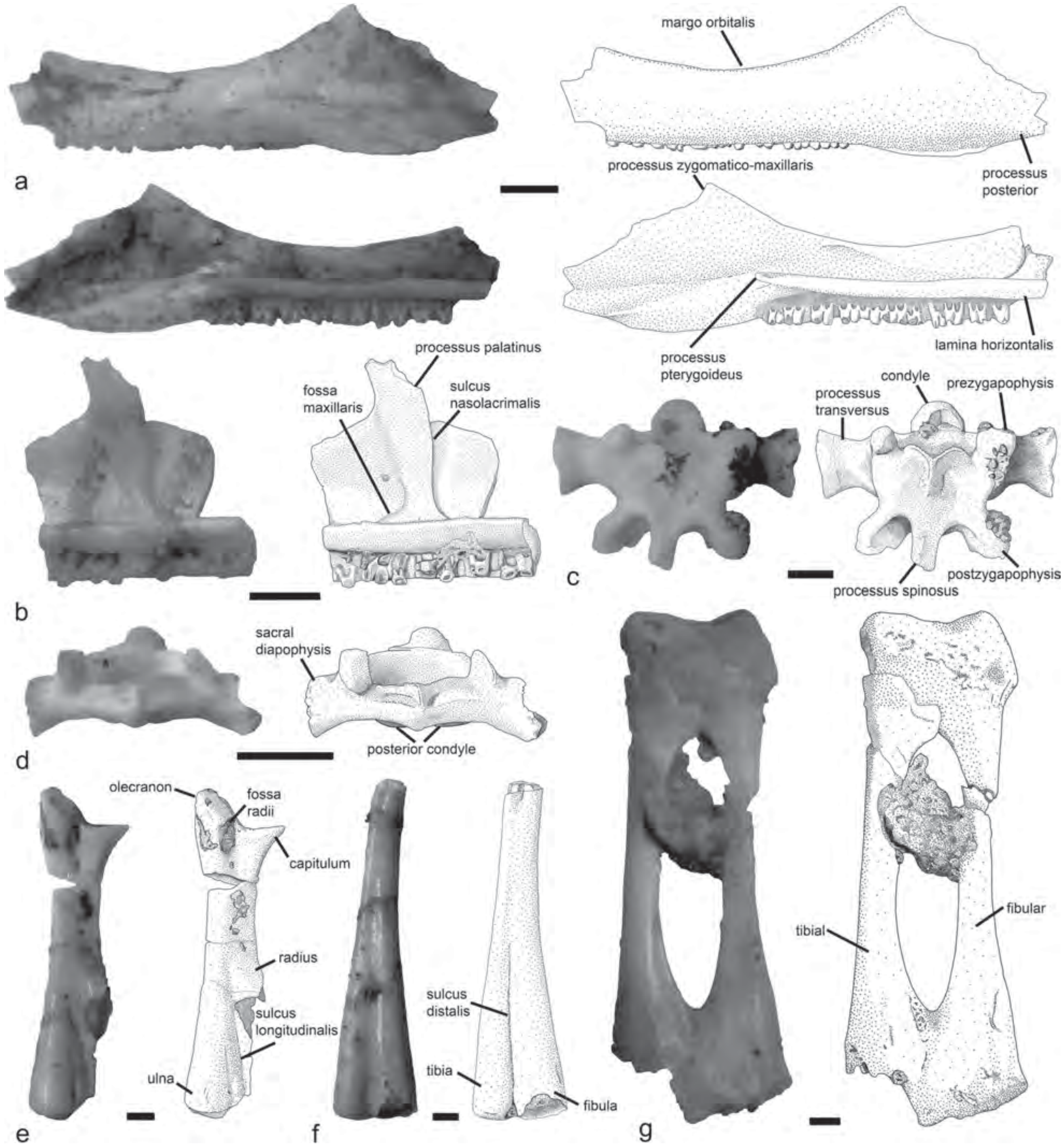

Fig. 3 Photographs (*left*) and interpretative sketches (*right*) of selected fossils of *Discoglossus* sp. **a** Proximal fragment of a left maxilla in lateral (*upper*) and medial (*lower*) views (IMEDEA 105361); **b** fragment of a right maxilla in medial view (IMEDEA 103310); **c** 4th presacral vertebra in dorsal view (IMEDEA 103156); **d** sacral vertebra in dorsal view (IMEDEA 105688); **e** left radioulna in posterior view (IMEDEA 105967); **f** distal fragment of a left tibiofibula in anterior view (IMEDEA 103542); **g** left tibiale-fibulare in posterior view (IMEDEA 103196). *Scale bars*, 1 mm

Olecranon and capitulum have a similar length and they form an angle of 123°. Proximally, the radioulna presents a deep fossa radii, as in extant *Discoglossus*.

IMEDEA 103542: Distal fragment of a left tibiofibula. It is slightly curved medially and displays an elongated central constriction. The morphology of the distal end of each bone (tibia and fibula) is subcircular in cross section and there is a slightly marked separation between them.

IMEDEA 103196: Left tibiale-fibulare (calcaneum-astragalus). The tibiale lacks distal end. The two bones are partially fused, both proximally and distally, and preserve calcified epiphyses. In the living *Discoglossus*, there are expansions at the end of the tibiale that increase the contact with the fibulare. These bones are more or less fused in old individuals, as in the fossil studied here. As in the two previous bones, this element has a low taxonomic value.

Comparison: According to Sanchiz (1998), Clarke (2007), and Biton et al. (2013, 2016), Discoglossinae, which includes the extant and fossil *Discoglossus* and *Latonia* as well as an extinct African Neogene genus (*Latoglossus*), is an osteologically well-delimited subfamily. The genus *Discoglossus* is identified by numerous osteological cranial characters, especially in the frontoparietal and maxilla (Sanchiz 1977c; Clarke and Lanza 1990; Bailon 1999). In the living *Discoglossus*, the maxillae display a developed processus palatinus (as in IMEDEA 103310) and a processus zygomatico-maxillaris (except in *Discoglossus montalentii*, in which it has been secondarily lost) with an angular dorsal margin. This characteristic of the processus zygomatico-maxillaris cannot be observed in the specimen IMEDEA 105361, because it is broken. Generally, the maxillae lack the posterior depression, although it can be exceptionally present in the genus (Blain et al. 2013), and display a teeth row reaching the lamina horizontalis, but without overreaching it. Most of these features can be observed in the IMEDEA 105361 maxilla, therefore allowing its attribution to *Discoglossus*, and not to *Latonia*. In *Latonia*, the maxilla frequently displays a posterior depression in medial view and a different degree of ornamentation in lateral view, whose variability depends on the species and the ontogenetic stage. In addition, the tooth row is longer than the lamina horizontalis and, in some cases, posteriorly overreaches the processus pterygoideus (see Roček 1994).

The NB-1 postcranial bones are slightly larger than those of the extant *Discoglossus*, but remarkably smaller than those of the early Pleistocene *Discoglossus* from Mallorca and Menorca. The IMEDEA 105967 radioulna is longer and slender than in the extant *Discoglossus*. It displays a deep fossa radii, also present in some species of *Alytes*. The fragmented tibiofibula IMEDEA 103542 has a low taxonomic significance, but the size, curvature and its subcircular section fit well with *Discoglossus*. No differences can be observed between the IMEDEA 103156 and the *Discoglossus* praesacral vertebrae, but the former differs from *Alytes* in size and in the presence of a more developed neural spine with a long processus spinosus. The sacral vertebra IMEDEA 105688 can be attributable to a juvenile *Discoglossus* as it displays a very incipient neural spine. *Alytes* displays similar sacral vertebrae, but they differ basically in the morphology of the sacral diapophyses. In *Alytes*, the sacral diapophyses are wide anteroposteriorly, like in *Discoglossus*, but narrower in their bases. IMEDEA 105688 lacks this trait, and thus it is attributed to *Discoglossus*.

Family Bufonidae Fitzinger, 1843
Genus and species indeterminate
(Fig. 4a–d)

Material examined: Praesacral vertebrae (IMEDEA 103032, 103193, 103463, 105910, 105917, 105921, 105969, 105970, 106495, 106496, 106497; Fig. 4a); praesacral vertebrae tentatively attributed to Bufonidae (IMEDEA 106494, 106498); sacral vertebrae (IMEDEA 103545, 103546; Fig. 4b, c); proximal fragment of radioulna (IMEDEA 103547); right ilium (IMEDEA 105728; Fig. 4d).

Description

All the praesacral vertebrae are procoelous. IMEDEA 103193 is probably a 5th praesacral vertebra. It displays a short neural arch and the cotyle and condyle are very flattened dorsoventrally. The processus transversus, inclined posteriorly, is located between the prezygapophysis and postzygapophysis. In the specimen IMEDEA 103193, a longitudinal widening of the dorsal region can be observed, possibly related with an incipient neural spine.

The two sacral vertebrae IMEDEA 103545 and IMEDEA 103546 are small and have an anterior cotyle and two posterior condyles. Both cotyle and condyles display an oval shape. Condyles are very close to each other but they do not contact. The sacral diapophysis is distally enlarged. Anteriorly, the sacral diapophysis contacts with the prezygapophysis. These sacral vertebrae display a developed posterior transversal crest. In IMEDEA 103546, the neural spine shows a tiny processus spinosus.

IMEDEA 105728 is a small right ilium without crista dorsalis and with a prominent tuber superior located above the acetabulum. The tuber superior has a rounded dorsal margin divided by a shallow groove, which confers it a bilobate aspect. This ilium displays a well-developed preacetabular fossa ending in a moderately expanded pars descendens. The pars ascendens is very short and has an incipient supraacetabular fossa. The angle between the pars cylindriformis and the pars descendens is around 90°. Rectilinear shallow grooves can be observed in the inferior part of the pars cylindriformis.

Comparison: Based on Bailon (1999), these remains are morphologically closer to the Bufonidae than to any other European anuran family. Alytidae and Bombinatoridae display opisthocoelous praesacral vertebrae, one anterior condyle in the sacral vertebrae (as in Ranidae) and a long pars ascendens on the ilia. In addition, in Bombinatoridae, the pars descendens is very small. Pelobatidae and Pelodytidae display procoelous vertebrae, with a long neural arch and with the cylindrical processus transversus located under the prezygapophysis in vertebrae 5 to 8. The sacral vertebrae of these two families have sacral diapophyses extremely wide anteroposteriorly and the ilia lack tuber superior. In Ranidae,

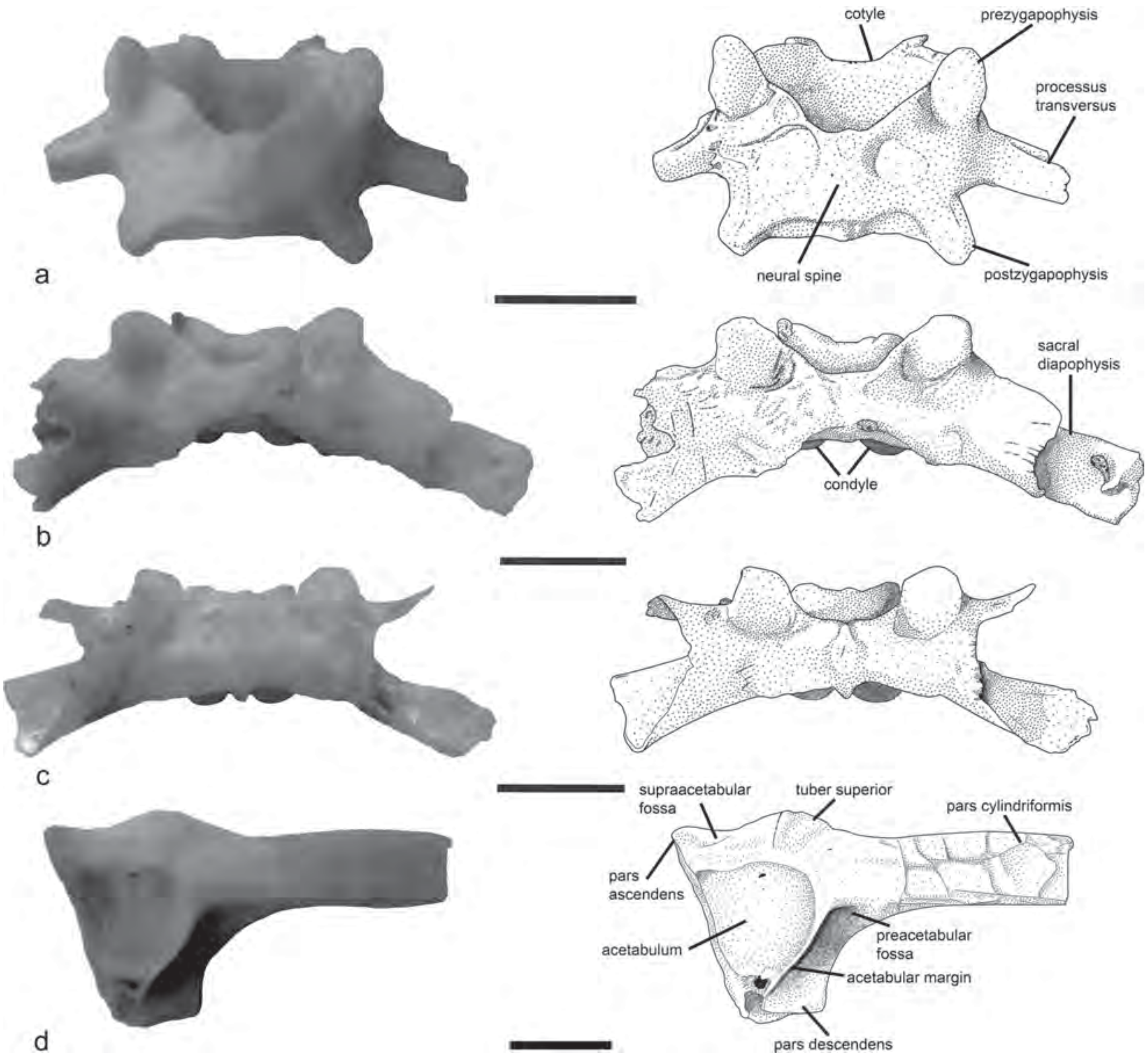

Fig. 4 Photographs (*left*) and interpretative sketches (*right*) of selected fossils of Bufonidae indet. **a** Fifth praesacral vertebra in dorsal view (IMEDEA 103193); **b**, **c** sacral vertebrae in dorsal view (IMEDEA 103545 and 103546, respectively); **c** right ilium in lateral view (IMEDEA 105728). *Scale bars*, 1 mm

the centrum of the praesacral vertebrae is small, with thin lateral walls. The sacral vertebra displays cylindrical sacral diapophyses. The ilia of Ranidae display a well-developed pars ascendens and a dorsal crest. The NB-1 material attributed here to Bufonidae shows its greatest similarity with Hylidae and Bufonidae. Nevertheless, there are several morphological differences between these two families: the cotyle and condyle of the praesacral vertebrae are more flattened and smaller in Hylidae than in Bufonidae. In Bufonidae, the praesacral vertebrae can display a more or less developed neural spine. In this sense, IMEDEA 103193 displays an incipient neural spine. In Hylidae, the sacral vertebra displays a more conspicuous prezygapophysis, whereas in Bufonidae it is more integrated in the sacral diapophyses, as in IMEDEA 103545 and IMEDEA 103546. The ilium of Hylidae shows a tuber superior with a rounded morphology and a pars descendens ventrally more expanded than in Bufonidae. The angle between pars descendens and pars cylindriformis is close to 90° in Bufonidae, while is higher in Hylidae. Although the pars descendens of IMEDEA 105728 is broken, it expands slightly onwards, forming an angle of 90° with the pars cylindriformis.

All European Neogene bufonids have been attributed to extant genera, and fossils described in deposits from the late

Miocene onwards have been identified as belonging to living species (Sanchiz 1977b). The remains described here do not allow a clear generic o specific attribution, but some sacral vertebrae and ilia can be used to approach it. The 5th–8th praesacral vertebrae lack any diagnostic trait allowing species identification, but the sacral vertebrae provide more relevant diagnostic criteria (Sanchiz 1977b). In *Epidalea calamita* and *Bufotes* spp., the anterior cotyle is slightly wider and more depressed than in *Bufo bufo. E. calamita* and *Bufotes* have a dorsal fossa at the root of each processus transversus, which are posterolaterally open in *E. calamita* and laterally open in *Bufotes*. These fossae are absent in *Bufo bufo*. When well developed, the neural spine is a highly diagnostic feature. In *Bufo bufo*, the sacral neural spine generally displays a wide A-shaped form, while in *Bufotes* is W-shaped (Ratnikov 2001). The sacral vertebrae IMEDEA 103545 and 103546 do not have a marked sacral neural spine, nor display any fossa at the base of the sacral diapophysis and present a cotyle significantly wider than high. Thus, their generic or even suprageneric attribution within the Bufonidae is not possible, as these remains are probably from juvenile individuals.

The posterior fragment of ilium IMEDEA 105728 has similarities with the *Bufotes*-group (*Bufo viridis*, *Bufotes balearicus*, *Bufo boulengeri* and *Bufo siculus*), such as a tuber superior relatively symmetrical and round, with a bilobated dorsal edge and a deep preacetabular fossa (Blain et al. 2010). This contrasts with *E. calamita* or *Bufo bufo*, which have a less developed or non-existent preacetabular fossa, respectively. The tuber superior in *E. calamita* is prominent and unilobed. In *Bufo bufo*, it is unilobed as well, but occasionally displays rudimentary grooves. The fossil ilia do not show any "*calamita* ridge" on the pars cylindriformis, unlike *E. calamita*. The pars descendens does not have the markedly convex outline observed in the African *Barbarophryne brongersmai* and *Sclerophrys regularis*, in which the angle between the pars cylindriformis and the pars descendens is also close to 90° (Delfino et al. 2009). All these taxa lack a dorsal crest on the pars cylindriformis and supraacetabular fossa (sensu Sanchiz 1977b).

Family Ranidae Fitzinger, 1843
Genus and species indeterminate
(Fig. 5)

Material examined: Sacral vertebra (IMEDEA 105971; Fig. 5); distal fragment of right humerus tentatively attributed to Ranidae (IMEDEA 106493).

Description

IMEDEA 105971: Sacral vertebra with an anterior condyle partially subdivided (presumably as result of a low degree of ossification), and significantly wider than the two posterior condyles. The posterior condyles are well separated medially and present a subcircular shape. The sacral diapophysis is robust and cylindrical, dorsoventrally compressed and lateroposteriorly oriented. It displays a developed sacral neural spine that is posteriorly bifurcated in two transverse ridges. These ridges are slightly bent backward before merging in the centre of the neural arch.

IMEDEA 106493: Distal fragment of a humerus, which is rectilinear and thin when observed in ventral view. The eminentia capitata is subspherical and centred on the axis of the diaphysis. The crista lateralis is slightly marked and the crista medialis is absent (indicating that it is a female/juvenile specimen). The epicondylus medialis and epicondylus lateralis are significantly reduced. The fossa cubitalis ventralis is small and shallow.

Comparison: Modern European frogs can be divided into two groups (e.g. Frost et al. 2006): brown frogs (genus *Rana*) and water frogs (genus *Pelophylax*). Several osteological characters —especially some in frontoparietalia and ilia—allow to discriminate between these groups (Roček 1982; Ratnikov 2001; Blain et al. 2015). However, the ranid remains obtained from NB-1 do not allow a clear attribution to any of these two groups.

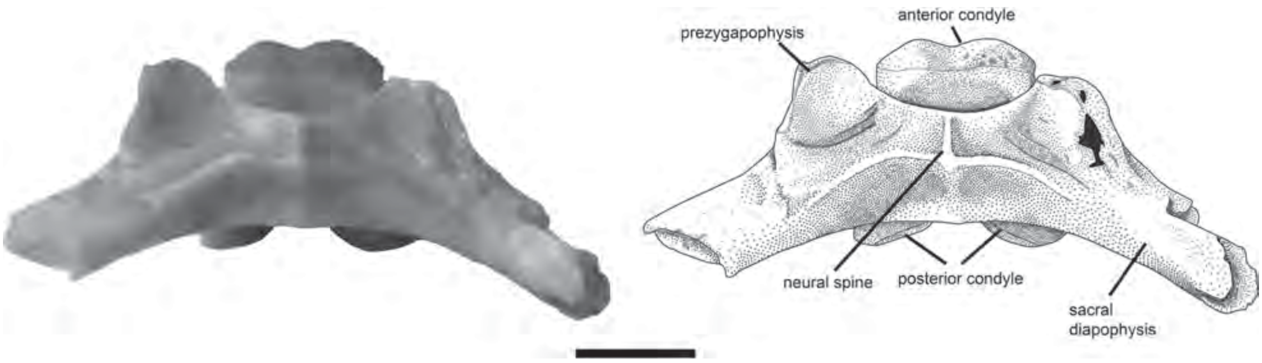

Fig. 5 Photograph (*left*) and interpretative sketch (*right*) of a sacral vertebra of Ranidae indet. in dorsal view (IMEDEA 105971). *Scale bar*, 1 mm

The sacral vertebra IMEDEA 105971 can be clearly attributed to a Ranidae as it displays an anterior condyle and cylindrical sacral diapophyses. According to Ratnikov (2001), the sacral vertebrae of Ranidae only enable identifications at a generic level (brown frogs or water frogs). In *Rana*, the transverse ridges of the sacral neural spine can be or inclined anteriorly or without inclination. On the other hand, *Pelophylax* displays a sacral neural spine inclined anteriorly, with the right and left branches bent backward prior merging in the centre of neural arch. The sacral vertebra IMEDEA 105971 shows very marked and not inclined transverse ridges, similarly to *Rana*, although these ridges bent backward slightly, prior to merging in the centre of neural arch, as in *Pelophylax*. Consequently, the attribution of IMEDEA 105971 to the brown frogs group (although it seems likely) cannot be confirmed.

The humerus also allows discriminating between brown frogs and water frogs, but only in males. Brown frogs usually display a slender humerus, and males have a crista medialis dorsally curved. Water frogs generally display a more robust diaphysis and the males have a very short crista medialis extended transversally. The humerus IMEDEA 106493 corresponds to a female/juvenile specimen since it lacks crista medialis, and thus it cannot be attributed to any of these groups.

Anura
Family, genus and species indeterminate

IMEDEA 103318, **106500**: Fragment of maxilla; IMEDEA 105965: fragment of left humerus; IMEDEA **103550**, **103551**: distal fragment of radioulna; IMEDEA 103548, 105968, 106499: fragments of tibiofibula; **IMEDEA 105962**: tibiofibula; IMEDEA 103544: phalanges.

These remains are fragments or poorly preserved complete bones that do not display enough diagnostic features, but they probably belong to the taxa studied above.

Discussion and conclusions

On the origin of the NB-1 anurans and colonisation chronology

The NB-1 anuran assemblage allows testing the two alternative biogeographic scenarios for the colonisation of the Balearic Islands proposed on the basis of molecular analyses of Alytinae. Martínez-Solano et al. (2004) estimated that the split between *A. muletensis* and *A. dickhilleni* took place c.3 Ma ago. This date suggested that the ancestor of *A. muletensis* arrived to Mallorca through an episode of overseas colonisation, as no land bridges between Mallorca and mainland were present after the MSC. Overseas dispersion can occur in anurans, although vicariance events have been mostly involved in the colonisation of the islands by them (Vences et al. 2003). On the contrary, Arntzen and García-París (1995), Fromhage et al. (2004) and Gonçalves (2007) suggested that *Alytes* spread over the partially desiccated western Mediterranean during the MSC, and that the ancestor of *A. muletensis* was later isolated on Mallorca due to the refilling of the Mediterranean basin at the end of the Messinian Event, c.5.33 My ago (Hsü et al. 1973; Krijgsman et al. 1999). The refilling of the Mediterranean basin also caused the almost simultaneous isolation of the lineages that subsequently gave origin to *A. maurus* in North Africa, *A. dickhilleni* in the Betic Mountains and *A. muletensis* in the Balearic Islands. The presence of remains of *Alytes* in the early Pliocene deposit of NB-1 rules out the overseas immigration hypothesis and it is in agreement with the proposal by Arntzen and García-Paris (1995) and other authors (Gonçalves 2007; Maia-Carvalho et al. 2014).

Genetic studies suggested that the *Discoglossus* clade appeared in the late Miocene (Fromhage et al. 2004; Pabijan et al. 2012), although fossils assigned to *Discoglossus* are known from the late Oligocene of Germany (Böhme 2008; Rage and Roček 2003) and the early Miocene of Sardinia (Venczel and Sanchiz 2006). The rediscovery of the Hula painted frog in the Lake Hula (Israel), formerly attributed to *Discoglossus*, allowed to finally identify it as *Latonia* (Biton et al. 2013). Thus, all extant species of *Discoglossus* have a western Mediterranean distribution. Environmental changes associated to the MSC could have influenced on the dispersal and isolation of the last common ancestor of extant *Discoglossus* species, such as *Discoglossus pictus*, *Discoglossus sardus*, *Discoglossus galganoi* and *Discoglossus scovazzi* (Zangari et al. 2006). During this dispersal event, an ancestral *Discoglossus* reached Mallorca, as documented by the NB-1 remains. The last evidence of the presence of *Discoglossus* on Mallorca comes from the early Pleistocene deposit of Pedrera de s'Ònix, suggesting that the extinction of the genus on this island took place at some indeterminate time after the sediment deposition in Pedrera de s'Ònix.

It has not been possible to identify the direct mainland ancestors of the other taxa studied here (i.e. the Bufonidae and the Ranidae). Nevertheless, their arrival to Mallorca probably also occurred during the MSC. In Europe, the oldest—but doubtful—"Ranidae" comes from the late Eocene of France (Rage 1984), whereas the oldest unquestionable Bufonidae come from the early Miocene of Spain and France (Sanchiz 1977c; Bailon and Hossini 1990; Roček and Rage 2000).

Environmental conditions during the MSC and dispersive capabilities of anurans under restrictive ambient temperature and water availability

The Balearic Islands were connected to the surrounding mainland during the MSC. The Messinian desiccation should have allowed the spread of a mainland fauna to the Balearics (e.g. van der Made et al. 2006; Bover et al. 2008). It has been widely accepted that during this episode a large part of the Mediterranean islands were surrounded by an inhospitable saline desert (Hsü 1983). Pollen sequences of the peri-Mediterranean region indicate that open and probably dry environments existed in the southern Mediterranean region before, during and after the salinity crisis (Fauquette et al. 2006). Favourable habitat corridors allowing the dispersal of terrestrial animals to the Balearics should have been present (e.g. Blondel and Aronson 1999). Although the Balearic Promontory could have been one of such corridors, relatives to most of the early Pliocene species of the Mallorcan endemic fauna have not been recorded so far in the Pliocene deposits of Eivissa, suggesting that it was probably not the only pathway. Although there is no direct evidence of such corridors, the massive erosion on the subaerial exposed continental margins during the great desiccation event is widely known (Rizzini et al. 1978; Ryan and Cita 1978; Just et al. 2010). The former mainland rivers drained over the emerged new lands, cutting in deep canyons that reached even the abyssal plains. If the water flow of these new rivers was large enough, they could have represented favourable dispersal corridors, especially for amphibians. In this sense, the anurans found in NB-1 provide some information about these probable corridors, mainly derived from the ecological requirements of extant frogs and toads. Most of the recorded anurans, especially Alytinae and Bufonidae, have crepuscular and nocturnal activity and they are not strictly water dependent during the adult stages. On the contrary, Ranidae and Discoglossinae are more strictly linked to aquatic environments, although with a variable degree of tolerance to brackish water. Ranidae include diurnal and nocturnal species, which decrease their activity during highest insolation hours. Within the Ranidae, some species are strictly aquatic, as *Pelophylax* (water frogs), which can be found in all types of freshwater bodies (although preferably in permanently wet environments), and have a high tolerance to brackish waters. Water availability and altitude are limiting factors in their geographical distribution. On the other hand, most of extant species of *Rana* (brown frogs) live in humid environments, but spend most of the adult life on the ground, just returning to water to breed.

Some of the mentioned traits above, such as nocturnal activity, low level of water dependance, tolerance to brackish water, etc., may have facilitated the long-range dispersal of several of these anurans (e.g. Alytinae, Bufonidae), favouring their arrival to Mallorca. The presence of water streams crossing the Messinian desert should have been necessary to allow the dispersal at least of the ranid and *Discoglossus* to the Balearic Islands.

The structure of current faunal communities from arid regions could be illustrative for the understanding of the Messinian colonisation event of Mallorca. In current arid regions, aquatic species commonly disperse across catchments, implying that movement away from streams is very common (e.g. Jaeger et al. 2005; Razeng et al. 2016). Several authors emphasise the importance of rainfall episodes for dispersal through rivers/streams in desert and semi-desert environments (e.g. Channing 1976; Spieler and Linsenmair 1998; Tockner et al. 2006). The Sahara Desert provides good examples of faunal dispersal across a desert region. It was initially considered to be an obstacle for faunal or human migrations and a Nile corridor route was proposed as a dispersal pathway. Nevertheless, the presence of palaeo-rivers recently recorded in the area suggests that they could have represented viable migration routes across the Sahara during humid periods (Drake et al. 2011; Coulthard et al. 2013). The riparian habitats associated to rivers are considered to be the most productive environments in desert or semi-desert regions (Free et al. 2013, 2015). These habitats (palaeo-rivers and their riparian associated habitats) could have acted as important corridors for the faunal dispersal during the MSC, when the mainland rivers drained to the abyssal plains giving rise to Messinian valleys and erosional surfaces in the Valencia Trough (Urgeles et al. 2010; García et al. 2011). Some torrent channels of the Serra de Tramuntana in Mallorca could have been tributaries of the rivers that flowed from mainland to the abyssal plain, linking lotic corridors and allowing the colonisation of Mallorcan by aquatic-related species. The use of riparian corridors by anurans as route to reach the Balearic Islands should be considered as a reasonable hypothesis to explain this colonisation event, and it can also explain the scarcity of related species between the Mallorcan, Menorcan and Eivissan early Pliocene vertebrate faunas.

The discovery of the NB-1 fauna allows exploring the local extinction of the last 5 My in the Balearic Islands. Just one anuran species, the still extant *A.* (*B.*) *muletensis*, was living on these islands when first humans settlers arrived. It is the sole anuran of the current Mallorcan fauna whose ancestors can be traced back until the NB-1 fauna. The second representative of the Alytidae present at NB-1 is most probably the ancestor of the *Discoglossus* recorded in several early Pleistocene Mallorcan and Menorcan sites. It is generally assumed that *Discoglossus* disappeared from Mallorca and Menorca during early Pleistocene or some time just after, because it has not been recorded in more recent sites. The other two anurans present in NB-1 (the bufonid and the ranid) are not recorded in any of the later sites from the Balearics and the chronology of their extinction on Mallorca is unknown. They are not present in the relatively rich deposit of Pedrera de s'Ònix nor in the not so rich deposit of Cova des Pas de Vallgornera. According to our knowledge, an early/middle Pliocene extinction chronology can be suggested for both the Bufonidae and the Ranidae. The extinction of *Discoglossus*, the bufonid and the ranid should have been caused by natural events, probably related to climatic changes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Terrestrial colonization of the Balearic Islands: New evidence for the Mediterranean sea-level drawdown during the Messinian Salinity Crisis

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ABSTRACT

More than 40 yr after the discovery of salt giants buried below the Mediterranean deep basin floor, debate on the Messinian Salinity Crisis (MSC) is still continuing about whether there was a large or only moderate drawdown in base level related to the deposition of deep evaporites during its peak. In this paper, we constrain the magnitude of this sea-level drawdown during the MSC. An analysis of the late Neogene faunas of the Balearic Islands, combined with the available geostructural data, shows that a minimum of 800–1200 m drawdown would be required to allow the colonization of the Balearic Islands by new continental-terrestrial fauna during the MSC peak, which provides solid new evidence in favor of a deep desiccated basin in the Mediterranean during the MSC.

INTRODUCTION

The Messinian Salinity Crisis (MSC) was a geological event that affected the entire Mediterranean region as well as global ocean circulation between 5.97 and 5.33 Ma (Krijgsman et al., 1999; Manzi et al., 2013). In the Mediterranean, the crisis was mainly characterized by isolation and/or reduced connection with the Atlantic Ocean, resulting in a new hydrological budget that favored the deposition of vast amounts of evaporites (salt and gypsum) in the marginal basins and abyssal plains, together with considerable erosion of the exposed margins (Hsü et al., 1973; CIESM, 2008).

As soon as the deep Mediterranean evaporites were discovered (Ocean Drilling Program and Deep Sea Drilling Project [ODP-DSDP] drill holes), intense debate arose about the most appropriate scenario for their formation. According to the initial model (so-called "deep desiccated basin"), the Messinian evaporites formed in a deep but desiccated Mediterranean, while the shelves and slopes underwent subaerial erosion due to fluvial rejuvenation triggered by a 1500 m sea-level drawdown (Hsü et al., 1973). This initial model provided a plausible explanation of the observed geological features and became the paradigm for the MSC.

Another model (corresponding to a "deep nondesiccated basin") proposed that the basin was not desiccated but instead completely filled with brine, suggesting that deep-water conditions may have persisted throughout the MSC (Debenedetti, 1976; Schmalz, 1991; Hardie and Lowenstein, 2004). Only a moderate base-level drawdown would be required in this scenario, and both slope erosion and evaporite emplacement would have occurred by density currents in a stratified deep-water environment (Roveri et al., 2014a).

The main criticisms of the deep desiccated basin model focused on the implications of the widely distributed clastic evaporites emplaced by deep-water gravity flows, which had been overlooked in previous studies (Lugli et al., 2015).

As no deep drilling has reached the entire MSC sequence in the Western Mediterranean, the nature of most of the evaporites and erosional surfaces is still unknown. The debate on both models continues and currently represents a scientific challenge (Roveri et al., 2014b). This paper aims to show that a major drawdown of the sea level is required to have allowed terrestrial colonization of the Balearic Islands during the MSC peak.

GEOLOGICAL SETTING

The Balearic Promontory (Fig. 1) is a 500-km-long, 120-km-wide continental rise, including the Balearic Islands, surrounded by the deep Algerian and Valencia/Liguro-Provençal basins (Acosta et al., 2002). It forms part of the northeastern prolongation of the Betic Range into the Mediterranean Sea.

A thin MSC-related unit (Bedded Unit [BU]; Fig. 1) has been recently identified all over the Balearic Promontory, generally 0–100 m thick, but it reaches a thickness of at least 300 m in the Mallorca Central Depression (Driussi et al., 2015). This unit is distributed in small subbasins at depths currently lying between 600 and 2000 m, while its connection with the known MSC units of the deep basins (Upper Unit [UU] and Mobile Unit [MU] in Fig. 1) currently remains uncertain. The other parts of the promontory were subject to erosion during the MSC (Margin Erosion Surface [MES] in Fig. 1).

The Neogene basins on the Balearic Promontory have been relatively stable in terms of vertical movements since the Miocene, so the sedimentary record, both onshore and offshore, is suitable for testing the possible scenarios related to the MSC events (Just et al., 2011; Maillard et al., 2014; Driussi et al., 2015; Mas, 2015).

METHODS

This study links two different methodologies: on one hand, the fauna fossil record (Fig. 2), and on the other hand, geological/geophysical data (Fig. 3). This approach allows the reconstruction of the sea-level drawdown needed to expose terrestrial pathways connecting mainland Europe to the Balearic Islands at the end of the Miocene.

The fossil bones of Pliocene sites in Mallorca were extracted from the rock matrix (bone breccias) by cyclically consolidating the visible bones with Paraloid-B67 resin (5%), and immersing them in 10% acetic acid solution for 48 h, followed by immersion in freshwater for 7 d, and air drying.

Maps and sections were taken from a large seismic database including academic seismic profiles obtained during several scientific cruises and oil-industry surveys, and these data sets were improved by recent high-resolution seismic profiles acquired on the Balearic Promontory during the "SIMBAD" oceanographic cruise (Maillard and Gaullier, 2013). The map and sections (with units in meters) taken from the seismic database assumed a Pliocene–Pleistocene unit velocity of 2290 m/s (Fig. 3). Paleobathymetry was estimated from restoration of the sections at the end of the Miocene before the sea-level drawdown. Post-MSC tectonic deformation was removed, as well as the effects of the Pliocene–Pleistocene unit loading and Miocene unit decompaction, both calculated with

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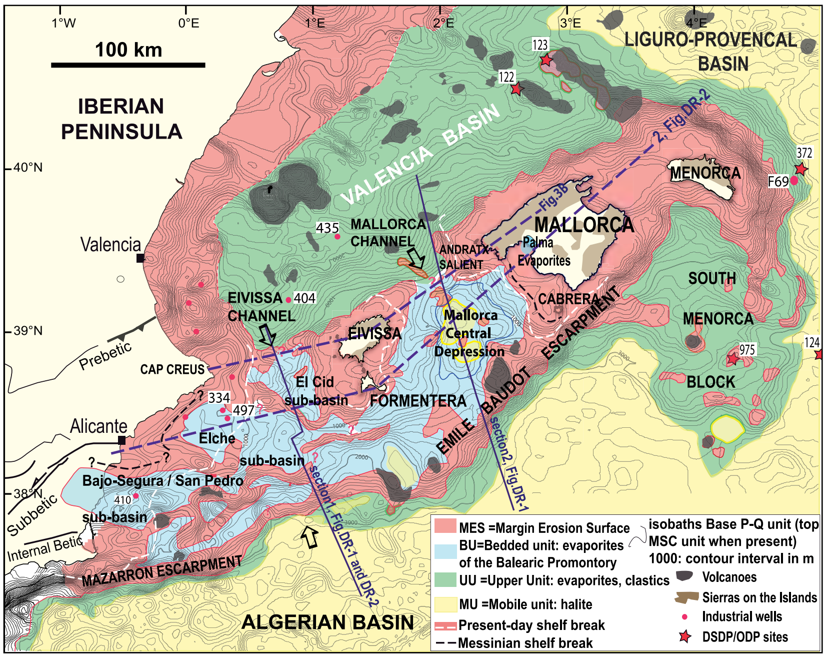

Figure 1. Distribution of Messinian Salinity Crisis (MSC) markers in Balearic Promontory (continental rise, including Balearic Islands). Map shows present-day depth to base of Pliocene–Quaternary (P-Q) unit, as well as (1) extent of MSC-related subbasins containing BU (in blue), and (2) areas affected by MES during erosion of MSC-related units (in red). DSDP—Deep Sea Drilling Project; ODP—Ocean Drilling Program.

a local isostatic model (Fig. DR2 in the GSA Data Repository[1]).

BIOSTRATIGRAPHY, COLONIZATION, AND PALEOBATHYMETRY

Different episodes of faunal colonization can be identified in the Miocene to Holocene fossil record of the Balearic Islands (Fig. 2; Bover et al., 2014). A first episode (the so-called *Gymnesicolagus* faunal assemblage) has been related to the Langhian-Serravallian regression (middle Miocene). A second episode, characterized by a new vertebrate fauna, has been recorded throughout the Pliocene–Pleistocene succession. Then, these new colonizing faunas evolved separately on the different islands (Fig. 2).

The colonization of the Balearic Islands by these new faunas is considered to have occurred during the Messinian, although the phylogenetic links between the mainland species and their insular descendants have not yet been clearly established. The recent discovery of Zanclean deposits on Mallorca and a reappraisal of the Pliocene sites on Menorca and Eivissa (Bover et al., 2014; Quintana et al., 2011; Quintana and Moncunill-Solé, 2014; Torres-Roig et al., 2017) shed new light on the fauna that arrived at the islands during the MSC, and on the chronology of this colonization episode. Evidence supports a very close relationship between the giant hamster *Apocricetus darderi* from the Zanclean section of Mallorca (MN14) and *Apocricetus alberti* from the Iberian Peninsula (MN13; Torres-Roig et al., 2017), providing robust evidence for a MSC-related origin of the Pliocene–Pleistocene faunal assemblage of Mallorca. Additionally, the large-sized gerbil *Debruijnimys* from Eivissa and an undescribed murid from MN14 of Mallorca are included in rodent genera that colonized the Iberian Peninsula during the MSC event. Some other island mammals (the caprine *Myotragus*, the shrew *Nesiotites*, and the leporids *Nuralagus* and *Hypolagus*) have been identified as likely descendants from mainland genera belonging to MN13. In addition, morphological traits (such as gigantism and hypsodonty increase) suggest that this fauna represents an early stage of isolated evolution.

The arrival of these faunas in the Balearic Islands can now be unequivocally related to their dispersal during the Messinian. Their colonization requires the existence of at least one terrestrial route connecting the Iberian Peninsula with the Balearic Islands. The narrow window in time is strongly supportive of the hypothesis of a terrestrial pathway for their appearance in a group and cannot be explained by random drift one-by-one over time from the mainland to faraway islands on flotsam.

Figure 1 shows the present-day depth of the base of the Pliocene–Pleistocene units. The areal extent of the MSC markers reflects the widespread nature of the MES, suggesting that subaerial erosion occurred over the entire Balearic shelf as well as on the structural highs located between the islands in the Mallorca and Eivissa channels (Just et al., 2011; Maillard et al., 2014; Driussi et al., 2015; Ochoa et al., 2015). The MES extends almost continuously from the Iberian Peninsula to the Balearic Islands through structural highs.

A cross section on the northern Balearic margin from mainland Spain (Cap de Creus) to Mallorca (Andratx salient; section 3B; Figs. 1 and 3) following the nearly continuous MES could be considered prime evidence to confirm the existence of a terrestrial connection between mainland Spain and the Balearic Islands. However, some of the bathymetric highs well expressed in the Eivissa Channel are related to post-MSC compression and/or volcanism (Acosta et al., 2001; Lastras et al., 2004), which led to small-scale folds and thrusts and to the large-scale bending observed on northwest-southeast cross sections (section 1; Fig. DR1). This Pliocene to present-day deformation may have produced 200–300 m of vertical uplift (Maillard and Mauffret, 2013). On the other hand, a large amount of post-MSC sedimentary loading (locally in the subbasins; Fig. 3A) could be responsible for subsidence, together with recent normal faulting (sections 1 and 2; Fig. DR1).

The paleogeomorphology of the area before the Pliocene may thus have been quite different. Restoration involves considering superimposed uplift and subsidence effects, where the Pliocene–Pleistocene unit is backstripped, and the late Miocene surface elevation is calculated with local isostatic compensation (Fig. DR2). In the Eivissa Channel, if the effects of post-MSC tectonics (300 m uplift) and unloading of the relatively constant-thickness Pliocene–Pleistocene unit are removed from this section, we can infer a paleodepth of 1000–1200 m maximum. This is in accordance with results showing that at least the upper slope of the Valencia basin was eroded (Urgeles et al., 2011; Cameselle and Urgeles, 2017). The rest of the Eivissa Channel should have been under shallow water during the MSC to allow deposition of the BU in the subbasins, followed by consequent post-MSC deformation (section 1; Fig DR1). The Elche basin, however, lying at around 900 m depth at the end of the Miocene (B, section 2; Fig. DR2), would have emerged with a sea-level drawdown of the order of 1000 m. This would imply that it was already filled by evaporites before the main drawdown. Indeed, the Elche subbasin is correlated with the Primary Lower Gypsum evaporites (Ochoa et al., 2015). In this case, a connection could

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[1] GSA Data Repository item 2018173, supplementary Figures DR1 and DR2, is available online at http://www.geosociety.org/datarepository/2018/ or on request from editing@geosociety.org.

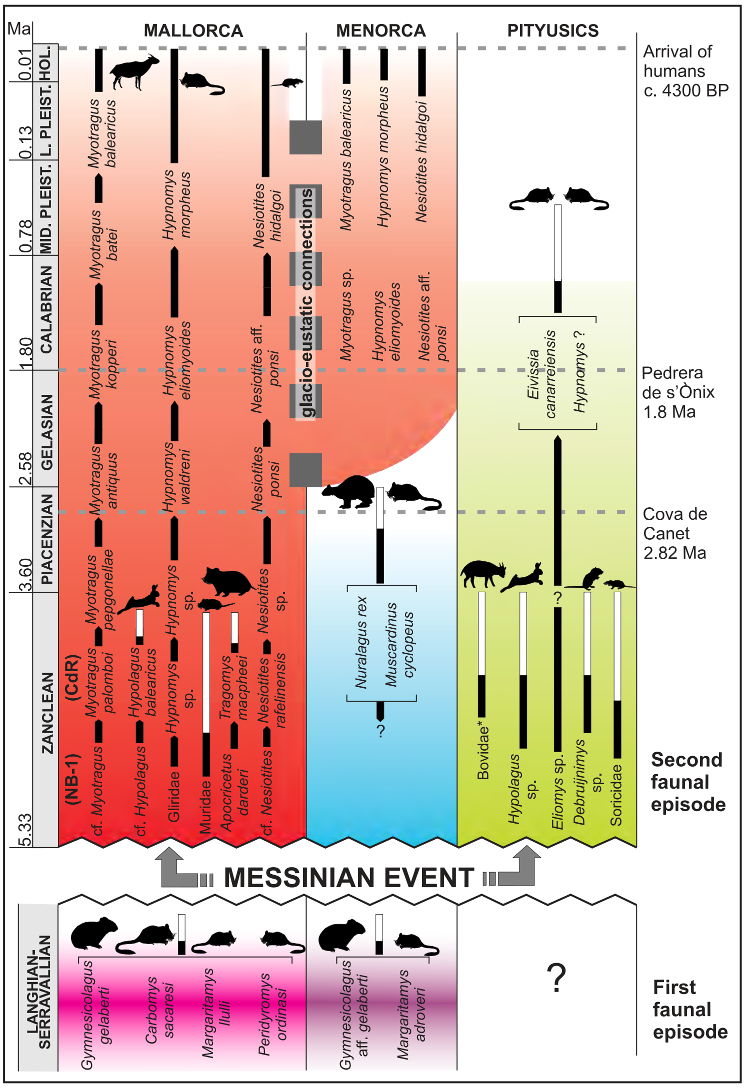

Figure 2. Diagram showing mammalian faunal succession of late Miocene–early Pliocene to Holocene in Balearic Islands. Different insular faunal episodes have been identified, where first episode (*Gymnesicolagus* faunal assemblage) has been related to Langhian-Serravallian regression (middle Miocene). Second episode, characterized by vertebrate fauna that arrived during MSC, is recorded throughout Pliocene–Pleistocene. New faunas evolved separately on different islands: *Myotragus* fauna on Mallorca, *Nuralagus* fauna on Menorca, later replaced by *Myotragus* fauna, and a poorly understood colonizing fauna—affected later by a Pliocene–Pleistocene extinction event—on Pityusic Islands (Eivissa and Formentera). Mallorca and Menorca merged during successive glacial events (gray squares). Gray horizontal discontinuous lines indicate paleomagnetic and radiocarbon ages. NB-1—Na Burguesa-1 faunal assemblage; CdR—Caló den Rafelino faunal assemblage. *Under study by Moyà-Solà and Quintana.

have occurred everywhere between mainland Iberian Peninsula and Eivissa during the MSC. Alternatively, the subbasins were perched and enclosed as small "lakes" of different water depth during the MSC, thus allowing mammalian colonization of the Balearic Islands via the northern Balearic margin (section 3B). This second hypothesis fits with the results in the Central Mallorca Depression, allowing salt deposition in a closed subbasin deeper than the Elche subbasin (B, section 2; Fig DR2).

Following section 3B, restoration reveals that a 1000 m sea-level drawdown would also have caused the emergence of the Mallorca Channel (Fig. 3B), suggesting a sea-level change of at least the same magnitude as the one allowing erosion along the entire path from the Eivissa Channel to Mallorca and implying a continuous terrestrial connection along the northern Balearic margin.

CONCLUSIONS

This analysis of the late Neogene insular fauna of the Balearic Islands, combined with the available structural data, enables us to infer the minimum sea level associated with desiccation of the Mediterranean during MSC, which favored the colonization of the Balearic Promontory by new continental-terrestrial fauna.

The paleobathymetry in the Eivissa and Mallorca Channels connecting the Iberian Peninsula and these islands was already 800–1200 m deep during the late Miocene. We conclude that the Mediterranean sea-level drawdown should have been at least equal to this paleodepth to allow the colonization of the Balearic Islands by terrestrial fauna during the MSC peak. The fauna observed in the Zanclean section of Mallorca provides strong new evidence supporting the deep desiccated basin model.

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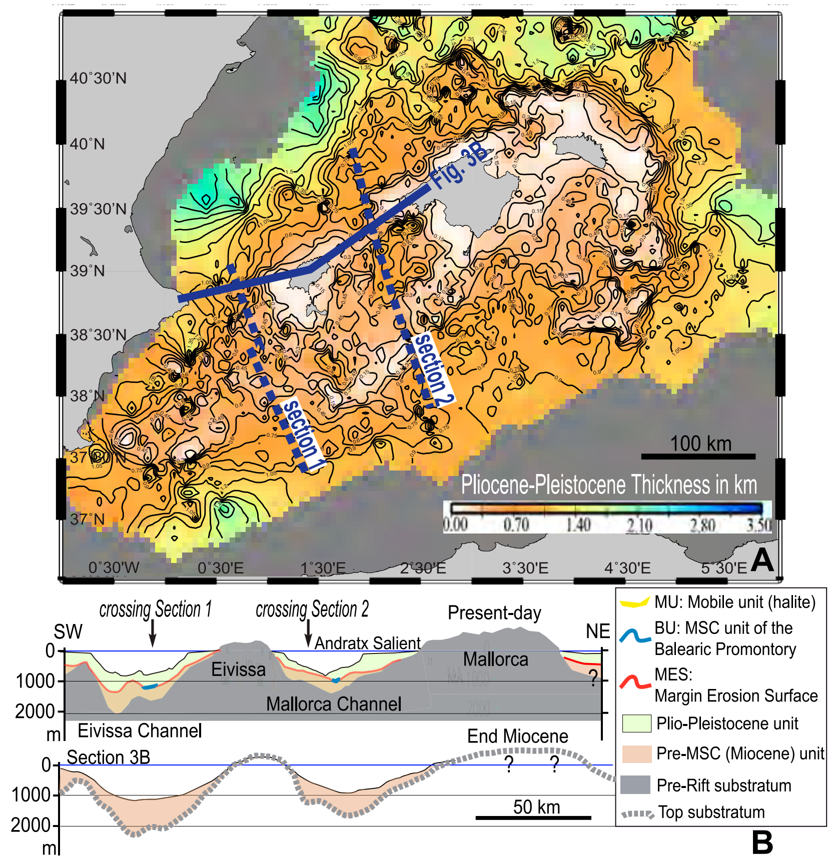

Figure 3. Depths and paleodepths of markers related to Messinian Salinity Crisis (MSC) on Balearic Promontory (continental rise, including the Balearic Islands). A: Map showing thickness of Pliocene-Pleistocene units (post-MSC deposits). B: Along-strike section of Balearic Promontory (for present-day) and restored paleodepth at end of Miocene. Section connects Cap Creus to southwest of Mallorca Island via Eivissa and Mallorca Channels. See comments in text. For restoration method, see text and Figure DR2 (text footnote 1). BU—Bedded Unit.

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A new giant cricetine from the basal Pliocene of Mallorca (Balearic Islands, western Mediterranean): biostratigraphic nexus with continental mammal zones

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ABSTRACT
A new insular giant species of *Apocricetus* (M1 length > 4.22 mm, upper teeth row length > 10.90 mm) is described from dental, mandibular and cranial material recovered at the Na Burguesa-1 site (Mallorca, Balearic Islands, western Mediterranean), a Zanclean palaeokarst deposit chronologically close to the refilling of the Mediterranean after the Messinian Salinity Crisis. *Apocricetus darderi* sp. nov. shows a close relationship with the mainland species *A. alberti* (MN13), an Iberian taxon, from which it differs in size, the presence of labial and lingual anterolophids in m1, triple anterolophulids frequently developed, a reduced anterosinusid in m2 and m3 and, occasionally, the presence of an ectomesolophid in m3. *Apocricetus darderi* sp. nov. becomes the first endemic Balearic mammal that can be confidently assigned as having a direct mainland relative, providing the first solid palaeontological evidence of a Messinian origin for the Plio-Pleistocene fauna of Mallorca. *Tragomys macpheei* from the Caló den Rafelino site (Early Pliocene, probably late MN14 or early MN15) displays a peculiar selenodont teeth pattern and a high degree of hypsodonty, and is considered to be either a direct descendant of *Apocricetus darderi* sp. nov. or a sister taxon derived from a common ancestor.

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Introduction

In the early twentieth century, after her pioneering palaeontological exploration of other Mediterranean islands, Miss Dorothea Bate initiated the scientific study of the fossil vertebrates of the Balearic Islands. Bate (1909) described the first endemic fossil mammal from the Pleistocene of Mallorca and Menorca, the mouse-like goat *Myotragus balearicus* Bate, 1909. Later, she described the giant dormouse *Hypnomys morpheus* Bate, 1918 and the giant shrew *Nesiotites hidalgo* Bate, 1944 from fossils found on both islands (Bate 1918, 1944). All these taxa exhibit traits linked to their long insular evolution. Until the end of the 1990s, several Late Pliocene and Pleistocene species were described belonging to the same phyletic lineages as these three mammals. These lineages, together with those of the endemic midwife toad *Alytes muletensis* (Sanchiz and Adrover 1979) and the endemic lizard *Podarcis lilfordi* (Günther 1874), form the so-called *Myotragus*-fauna, whose origin on Mallorca is considered to be Messinian in age (Bover et al. 2008). Until a decade ago, it was assumed that the *Myotragus*-fauna evolved gradually and without undergoing any change in its faunal composition, which allowed the establishment of local biozones whose absolute ages nevertheless remain undetermined.

The discovery of the Caló den Rafelino deposit on Mallorca (Bover et al. 2007) has increased our knowledge of the composition of the *Myotragus*-fauna during the Pliocene. At this locality, five different mammals have been described, representing a new genus, four new species and one species identified only at generic level: *Nesiotites rafelinensis* Rofes, Bover, Cuenca-Bescós and Alcover, 2012 (but with a controversial status: see Furió and Pons-Monjo 2013; Rofes et al. 2013), *Tragomys macpheei* Agustí, Bover and Alcover, 2012; *Hypnomys* sp., *Hypolagus balearicus* Quintana, Bover, Alcover, Agustí and Bailon, 2010 and *Myotragus palomboi* Bover, Quintana and Alcover, 2010. The archaic traits of *M. palomboi* and the derived features of the cricetid *Tragomys macpheii* in comparison with their supposed continental relatives suggest an Early Pliocene age for CdR (Bover et al. 2010; Agustí et al. 2012). This proposal fits well with the hypothesis of the arrival of this fauna on the island during the Messinian Salinity Crisis (5.97–5.33 Ma ago; Gautier et al. 1994; Krijgsman et al. 1999; Manzi et al. 2013).

The Messinian Salinity Crisis represents one of the most fascinating events in the geological history of the Mediterranean Sea: the drying up of the Mediterranean resulted from the closing of the connection with the Atlantic Ocean (Hsü et al. 1973, 1978). This event had major climatic and biogeographic consequences, allowing the mammalian exchange between Europe and Africa (Agustí et al. 2006; van der Made et al. 2006). This exchange involved the dispersal of mammals of African origin into Europe (e.g. the rodents *Paraethomys* Petter, 1968 and *Debruijnimys* Castillo and Agustí, 1996; the hippopotamus *Hexaprotodon*

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Falconer and Cautley, 1836; and the camel *Paracamelus* Schlosser, 1903) and the spread of mammals of European origin into Africa (e.g. the pika *Prolagus* Pomel, 1853 and the murid *Occitanomys* Michaux, 1969). The Messinian Salinity Crisis led to the colonisation of the Western Mediterranean Islands via terrestrial connections (e.g. van der Made et al. 2006). The Pityusic Islands were colonised by *Debruijnimys* at this time, which is also assumed to correspond to the arrival of the *Myotragus*-fauna on Mallorca (Bover et al. 2008).

Although current evidence points to *Aragogoral* Alcalá and Morales, 1997 (Upper Vallesian, MN10) or *Norbertia* Köhler, Moyà-Solà and Morales, 1995 (Turolian-Ruscinian boundary, MN13/14) (Bover et al. 2010) as potential direct ancestors of *Myotragus*, the phylogenetic relationships of *M. palomboi* with its presumed mainland ancestor are not clearly documented. This phylogenetic uncertainty rules out an accurate biostratigraphic correlation with continental mammal zones (MN zones), since the evidence still remains to be firmly established. The unbalanced character and low diversity of the *Myotragus*-fauna of CdR, as well as the derived features of its mammalian elements, especially the gigantic size and ruminant-like dental pattern of *T. macpheei*, tend to support a long evolution of this fauna under insular conditions.

In 2012, a new Early Pliocene site, Na Burguesa-1, was discovered in Palma (Mallorca). This site has yielded the remains of up to six species of mammals, belonging to the Soricinae, Cricetinae, Muridae, Gliridae, Leporidae and Bovidae (Bover et al. 2014). Regarding the rodents: (1) the cricetine corresponds to a large species that fits well with *Apocricetus* Freudenthal, Mein & Martín Suárez, 1998, which might be the ancestor of *Tragomys macpheei*, (2) the first representative of a murid detected in the fossil record of the Balearic Islands, and (3) a glirid that represents a primitive ancestor of *Hypnomys*, the only rodent lineage of the *Myotragus*-fauna to survive beyond the Pliocene, evolving into *Hypnomys morpheus* and becoming extinct with the arrival of the first humans.

The aim of this study is to describe and name a new cricetine from Na Burguesa-1, and explore its relationships with mainland cricetines in order to establish a biostratigraphic correlation of the *Myotragus*-fauna with continental mammal zones.

Location, materials and methods

The fossils were extracted from the karstic deposit of Na Burguesa–1, located at the South-Western end of the Serra de Tramuntana of Mallorca, Balearic Islands (Figure 1). The deposit is formed of material filling, a fissure in Lower Liassic grey limestones. It consists of a fossil-rich breccia of sharp limestone chips embedded in a matrix of red-brown silts strongly cemented by calcite (for more details, see Torres-Roig et al. 2017). The material is curated at the Institut Mediterrani d'Estudis Avançats (Esporles, Mallorca; acronym used in the collection catalogue: IMEDEA).

The palaeontological material was extracted by treatment with acetic acid and then consolidated with Paraloid B-72. Scanning electron microscope (HITACHI S-3400N) photographs were taken at the Scientific and Technical Services of the Universitat de les Illes Balears. Measurements were based on images obtained

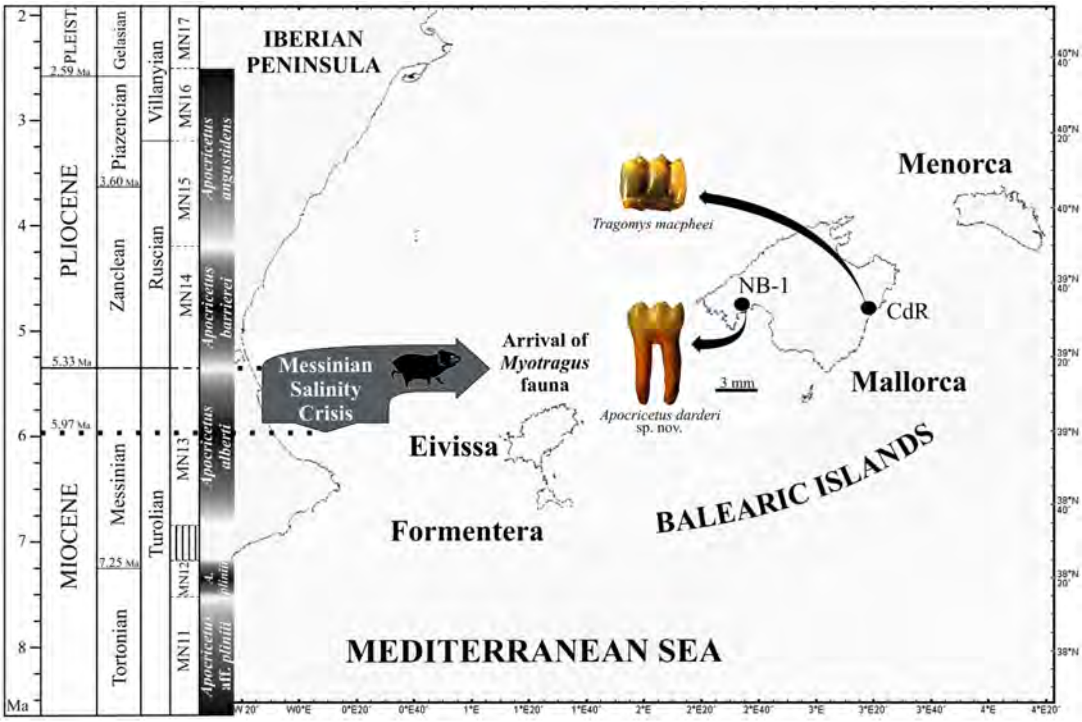

Figure 1. Geographical location of the early Pliocene palaeontological deposits of Na Burguesa-1 (NB-1) and Caló den Rafelino (CdR), Mallorca (Balearic Islands), and biostratigraphic distribution of the genus *Apocricetus* from the late Miocene to the Pliocene. MN units based on Agustí et al. (2001) and MN13/MN14 boundary after Hernández-Fernández et al. (2004).

with a digital camera DFC420 attached to a Leica S8 APO stereomicroscope using ImageJ software (Rasband 2009).

The nomenclature used for tooth description (Figure 2) follows Mansino et al. (2014) and Oliver and Peláez-Campomanes (2013). Lower molars are referred to as m1,2,3; upper molars as M1,2,3. Measurements were carried out according to Daams and Freudenthal (1988) and are given in millimetres.

Abbreviations – MSC: Messinian salinity crisis. NB-1: Na Burguesa–1 site. CdR: Caló den Rafelino site.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer, 1817

Subfamily Cricetinae Fischer, 1817

Genus *Apocricetus* Freudenthal, Mein & Martín Suárez, 1998

Apocricetus darderi sp. nov.

(Figures 3–7)

Etymology – The species is named in honour of Dr. Bartomeu Darder i Pericàs (1894–1944), a distinguished Mallorcan geologist who contributed to our current knowledge of the geology of the island, mainly the Central and Eastern mountain ranges.

Type Locality and Horizon – Na Burguesa-1 (Palma, Mallorca). Early Pliocene (MN14).

Holotype – Left mandible, IMEDEA 94726 (Figures 5(A) and 7(A), (B)).

Paratypes – **33 m1** (IMEDEA 94860, IMEDEA 94861, IMEDEA 104208, IMEDEA 104211, IMEDEA 104212, IMEDEA 104224 to IMEDEA 104226, IMEDEA 104230, IMEDEA 104234, IMEDEA 104255, IMEDEA 104549 to 104557, IMEDEA 104998 to IMEDEA 105001, IMEDEA 106082 to IMEDEA 106089), **26 m2** (IMEDEA 94862, IMEDEA 94863, IMEDEA 104209, IMEDEA 104217, IMEDEA 104218, IMEDEA 104236, IMEDEA 104243, IMEDEA 104559 to IMEDEA 104564, IMEDEA 105002, IMEDEA 105003, IMEDEA 106090 to IMEDEA 106092, IMEDEA 106094 to IMEDEA 106101), **29 m3** (IMEDEA 94864, IMEDEA 94866, IMEDEA 94867, IMEDEA 104214, IMEDEA 104220, IMEDEA 104227, IMEDEA 104233, IMEDEA 104237, IMEDEA 104241 to IMEDEA 104244, IMEDEA 104247, IMEDEA 104248, IMEDEA 104252, IMEDEA 104565 to IMEDEA 104572, IMEDEA 104574, IMEDEA 106102 to IMEDEA 106107, IMEDEA 106109), **15 M1** (IMEDEA 104213, IMEDEA 104215, IMEDEA 104528 to IMEDEA 104530, IMEDEA 104533, IMEDEA 104680, IMEDEA 104682, IMEDEA 104992, IMEDEA 104993, IMEDEA 106061 to IMEDEA 106066), **24 M2** (IMEDEA 94865, IMEDEA 104210, IMEDEA 104219, IMEDEA 104221, IMEDEA 104223, IMEDEA 104235, IMEDEA 104250, IMEDEA 104534 to IMEDEA 104542, IMEDEA 104995, IMEDEA 106067 to IMEDEA 106073, IMEDEA 106093), **25 M3** (IMEDEA 94868, IMEDEA 104222, IMEDEA 104229, IMEDEA 104232, IMEDEA 104238, IMEDEA 104240, IMEDEA 104246, IMEDEA 104249, IMEDEA 104251, IMEDEA 104543 to IMEDEA 104548, IMEDEA 104996, IMEDEA 104997, IMEDEA 106074 to IMEDEA 106081), **36 mandibles** (IMEDEA 94722 to 94724, IMEDEA 94734, IMEDEA 94800, IMEDEA 104145 to IMEDEA 104148, IMEDEA 104150, IMEDEA 104651, IMEDEA 104652, IMEDEA 104654 to 104657,

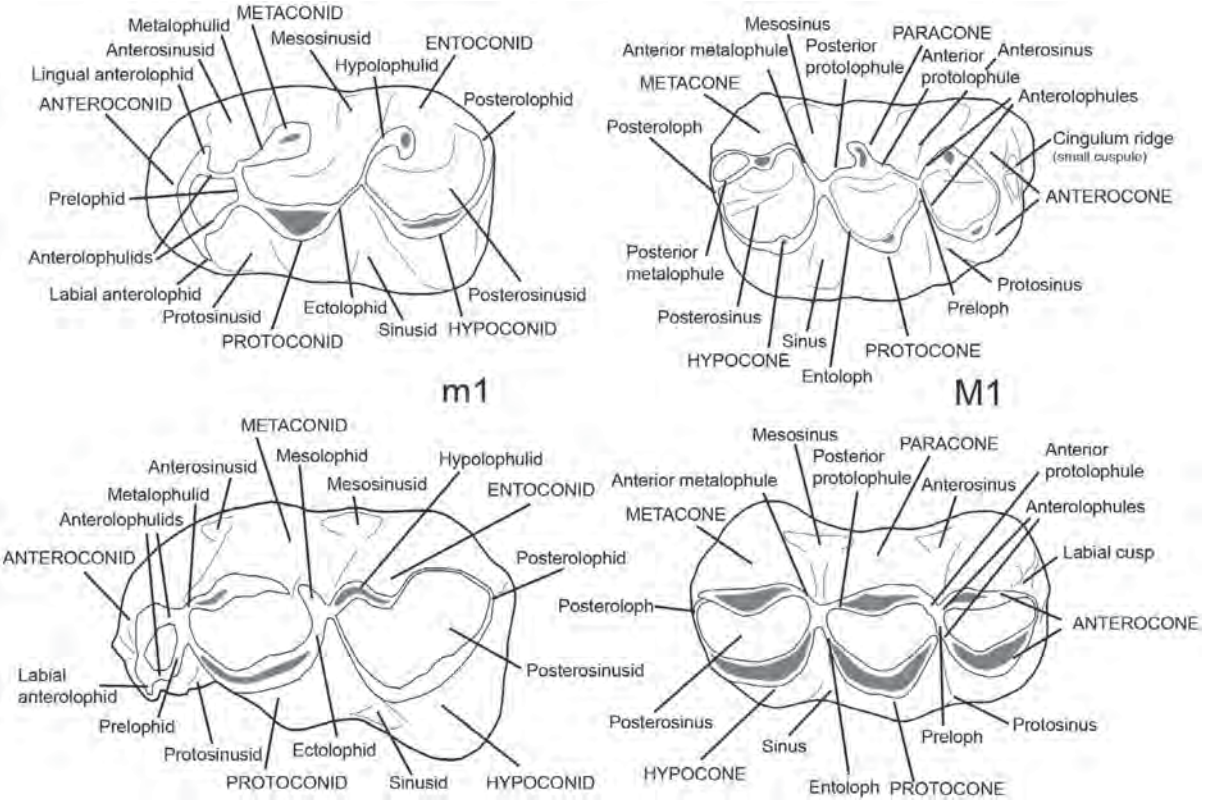

Figure 2. Nomenclature of the m1 and M1 of *A. darderi* sp. nov (above) and *T. macpheei* (below).

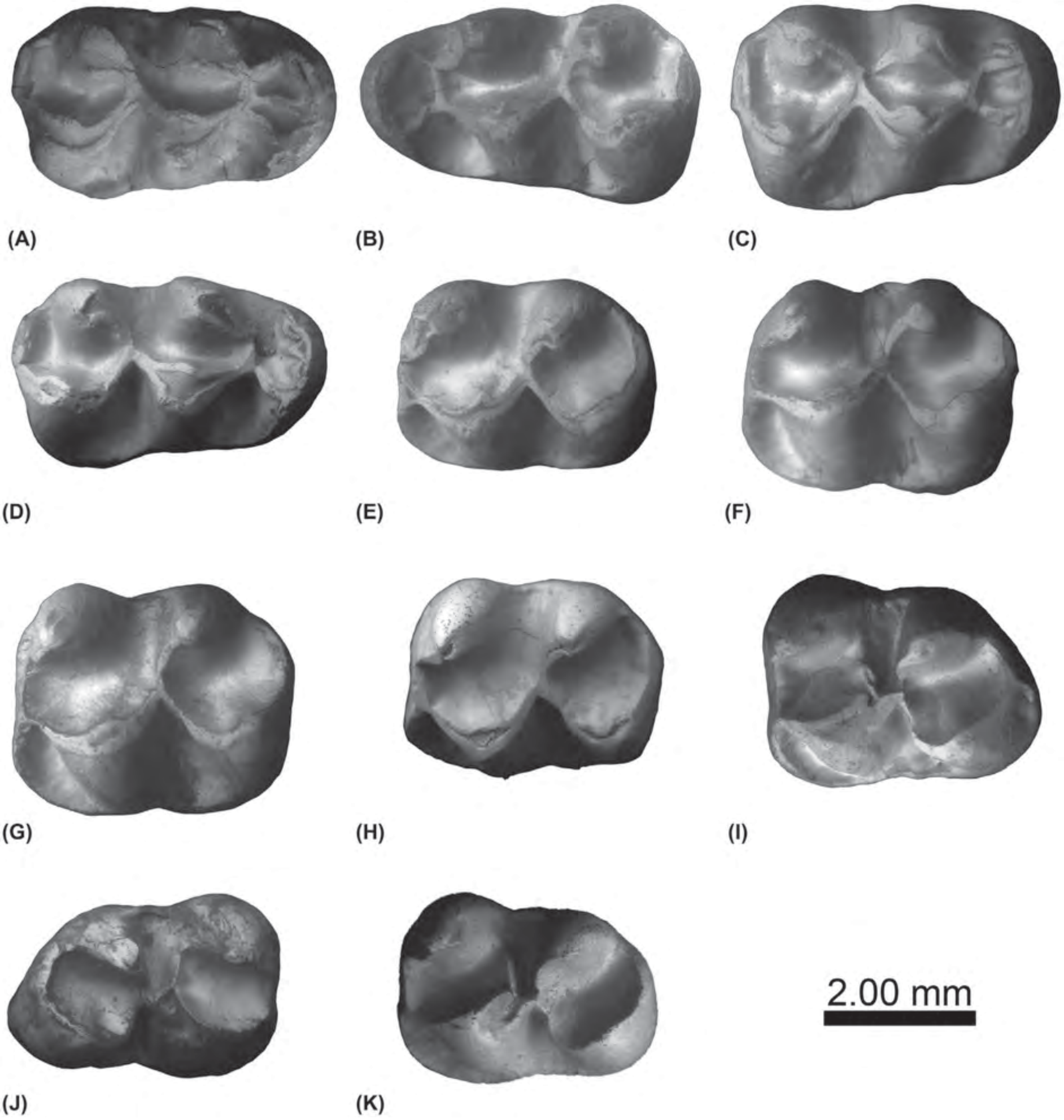

Figure 3. Isolated lower teeth of *A. darderi* sp. nov. from NB-1, Mallorca. (A) right m1, IMEDEA 104224; (B) left m1, IMEDEA 104226; (C) right m1, IMEDEA 104557; (D) right m1, IMEDEA 106086; (E) left m2, IMEDEA 104218; (F) left m2, IMEDEA 104563; (G) left m2, IMEDEA 105003; (H) left m2, IMEDEA 106091; (I) left m3, IMEDEA 94864; (J) right m3, IMEDEA 94867; (K) left m3, IMEDEA 104566. Scale bar 2 mm.

IMEDEA 104659, IMEDEA 104661, IMEDEA 104663 to 104665 (the last number corresponds to 2 mandibles of the same individual), IMEDEA 104969 to 104971, IMEDEA 104973, IMEDEA 106188, IMEDEA 106189, IMEDEA 106294 to 106301), **18 maxillae** (IMEDEA 104,151, IMEDEA 104,177, IMEDEA 104,181, IMEDEA 104669, IMEDEA 104673, IMEDEA 104676, IMEDEA 104677, IMEDEA 104679, IMEDEA 104974, IMEDEA 106302 to IMEDEA 106309, IMEDEA 106311). **Three fragmented skulls** (IMEDEA 94797, 104129 and 104796) and **an isolated occipital** (IMEDEA 104134).

Diagnosis – Largest *Apocricetus* described so far [larger than *A.* aff. *plinii*, *A. plinii* (Freudenthal, Lacomba and Martín-Suárez, 1991), *A. alberti* Freudenthal, Mein and Martín-Suárez, 1998; *A. barrierei* (Mein and Michaux, 1970) and *A. angustidens* (Depéret, 1890–1897)]. Crest-like anteroconid of m1 subdivided into two or three lobes. Well-developed labial anterolophid and small lingual anterolophid in m1. Anterolophulid of m1 frequently double, but may be simple or triple. Reduced anterosinusid sometimes present in m2 and m3. Mesolophid practically absent in m1, absent in m2 and present in all

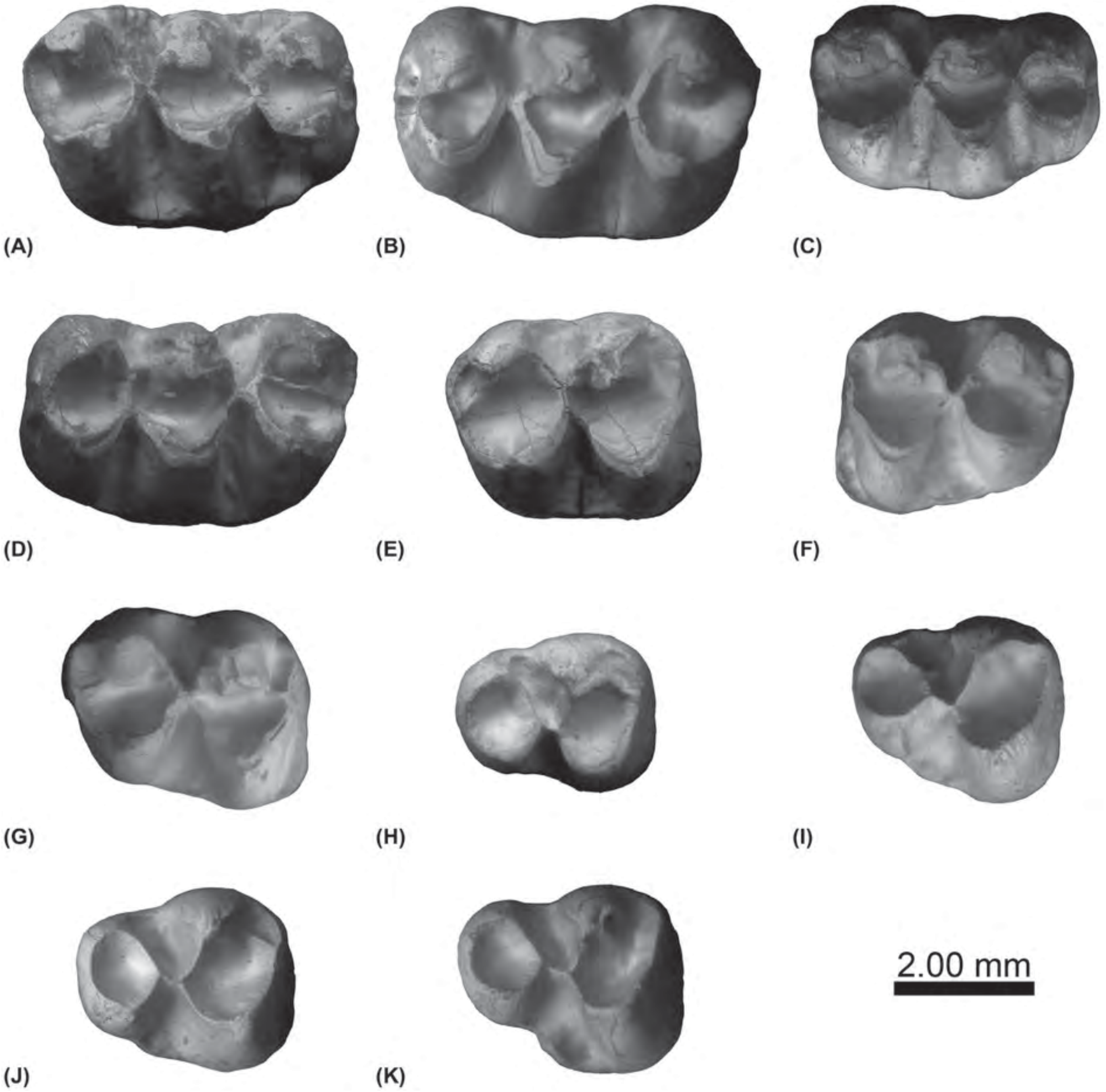

Figure 4. Isolated upper teeth of *A. darderi* sp. nov. from NB-1, Mallorca. (A) right M1, IMEDEA 104213; (B) left M1, IMEDEA 104215; (C) right M1, IMEDEA 104533; (D) left M1, IMEDEA 104680; (E) right M2, IMEDEA 104219; (F) left M2, IMEDEA 104535; (G) right M2, IMEDEA 104538; (H) right M3, IMEDEA 94868; (I) right M3, IMEDEA 104240; (J) right M3, IMEDEA 104251; (K) right M3, IMEDEA 104546. Scale bar 2 mm.

available m3. Usually m3 is longer than m2. Shape of m3 frequently subtriangular (the posterior side somewhat narrower than the anterior). Anterior protolophule frequent in M1, rare in M2 and present in 50% of M3. Ectoloph not developed in M1 nor in M2, practically absent in M3. Mesoloph absent in upper molars. Posterior metalophule frequently developed in M1 and very frequently in M2. The edges of labial cusps of upper molars sometimes carved.

Differential diagnosis – Larger than all known mainland cricetines. Only the endemic insular taxa *Tragomys macpheei* from CdR, *Hattomys gargantua* Freudenthal, 1985 and *Mystemys giganteus* Savorelli and Masini, 2016 from Gargano (Italy) are significantly larger than *A. darderi* sp. nov.

A. darderi sp. nov. differs from the other species of *Apocricetus* (*A.* aff. *plinii*, *A. plinii*, *A. alberti*, *A. barrierei* and *A. angustidens*) by the presence of labial (100%) and lingual (31.9%) anterolophid in m1, a relatively high frequency of triple anterolophulids (21.3%), a reduced anterosinusid in m2 (13%) and m3 (34.7%) and, rarely, an ectomesolophid in m3 (12.2%).

A. darderi sp. nov. differs from *T. macpheei* by having molars that are not hypsodont or selenodont; absence of mesolophid in m1

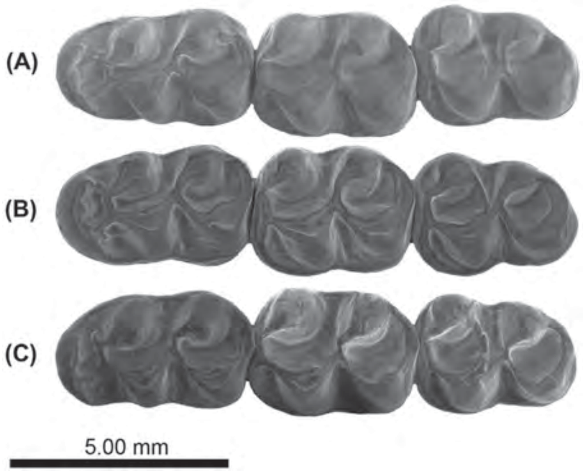

Figure 5. Lower teeth rows of *A. darderi* sp. nov. from NB-1, Mallorca. (A) left mandible, IMEDEA 94726 (holotype); (B) left mandible, IMEDEA 104661; (C) left mandible, IMEDEA 104971. Scale bar 5 mm.

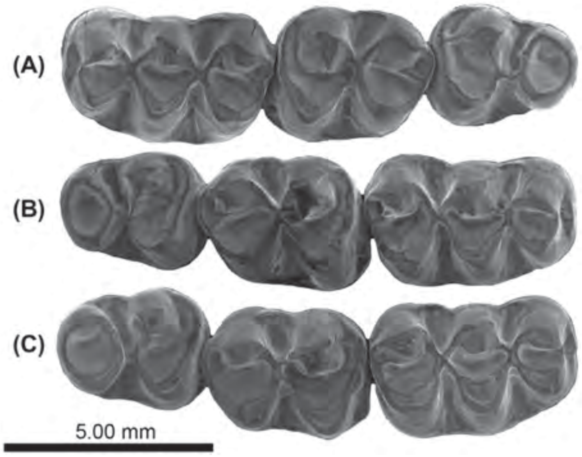

Figure 6. Upper teeth rows of *A. darderi* sp. nov. from NB-1, Mallorca. (A) left maxilla, IMEDEA 104177; (B) right maxilla, IMEDEA 104677; (C) right maxilla, IMEDEA 106304. Scale bar 5 mm.

and m2; m3 longer than m2; presence of an anterior cingulum ridge in M1; anterior protolophule of M1 present as a low crest; anterior protolophule present in 14.7% of the M2; mesosinus divided by the posterior protolophule; in M3, as in M2, an anterior protolophule may be present.

Measurements – See Tables 1–4.

Description of the type material (number of specimens in brackets)

Lower dentition

m1 – Simple crest-like anteroconid (28) (Figures 3(B) and 5(A)); bifid (12) (Figures 3(A) and 5(C)), or trifid (7) (Figures 3(C), (D) and 5(B)). Wide prelophid present (43). Anterolophulid simple and labial without lingual spur (6) (Figure 3(D)), simple and labial with a small lingual spur (2) (Figure 5(C)), double (31) (Figures 3(B), (C) and 5(A), (B)), or triple (10) (Figure 3(A)). Usually both anterolophulids converge to the prelophid and only in two specimens are parallel, while in other two the lingual anterolophulid has a central position. There is a short labial anterolophid in all specimens. Lingual anterolophid very short (15) (Figure 3(C)), long (1), or reaching the metaconid (4). Mesolophid present in two specimens only. Ectomesolophid always absent. Anterior metalophulid always present, posterior metalophulid only in five cases (Figure 3(C)). One specimen has a posterior hypolophulid. The posterolophid, always connected to the base of the entoconid, closes the posterosinusid. The m1 displays two long roots.

m2 – Well-developed labial anterolophid which descends to the base of the protoconid, confining a wide and deep protosinusid. A small lingual anterolophid may be present (6), delimiting a narrow anterosinusid (Figure 3(G)). A short anterior metalophulid is always present. Mesolophid and ectomesolophid always absent. Usually two low cingulum ridges close the mesosinusid and the sinusid, and a low posterolophid is directed towards the base of the entoconid, closing the C-shaped posterosinusid. The m2 has two roots.

m3 – Mansino et al. (2014) established five m3 categories (1: extremely triangular, 1.35–1.31; 2: very triangular, 1.30–1.26; 3: moderately triangular, 1.25–1.21; 4: subtriangular, 1.20–1.11; 5: subrectangular, 1.10–1.0). We recognise a group of molars with moderately triangular shape (Category 3: six out of 51 specimens, 11.8%), another one with slightly triangular shape (Category 4: 40 specimens, 78.4%) and a third group with subrectagular shape (Category 5: five specimens, 9.8%). As in m2, m3 shows a well-developed labial anterolophid that reaches the base of the protoconid. This crest surrounds the protoconid, reaching the sinusid (11) (Figures 3(I), (K) and 5(B)). A short lingual anterolophid is present (17), delimiting a narrow anterosinusid (Figures 3(I), (K) and 5(A), (B)). A short anterior metalophulid is always present. Mesosinusid and sinusid closed by two low cingulum ridges. The mesolophid is always present; it may be short (14) (Figures 3(I) and 5(A)) or long (15), reaching the base of the metaconid (Figures 3(J), (K) and 5(B), (C)). A small ectomesolophid is present (6) which connects to the posterior wall of the protoconid (Figure 3(J), (K)). A low posterolophid is always directed to the base of the entoconid and closes the posterosinusid. The m3 has two roots.

Upper dentition

M1 – An anterior cingulum ridge on the base of the anterocone delimits a small cuspule (25) (Figures 4(D) and 6(C)). This cuspule is divided by a small ridge (21) (Figures 4(B) and 6(A), (B)). Anterior cingulum absent in four specimens (Figure 4(C)). Double anterocone formed by two cusps connected anteriorly. The anterolophule is always double, and sometimes forked (8) (Figure 3(B), (C)). Short preloph (21) (Figures 4(D) and 6(A–C)). The posterior protolophule is always present. A small anterior protolophule is present (24) (Figures 4(B), (D) and 6(A–C)) or absent (5) (Figure 4(C)). Mesoloph and ectomesoloph always absent. A well-developed anterior metalophule is always present and a posterior metalophule sometimes appears (12) (Figures

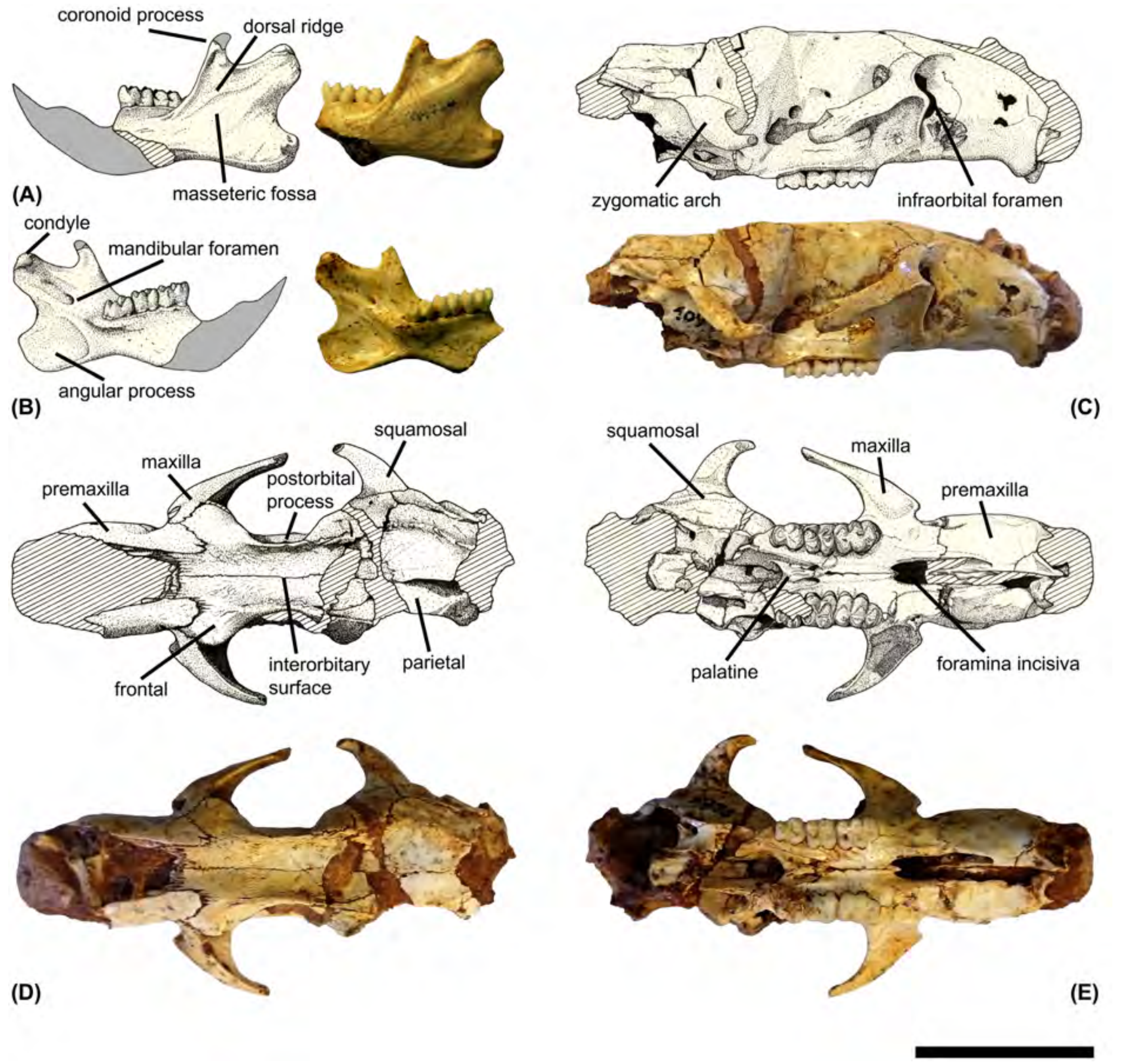

Figure 7. Photographs and drawings of the left mandible IMEDEA 94726 (holotype) in (A) lateral and (B) medial views, and the skull IMEDEA 104796 in (C) lateral, (D) dorsal and (E) ventral views. Grey shaded areas, based on other specimens, indicate reconstruction of the hypothetical bone shape. Scale bar 2 cm.

Table 1. Measurements of the teeth of *A. darderi* sp. nov.

		Length				Width				
Element	*N*	min	mean	max	σ	min	mean	max	σ	L/W
m1	64	3.82	4.25	4.71	0.18	2.35	2.67	3.07	0.17	1.59
m2	57	3.32	3.59	3.87	0.12	2.34	2.82	3.16	0.16	1.27
m3	60	3.31	3.71	4.25	0.17	2.37	2.71	2.95	0.15	1.37
M1	33	4.22	4.68	4.99	0.18	2.75	3.06	3.33	0.14	1.53
M2	42	3.35	3.65	3.96	0.12	2.74	3.07	3.41	0.16	1.19
M3	43	2.88	3.26	3.54	0.17	2.41	2. 72	3.07	0.16	1.20

4(D) and 6(A), (C)). The basal cingulum is more developed in the mesosinus than in the sinus. A posteroloph, always connected directly to the posterior wall of the metacone, closes the posterosinus. The M1 has four roots.

M2 – A well-developed labial anteroloph is always present, enclosing a deep anterosinus. The labial anteroloph always reaches the base of the paracone, being long (31) (Figures 4(E), (F) and 6(A–C)) or short (3) (Figure 4(G)). A short lingual anteroloph is

Table 2. Measurements of upper and lower teeth row of *A. darderi* sp. nov.

		Length			
Teeth row	*N*	min	mean	max	*σ*
Mandible	31	10.71	11.51	12.31	0.42
Maxilla	18	10.90	11.35	11.88	0.34

Table 3. Measurements of skulls of *A. darderi* sp. nov.

	Skulls			
IMEDEA	94797	104129	104796	104134
Maximum width of nasals	–	9.03	–	–
Diastema length	–	16.65	16.44	–
Zygomatic width	–	–	30.90*	–
Interorbitary width	7.25	6.90	4.44	–
Frontal length	22.68	–	–	–
Parietal length	7.30	–	6.50	–
Rostral length**	–	28.36	28.06	–
Palatal length	–	11.35	11.89	–
Palatal width	–	4.60	5.20	–
Choana width	–	5.75	4.11	–
Maximum width of the occipital condyles	–	–	–	12.03

*Estimated measure;
**Measured from the posterior edge of the incisor alveolus to the posterior edge of M3.

Table 4. Measurements of jaws of *A. darderi* sp. nov.

	Jaws				
	N	Min	Mean	Max	*σ*
Maximum length	7	28.85	33.59	36.26	2.60
Diastema length	23	7.91	9.48	10.56	0.81
Infrarostral length*	23	15.10	20.34	21.95	1.05
Ramus height	5	14.29	16.71	18.26	1.89

*Measured from the posterior edge of the incisor alveolus to the posterior edge of m3.

present at the base of the crown, enclosing a reduced protosinus (27) (Figures 4(F), (G) and 6(A–C)). The posterior protolophule is always present, while the anterior protolophule is only present in five specimens (Figure 4(G)). Mesoloph and ectomesoloph always absent. Anterior metalophule always present. The posterior metalophule is well developed (24) (Figures 4(E–G) and 6(A–C)). Labial and lingual basal cingula close the mesosinus and the sinus, respectively. The posteroloph is always curved and connects directly with the posterior wall of the metacone, closing the posterosinus. As in M1, M2 has 4 roots.

M3 – A well-developed labial anteroloph is always present, connecting to the anterior wall of the paracone. A reduced lingual anteroloph is present at the base of the crown (15) (Figure 6(A–C)). The posterior protolophule is always present. Anterior protolophule complete (18) (Figures 4(H), (J) and 6(A), (C)). The mesoloph is always absent and an ectoloph, connecting paracone to metacone, is present only in three specimens (Figure 4(I)), the other three showing a small spur on the paracone (Figure 6(C)). The metalophule is always anterior. Labial and lingual basal cingula close the mesosinus and the sinus. There are five specimens showing the posteroloph on the postero-lingual side of the teeth, connecting it to the basal cingulum of the sinus (Figure 4(I)), whereas five molars show a small lingual spur on this side (Figure 6(A), (B)). The other posterolophs connect directly with the posterior wall of the metacone, closing a reduced subcircular posterosinus. A marked mesocingulum on the labial side of the metacone connecting the cusp with the mesosinus (14) (Figures 4(H), (I) and 6(B)). The M3 displays three roots.

Skull – IMEDEA 94797 corresponds to a partial skull, with preservation of a small portion of the right premaxilla, both frontals, part of the posterior right zygomatic arch (squamosal), both parietals and the anterior part of the interparietal. IMEDEA 104129 is a well-preserved skull lacking nasals and braincase. IMEDEA 104796 is the most complete skull, with the right zygomatic arch preserved practically intact (without jugal) and a part of the braincase; the nasals are not preserved either (Figure 7C–E). The occipital bone IMEDEA 104134 is practically complete and the foramen magnum is preserved.

IMEDEA 104129 and 104796 show a broad rostrum. The infraorbital foramen is wider above than below. All the skulls have very prominent supraorbital ridges that extend to less marked ridges on the temporal areas. The frontals are markedly inflated near the anterior part of the orbits and have a concave interorbitary surface. The postorbital processes are very reduced, slightly angular and located on the postero-dorsal margin of the orbit. In lateral view, the zygomatic arch is located high on the braincase. The incomplete zygomatic arch of IMEDEA 104796 appears to possess a short jugal. In the specimens IMEDEA 104129 and 104796, the foramina incisiva do not reach the M1 and the posterior end of the palatine is located at the level of the M3.

Jaw – 35 partial and two complete jaws (IMEDEA 104656 and 106188) have been recovered from NB-1. Overall, they show a tiny coronoid process, which is slightly curved posteriorly at its tip. In medial view, the tip of the coronoid process does not overreach the mandibular foramen. The condyle is almost vertical and relatively close to the m3. The angular process is greatly expanded and its separation from the condyle is represented by a shallow curved edge. The dorsal ridge of the masseteric fossa is significantly pronounced, providing a deep space on the coronoid process for the attachment of the anterior and posterior temporalis muscles.

Comparative analysis

Biometric aspects

A continuous trend of increasing size with time is well documented in continental *Apocricetus*. Although size has been widely used as a proxy for species identification in the *Apocricetus* lineage, the size range of some species overlaps with their immediate ancestors and descendants, particularly in the earliest forms (i.e. *A.* aff. *plinii* – *A. plinii* – *A.alberti*). Consequently, size is not the best criterion for discriminating species of *Apocricetus*, except for the more recent species (*A. barrierei* and *A. angustidens*) (Mansino et al. 2014; Ruiz-Sánchez et al. 2014). *A. darderi* sp. nov. is much larger than any continental *Apocricetus* (Figure 8), owing to its insular evolution. Following Ruiz-Sánchez et al. (2014) and Mansino et al. (2014), the m2 to m3 length ratio (i.e. m2 length/m3 length) decreases from the earliest species to the more recent (with some exceptions, probably due to sample size). Generally, m2 and m3 are well differentiated in *A.* aff. *plinii* and *A. plinii*, with m2 longer than m3 (ratio > 1), while this ratio is <1 in *A.*

darderi sp. nov., as more commonly observed in *A. alberti* and *A. barrierei*.

Although there are few available teeth of *Tragomys* (especially third molars, *n* = 2), its first and second molars are larger than those of *A. darderi* sp. nov. For these molars, the L/W ratio is clearly higher in *T. macpheei* (Table 1 in Agustí et al. 2012) than in *A. darderi* sp. nov. (Table 1).

Morphological differences in lower molars with respect to Apocricetus *spp.*

According to Mansino et al. (2014), the morphology of the anteroconids and anterolophulids of m1, the presence of a prelophid in m1, the frequency of anterosinusids and mesolophids in m2 and m3, and the shape of m3 are diagnostic traits which justify the distinction of the species of *Apocricetus*.

In the earliest species, the divisions of the anteroconid are well defined. *A.* aff. *plinii* from Crevillente-23 can display two or three lobes, while *A. plinii* Crevillente-15 usually has two lobes (Freudenthal et al. 1991, 1998). *A. alberti* from Venta del Moro shows predominantly two lobes or a crest-like anteroconid and rarely three lobes (Mansino et al. 2014). On the other hand, in the more recent species of the lineage, a crest-like anteroconid commonly occurs, although occasionally it can display two weak lobes (Freudenthal et al. 1998; Ruiz-Sánchez et al. 2014). A crest-like anteroconid frequently occurs (59.6%) in *A. darderi* sp. nov., although a significant percentage of anteroconids are subdivided into two (25.5%) or three (14.9%) lobes.

The anterolophulid of *A.* aff. *plinii* from Crevillente-23 and *A. plinii* from Crevillente-15 is simple or forked (with a branch directed to each anteroconid cuspid; Freudenthal et al. 1991, 1998), while a double anterolophulid arising from a prelophid is commonly found in *A. barrierei* from La Bullana-2B and 3B and *A. angustidens* from Serrat den Vaquer (Freudenthal et al. 1998; Ruiz-Sánchez et al. 2014). Instead, *A. alberti* shows a combination of features from both the earliest and the more advanced species. 35.8% of the specimens from Venta del Moro possess a double anterolophulid (double+forked) and 46.2% have a prelophid (Mansino et al. 2014, see Table 2). In *A. darderi* sp. nov., the anterolophulid is predominantly double convergent (61.7%), but it may be triple (21.3%), simple (12.8%) or double parallel (4.2%). 91.5% of the specimens have a prelophid (Table 5).

The m2 and m3 anterosinusid is absent in *A. alberti* from Venta del Moro as well as in *A. barrierei* from La Bullana-2B and 3B (Mansino et al. 2014; Ruiz-Sánchez et al. 2014). However, the anterosinusid in *A.* aff. *plinii* from Crevillente-23 is better

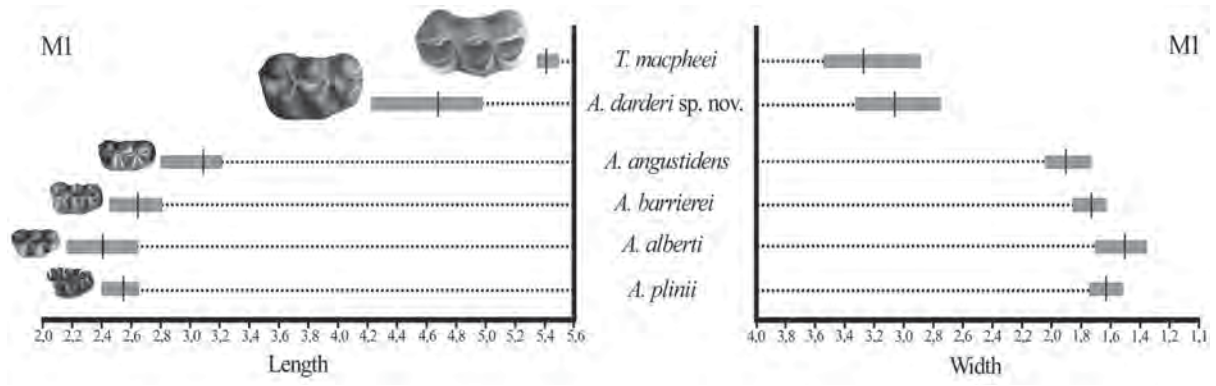

Figure 8. Maximum, minimum and mean length and width of the M1 in *A. plinii* from Crevillente-15 (Freudenthal et al. 1991), *A. alberti* from Venta del Moro A (Mansino et al. 2014), *A. barrierei* from La Bullana 2B (Ruiz-Sánchez et al. 2014), *A. angustidens* from Mont-Hélène (Freudenthal et al. 1998), *A. darderi* sp. nov. from Na Burguesa-1 and *T. macpheei* from Caló den Rafelino (Agustí et al. 2012).

Table 5. Variation of characters in the lower molars of *A. darderi* sp. nov.

	m1	m2	m3
Anteroconid	Crest-like: 28/47 (59.57%) 2 lobes: 12/47 (25.53%) 3 lobes: 7/47 (14.90%)	–	–
Anterolophid	Labial: 47/47 (100%) Lingual: 15/47 (31.91%)	Labial: 46/46 (100%) Lingual: 6/46 (13.04%)	Labial: 49/49 (100%) Lingual: 17/49 (34.69%)
Anterolophulid	Simple: 6/47 (12.77%) Double convergent: 29/47 (61.70%) Double parallel: 2/47 (4.25%) Triple: 10/47 (21.28%)	– – – –	– – – –
Prelophid	Present: 43/47 (91.49%) Absent: 4/47 (8.51%)	–	–
Mesolophid	Present: 2/47 (4.26%)	Absent	Short: 14/49 (28.57%) Long: 35/49 (71.43%)
Ectomesolophid	Absent	Absent	Present: 6/49 (12.24%)
Metalophulid	Anterior: 47/47 (100%) Posterior: 5/47 (10.64%)	Anterior: 46/46 (100%) Posterior: 0	Anterior: 49/49 (100%) Posterior: 0
Posterior hypolophulid	Present: 1/47 (2.13%)	–	–

developed in m3 than in m2, while it appears only in some m3 of *A. angustidens* from Serrat den Vaquer (Freudenthal et al. 1998). *A. plinii* from Crevillente-15 has a reduced anterosinusid, which is present in 64.7% of m2 and in 44.5% of m3 (Freudenthal et al. 1991, 1998; Mansino et al. 2014). In *A. darderi* sp. nov., only a small anterosinusid is present in 13% of m2 and 34.7% of m3.

In *A. plinii* from Crevillente-15, a labial anterolophid surrounds the protoconid in 11.1% of m2 and 26.3% of m3 (Freudenthal et al. 1991), whereas, in *A. alberti* from Venta del Moro, it appears in 14% (1 out of 71) of m2 and 3.8% (2 out of 53) of m3 (Mansino et al. 2014). This feature has not been observed in the more recent species (Mansino et al. 2014). In *A. darderi* sp. nov., 21.7% of m2 and 24.5% of m3 display a well-developed labial anterolophid that surrounds the protoconid. The presence of a mesolophid in m2 of *A. alberti* from Venta del Moro is uncommon (7.8%), although 31.3% of m2 have a reduced spur (Mansino et al. 2014). In *A.* aff. *plinii* from Crevillente-23, the mesolophid is present in 34.6% of specimens (Freudenthal et al. 1998), whereas it is absent in *A. plinii*, *A. barrierei* and *A. angustidens*, as well as in *A. darderi* sp. nov.

The frequency of the mesolophid in m3 in the *Apocricetus* lineage decreases progressively with time (Mansino et al. 2014). In *A.* aff. *plinii* from Crevillente-23, a mesolophid is present in 91.4% of the specimens, while *A. plinii* from Crevillente-15 shows a frequency of 86.4%. Its frequency in *A. alberti* from Venta del Moro reaches 78.7%. In *A. barrierei* from La Bullana-2B and 3B, it is present in 46.2% of specimens, while it appears in 46.7% of the specimens of *A. angustidens* from Serrat den Vaquer. In *A. darderi* sp. nov., the mesolophid of m3 is present in all the specimens and reaches the base of the metaconid in 71.4% of cases.

The shape of m3 changes along the *Apocricetus* lineage (Freudenthal et al. 1998; Mansino et al. 2014; Ruiz-Sánchez et al. 2014). This trait can be assessed using the anterior width/posterior width ratio (Mansino et al. 2014). Higher values indicate a narrower posterior side (triangular shape), while lower values close to 1 correspond to teeth with a posterior side equivalent to the anterior (rectangular shape). During the evolution of the lineage of the mainland *Apocricetus*, there is a change in shape of m3 from subtriangular to a subrectangular pattern, *sensu* Mansino et al. (2014). *A. plinii* from Crevillente-15 and *A. alberti* from Venta del Moro fall mainly in category 4 (95.7 and 84.3%, respectively), but some m3 of *A. alberti* are subrectangular (category 5). The m3 of *A. barrierei* from La Bullana-2B and 3B and *A. angustidens* from Mont-Hélène fall invariably in categories 4 (60.9 and 50%, respectively) and 5 (39.1 and 50%, respectively) (see Mansino et al. 2014, Figure 8). The shape of m3 in *A. darderi* sp. nov. falls in the latter three categories, but predominantly in category 4 (78.4%).

Morphological differences in upper molars with respect to* Apocricetus *spp.

According to Freudenthal et al. (1991, 1998), Ruiz-Sánchez et al. (2014) and Mansino et al. (2014), the following major diagnostic traits in the upper molars can be used to identify species within the lineage: (1) presence/absence of an anterior cingulum ridge in M1, (2) number and morphology of anterolophules in M1, (3) degree of development of a preloph, (4) presence/absence of a mesoloph in M1 and M2, and (5) presence and degree of development of an anterior protolophule and a posterior metalophule on upper molars.

In *A.* aff. *plinii*, *A. plinii* and *A. alberti* from their type localities, the anterior cingulum ridge of M1 is absent (Freudenthal et al. 1991, 1998). However, a weak cingulum is present in 13.5% of the specimens *of A. alberti* (Mansino et al. 2014). This cingulum is absent or weak In *A. barrierei* (16.7%, Ruiz-Sánchez et al. 2014), whereas it is well developed in *A. angustidens*. The anterior cingulum ridge of *A. darderi* sp. nov. is present and well developed in 86.2% of specimens, being simple in 13.8% and divided by a short central crest in 72.4% (Table 6).

In *A.* aff. *plinii* from Crevillente-23 and *A. plinii* from Crevillente-15, the anterolophule may be simple or forked, the latter lacking a preloph. In *A. alberti* from Venta del Moro, it may be simple (7.5%), forked (57.5%) or double with a preloph (35%), the latter being diffuse in some specimens (Mansino et al. 2014). *A. barrierei* from La Bullana-2B and 3B has a well-developed double anterolophule with a short preloph that is more marked than in *A. alberti* (Mansino et al. 2014; Ruiz-Sánchez et al. 2014). In *A. darderi* sp. nov., the anterolophule may be double (72.4%) or forked (27.6%), and 72.4% of the specimens have a preloph.

Both *A.* aff. *plinii* from Crevillente-23 and *A. plinii* from Crevillente-15 show a mesoloph in M1 and M2, whereas it is absent in the rest of the species, including *A. darderi* sp. nov.

The earliest species of the lineage display an anterior protolophule (50–60% of the M1; Mansino et al. 2014), while it is less frequently developed in the more recent species (Ruiz-Sánchez

Table 6. Variation of characters in the upper molars of *A. darderi* sp. nov.

	M1	M2	M3
Anterocone (Cingulum ridge)	Simple cuspule: 4/29 (13.79%) Divided cuspule: 21/29 (72.41%) Absent: 4/29 (13.80%)	–	–
Anteroloph	–	Labial: 34/34 (100%) Lingual: 27/34 (79.41 %)	Labial: 37/37 (100%) Lingual: 15/37 (40.54%)
Anterolophule	Double: 21/29 (72.41%) Forked: 8/29 (27.59%)	– –	– –
Preloph	Present: 21/29 (72.41%) Absent: 8/29 (27.59%)	–	–
Protolophule	Anterior: 24/29 (82.76%) Posterior: 29/29 (100%)	Anterior: 5/34 (14.71%) Posterior: 34/34 (100%)	Anterior: 18/37 (48.65%) Posterior: 37/37 (100%)
Mesoloph	Absent	Absent	Absent
Ectoloph	Absent	Absent	Paracone spur: 3/37 (8.11%) Complete: 3/37 (8.11%)
Metalophule	Anterior: 29/29 (100%) Posterior: 12/29 (41.38%)	Anterior: 34/34 (100%) Posterior: 24/34 (70.59%)	Anterior: 37/37 (100%)

et al. 2014). The posterior metalophule is present in 45.5% of specimens of *A.* aff. *plinii* from Crevillente-23, 23.1% of *A. plinii* from Crevillente-15, 17.1% of *A. alberti* from Venta del Moro, while it is practically absent in *A. barrierei* from La Bullana-2B and 3B, and totally absent in *A. angustidens* from Mont-Hélène (Mansino et al. 2014). In *A. darderi* sp. nov., the anterior protolophule appears in 82.8% of the specimens, and the posterior metalophule in 41.4% of the M1.

The anterior protolophule of M2 is present in almost all specimens of the earliest species (100% in *A.* aff. *plinii* from Crevillente-23), while its frequency progressively decreases in the more recent species (23.1% in *A. angustidens* from Mont-Hélène) (Mansino et al. 2014). The posterior metalophule shows a gradual decrease in frequency from 51.7% in *A.* aff. *plinii* to 35.3% in *A. barrierei* from La Bullana-2B and 3B (Mansino et al. 2014), becoming absent in *A. angustidens* from Mont-Hélène (Freudenthal et al. 1991, 1998; Ruiz-Sánchez et al. 2014). In *A. darderi* sp. nov., the anterior protolophule appears in 14.7% of M2, and the posterior metalophule in 70.6% of the molars.

A well-developed anterior protolophule of M3 is always present in the earliest species of the *Apocricetus* lineage. In *A. barrierei* from La Bullana-2B and 3B, it may be elongated or absent, depending on the palaeontological site. In *A. angustidens*, it is present in 33.3% of the specimens from Mont-Hélène (Freudenthal et al. 1998; Ruiz-Sánchez et al. 2014). In *A. darderi* sp. nov., 48.6% of the M3 display an anterior protolophule.

Morphological differences in lower molars with respect to Tragomys macpheei

The most distinctive trait of *T. macpheei* compared with *A. darderi* sp. nov. is the high degree of hypsodonty and selenodonty of its lower molars. As *T. macpheei* is a putative descendant of *A. darderi* sp. nov., the selenodont pattern exhibited in the former could have resulted from the modification of the condition found in *A. darderi* sp. nov. through the appearance of new crests and a general remodelling of teeth.

Compared to *A. darderi* sp. nov., *T. macpheei* displays an m1 with a reduced anteroconid, which comprises two weak lobes. *T. macpheei* has only a small labial anterolophid, while *A. darderi* sp. nov. usually shows, in addition, a lingual anterolophid (31.9%). The anterolophulids of *T. macpheei* are double, one labial, generally very thick, and another lingual, short and slightly thinner than the labial. *A. darderi* sp. nov. exhibits from one to three narrow anterolophulids. *T. macpheei* has a well-developed prelophid, but it does not connect with the protoconid (i.e. the protoconid anterior arm connects directly with the anterior metalophulid in the lingual extremity of the prelophid). This feature does not appear in *A. darderi* sp. nov. The posterior metalophulid has never been observed in *T. macpheei*, whereas it is uncommon (10.6%) in *A. darderi* sp. nov. Additionally, all m1 of *T. macpheei* show a crest interpreted as a mesolophid by Agustí et al. (2012), although it could be alternatively considered as a newly formed crest linked to the selenodonty-derived pattern. The mesolophid is practically non-existent in *A. darderi* sp. nov. (4.3%).

The anterior half of m2 in *T. macpheei* is proportionally more developed than in *A. darderi* sp. nov. *T. macpheei* shows predominantly a narrow protosinusid delimited by the labial anterolophid, and the lingual anterolophid is absent, while there is a wide protosinusid in *A. darderi* sp. nov., in some cases associated with a lingual anterolophid (13%). As observed in m1, the specimens of *T. macpheei* show a crest that could be interpreted as a mesolophid or a newly formed crest linked to the selenodonty derived pattern, which may reach the base of the metaconid; it is absent in *A. darderi* sp. nov.

The two available m3 of *T. macpheei* display a well-developed labial anterolophid, as in *A. darderi* sp. nov., although the latter species may also have a lingual anterolophid (34.7%). In both *T. macpheei* teeth, the mesolophid connects with the metaconid. There are some specimens of *A. darderi* sp. nov. that show a short mesolophid that does not reach the metaconid (28.6%). *T. macpheei* lacks an ectomesoloph, while this crest is present in 12.2% of the specimens of *A. darderi* sp. nov. Unfortunately, the *T. macpheei* sample available for study is very limited, and some of the recorded differences could only be properly evaluated after collecting additional specimens of this highly modified species.

Morphological differences in upper molars with respect to T. macpheei

The anterocone of M1 of *T. macpheei* displays from 1 to 3 small anterior ridges descending to the base of the crown through the anterior wall of the anterocone, while *A. darderi* sp. nov. possesses an anterior cuspule that may or may not be divided by a small crest. *T. macpheei* has a well-formed double anterolophule and preloph, that in some specimens may be weakly connected to the anterior arm of the protocone. This connexion is more clear in *A. darderi* sp. nov.

T. macpheei shows an anterior and a posterior protolophule, as in *A darderi* sp. nov., although, in the former, the anterior protolophule reaches the apex of the paracone. Moreover, *T. macpheei* has only an anterior metalophule, while 41.4% of the specimens of *A. darderi* sp. nov. also display a posterior metalophule.

The M2 of *T. macpheei* has a labial anteroloph that reaches the base of the paracone, as in *A. darderi* sp. nov., but it is much more developed with an extension in the anterolabial wall that reaches the base of the crown. Whereas *T. macpheei* has a very small basal ridge on the anterolabial wall of the protocone, *A. darderi* sp. nov. may display a reduced lingual anteroloph (79.4%) at the base of the crown. *T. macpheei* displays a spur on the protocone anterior arm, probably a vestige of the anterior protolophule. On the other hand, in 14.7% of the specimens of *A. darderi* sp. nov., the anterior protolophule is well developed. The connection between the posterior arm of the protocone with the hypocone anterior arm is weak in *T. macpheei*, whereas this contact is well defined in *Apocricetus darderi* sp. nov. The posterior metalophule is always absent in *T. macpheei*.

In *T. macpheei*, there is a spur on the anterolingual side of the paracone of the M3, perhaps corresponding to a vestigial anterior protolophule. The posterior protolophule is thick and well developed. *A. darderi* sp. nov. shows an anterior protolophule in 48.6% of the specimens and a thin posterior protolophule in all cases. While the ectoloph is well formed in *T. macpheei*, it is completely developed in *A. darderi* sp. nov., where a spur is formed on the paracone in only 8.1% of the specimens analysed. The sinus of *T. macpheei* is more reduced than in *A. darderi* sp. nov.

Skull and mandible of **A. darderi** *sp. nov.*

The absence of skulls attributed to the mainland species of *Apocricetus* or the insular *T. macpheei* precludes any comparison with the new species. On the contrary, the holotype of *Hattomys gargantua* (RGM 263 555) consists of a nearly complete skull. It shows great structural similarities with *A. darderi* sp. nov., especially as regards the high position of the zygomatic arch in lateral view, the position of the foramina incisiva in relation to M1, and the extension of the posterior margin of the palatine with respect to M3.

In the same way, the absence of jaws from the mainland species of *Apocricetus* or from the insular cricetines *Hattomys* and *Tragomys* rules out any comparison with *A. darderi* sp. nov. Compared with the extant *Cricetus* (Linnaeus, 1758), *Mesocricetus auratus* Waterhouse, 1839 and *Phodopus* Miller, 1910 spp., the jaw of *A. darderi* sp. nov. shows a remarkably peculiar and distinctive morphology. In fact, these extant cricetines possesses a long and highly curved coronoid process that exceeds the mandibular foramen, especially in *M. auratus*. Their condyles are situated in a lower position compared to *A. darderi* sp. nov., and the distance between the condyles and the m3 is longer. In these extant taxa, the mandibular edge separating the angular process and the condyle is always deep, and the angular process is narrow; these features mean that the angular process has a longer appearance.

Discussion and conclusions

Apocricetus was defined by Freudenthal et al. (1998) to include medium to large-sized species of cricetines characterised by m1 and m2 lacking a mesolophid, m1 with a labial (either single or double) anterolophulid, and a long m3. In the upper molars, the anterior protolophules and the posterior metalophules are reduced or absent (Freudenthal et al. 1998). So far, the genus includes five forms: *A.* aff. *Plinii*, *A. plinii*, *A. alberti*, *A. barrierei* and the type species *A. angustidens*. The genus ranges from the Early Turolian, MN11 (*A.* aff. *plinii*) to the Early Villanyan, MN16 (*A. angustidens*) (Bachelet et al. 1990; Freudenthal et al. 1998). An increase in size (Freudenthal et al. 1998) and several morphological changes have occurred during the evolution of *Apocricetus*, such as the shape of m3, which shows a predominantly subtriangular outline in the earliest species and subrectangular in the most recent (Mansino et al. 2014). The morphological changes of *Apocricetus* during its evolution have become an essential tool for establishing a biostratigraphic framework between the Late Miocene and the Late Pliocene in southern Europe (Freudenthal et al. 1998; García-Alix et al. 2008a, 2008b; Minwer-Barakat et al. 2012; Mansino et al. 2014; Ruiz-Sánchez et al. 2014). The discovery of a representative of this lineage in Mallorca shows that a stock of the Late Turolian (MN 13) *A. alberti* reached the island during the MSC, coinciding with the biostratigraphic range of *A. alberti*. Thus, a population was established that became isolated 5.33 Ma ago and evolved under insular conditions. The isolation of this population gave rise to the cricetine described herein, which probably evolved later into *T. macpheei* displaying an unusual goat-like dentition. An alternative interpretation of the relationship between *A. darderi* and *T. macpheei* is to consider them as sister species derived from a common ancestor.

The new insular cricetine described here, despite its giant size, shows remarkable morphological features commonly displayed by members of the genus *Apocricetus*. Considering both the evolution of small mammals introduced by humans onto islands and the fossil record of autochthonous small mammals, the first effect of insular mammalian evolution frequently involves a change in body size, eventually followed by morphological modifications that can blur the phylogenetic relationships with continental ancestors. Once acquired new dentition patterns, new increases of body size are frequently recorded.

The attribution of the cricetine of NB-1 to the genus *Apocricetus* is based on (1) the absence of a mesolophid in m1 and m2, (2) the predominant presence of a double anterolophulid in m1, and (3) a long m3 with respect to m2. *A. darderi* sp. nov. is characterised by a combination of the following features: giant size; large variability in morphology of anteroconid and number of anterolophulids in m1; presence of a labial and, less frequently, a lingual anterolophid in m1; presence in some specimens of a reduced anterosinusid in m2 and m3, and very rarely a ectomesolophid in m3.

The morphological analysis suggests that *A. darderi* sp. nov. is closely related to an advanced form of *A. alberti* from the Late Miocene of Iberian Peninsula (Late Turolian, MN13). This hypothesis is based on:

1. Although practically half of the m1 of *A. darderi* sp. nov. and *A. alberti* display a crest-like anteroconid, both species show m1 with an anteroconid divided into two or three lobes.
2. The variability of anterolophulids present in m1 is only slightly higher in *A. darderi* sp. nov. than in *A. alberti*, while it is lower in *A.barrierei* and *A. angustidens*. On the other hand, both species (*A. darderi* sp. nov. and *A. alberti*) show highly frequent occurrence of a prelophid.
3. In *A. darderi* sp. nov., some m2 and m3 display a labial anterolophid that surrounds the protoconid to reach the sinusid, as in *A. plinii* and *A. alberti*.
4. The frequency of occurrence of a mesolophid in m3 in *A. darderi* sp. nov. matches that of *A. alberti*, while the frequency in *A. barrierei* is lower.
5. The predominant shape of m3 in *A. darderi* sp. nov. (i.e. category 4) is coincident with *A. alberti*.
6. The absence of a mesoloph in M1 and M2 in *A. darderi* sp. nov. is similar to the condition found in *A. alberti*, *A. barrierei* and *A. angustidens*.
7. The absence of a mesolophid in m2 of *A. darderi* sp. nov. differs from the significantly frequent occurrence (39.1%) in *A. alberti*, while it is also absent in *A. barrierei*.
8. The anterolophule of M1 of *A. darderi* sp. nov. is predominantly double and has a preloph, just as observed in *A. barrierei*.

In view of the evolutionary trends recorded in the lineage from *A.* aff. *plinii* to *A. angustidens*, several additional features point to an independent evolution of the peculiar *A. darderi* sp. nov.:

1. *A. darderi* sp. nov. displays a well-developed anterior cingulum ridge in M1; although this ridge may be

present in *A. alberti*, it is in any case less well developed. It is rare In *A. barrierei*, but is widespread and well developed in *A. angustidens*.

(2) In general terms, the anterior protolophule in the upper molars tends to decrease in frequency from the earliest to the more recent species of *Apocricetus*. *A. darderi* sp. nov. shows a higher frequency of occurrence of anterior protolophules on the M1 than in the earliest species of the genus. On the other hand, the anterior protolophule of M2 in *A. darderi* sp. nov. is less frequent than in the more recent species of *Apocricetus*, and the frequency of the anterior protolophule of M3 is intermediate between the frequencies recorded in *A. barrierei* and *A. angustidens*.

(3) In the same way, the occurrence of posterior metalophules in M1 and M2 tends to decrease in frequency from the earliest species to the latest. The posterior metalophule of M1 of *A. darderi* sp. nov. shows a frequency close to that observed in *A.* aff. *plinii*, while the frequency of occurrence of the posterior metalophule of M2 in *A. darderi* sp. nov. is considerably higher than in the earliest species.

Some of the above features, especially in the upper molars, have a low power of resolution to establish the relationships between the different species of *Apocricetus*. Instead, the lower molars appear to provide a better resolution to discriminate among species. Our study demonstrates the close link of *A. darderi* sp. nov. with the more advanced mainland populations of *A. alberti*, thus representing the closest relationship ever established between a Neogene mainland taxon and its Mallorcan descendant. This provides the best currently available biostratigraphic correlation with a continental mammal zone. Despite its gigantism and derived features associated with insular evolution, *A. darderi* sp. nov. retains a number of archaic characters that link it with early members of the genus *Apocricetus*. Such is the case for the frequently double but also triple anterolophulid, the retention of a reduced anterosinusid on some m2 and m3, the subtriangular shape of the m3 and the frequent occurrence of a posterior metalophule in M1. Thus, *A. darderi* sp. nov. seems to be closely related to *A. alberti*, a characteristic species of the MN 13 (latest Miocene) continental faunas. However, as observed with *T. macpheei* from CdR, the giant size of *A. darderi* sp. nov. and the singularity of the fauna from NB-1 (unbalanced and relatively poor species diversity) indicate that the fauna was already insular, i.e. isolated after the Pliocene flooding of the Mediterranean Basin. Thus, despite its MN 13 'aspect', the NB-1 fauna should be considered as coeval with the early Pliocene faunas of the continent commonly assigned to MN 14.

A re-analysis of *T. macpheei* leads us to consider *A. darderi* sp. nov. as its direct ancestor or as a sister taxa evolved from a common ancestor. Both are the sole cricetines present in the Mallorcan Neogene, and *T. macpheei* displays highly derived dental characters. The presence of mesolophids in m1 and m2 in *T. macpheei*, the high development of crests such as the anterior protolophule and the posterior protolophule in M1, or the ectoloph in M2 and M3, mean that this species displays a particular selenodont pattern. Moreover, *T. macpheei* shows a relative increase in molar length and a major reduction of m3 with respect to m2, as well as a high degree of hypsodonty.

Apart from the acquisition of a high degree of hypsodonty and selenodonty, the most noteworthy trend in the lineage from *A. darderi* sp. nov. (or from the common ancestor) to *Tragomys macpheei* involves the important development attained by the M1 with respect to the upper teeth row and the narrowing of teeth, especially the second molars. These four traits are not displayed in *Apocricetus* as defined by Freudenthal et al. (1998), and confirm *Tragomys* as a separate genus derived from *Apocricetus*. According to our interpretation, an advanced stock of *Apocricetus alberti* colonised Mallorca during the MSC. After the refilling of the Mediterranean Basin, this stock started to evolve under insular conditions. The giant *A. darderi* sp. nov. and the highly modified *T. macpheei* subsequently appeared on Mallorca during the isolated evolution of *A. alberti*. If *A. darderi* sp. nov. is confirmed as the ancestor of *T. macpheei*, the fauna from CdR should be considered as a direct descendant of the NB-1 fauna and could be correlated with the upper part of MN14 or perhaps the beginning of MN15.

It is hard to determine accurately the time span that separates the first isolated (i.e. post-Messinian) populations of *A. alberti* on Mallorca from the appearance of its descendant *A. darderi* sp. nov., although it was probably very short in geological terms (perhaps a few thousand years). The huge difference in size between these species, combined with the somewhat similar teeth morphology, fits well with our current knowledge of the evolution of mammals on islands. It has been repeatedly observed that changes in body size are very rapid on islands, especially in rodents (e.g. Millien 2006), while other traits such as teeth morphology evolve slowly (Agustí 1986) and can be followed by a renewed increase in body size. The proposed relationship between *A. alberti* and *A. darderi* suggests that the Eastern Iberian Peninsula is the most probable source region for the Mallorcan taxon.

Although it might be considered unwise to classify species of the same insular phyletic lineage in two different genera, the great similarity in teeth morphology between *A. darderi* sp. nov. and the other species of the genus, together with their remarkable differences with respect to *T. macpheei*, argue in favour of adding the NB-1 cricetine to the genus proposed here. The alternative, i.e. including *Apocricetus* in *Tragomys*, is not favoured since it would imply changing the diagnosis of the genus *Tragomys* to incorporate the moderately modified *A. darderi* sp. nov.

The insular endemic fossil cricetines from the Western Mediterranean Mio-Pliocene consist of *A. darderi* sp. nov. and *T. macpheei* (Mallorca), as well as the lineages of *Hattomys* and *Mystemys giganteus* from the Gargano promontory (Italy). *Hattomys* includes several species, the largest one being *Hattomys gargantua*, which displays an M1 attaining 6 mm in length. Despite the common trend towards gigantism, *Hattomys* differs from both *A. darderi* sp. nov. and *T. macpheei* in the complexity of its anteroconid, the variable presence and morphology of the mesolophid of the lower molars, and the presence of a long mesoloph on the upper molars. However, *Hattomys* also shows some similarities with *A. darderi* sp. nov. i.e.: variable number of anterolophulids (1 to 3), third molars not very reduced and presence of flanges on the anterior and posterior ends of the labial cusps on upper molars (Freudenthal 1985; Savorelli 2013). This latter is one of the singular traits displayed by the upper molars of *Hattomys*. The recently described *Mystemys giganteus* by Savorelli and Masini (2016) is a highly distinctive insular taxon, with exceptionally large M1 teeth (length attaining 6.23 mm) and a primitive molar pattern, moderately hypsodont dental crown, as well as robust and swollen cusps. Its subfamily attribution is uncertain, but even though the few teeth described could be actually referred to the subfamily Cricetinae, this taxon clearly has no direct connection with the evolution of a large species of *Apocricetus* on Mallorca.

The origin of *Hattomys* is still not clear, but it probably derives from a continental cricetid of the Late Miocene. According to Freudenthal (1985), the dental patterns of *Cricetus kormosi* Schaub, 1930 and *Hattomys* might be closely related. If this relationship is confirmed, we cannot rule out the possibility that *Hattomys* also originated from *A. alberti*, taking into account that the earliest faunas from Gargano are correlated with the Turolian of Crevillente (Spain), and that the specimens initially attributed to *Cricetus kormosi* from Spain and southern France were subsequently attributed to *A. alberti* by Freudenthal et al. (1998). In both instances, a peculiar insular evolution took place, leading to gigantism and the acquisition of a particular teeth morphology.

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Morphological divergence in giant fossil dormice

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Insular gigantism—evolutionary increases in body size from small-bodied mainland ancestors—is a conceptually significant, but poorly studied, evolutionary phenomenon. Gigantism is widespread on Mediterranean islands, particularly among fossil and extant dormice. These include an extant giant population of *Eliomys quercinus* on Formentera, the giant Balearic genus †*Hypnomys* and the exceptionally large †*Leithia melitensis* of Pleistocene Sicily. We quantified patterns of cranial and mandibular shape and their relationships to head size (allometry) among mainland and insular dormouse populations, asking to what extent the morphology of island giants is explained by allometry. We find that gigantism in dormice is not simply an extrapolation of the allometric trajectory of their mainland relatives. Instead, a large portion of their distinctive cranial and mandibular morphology resulted from the population- or species-specific evolutionary shape changes. Our findings suggest that body size increases in insular giant dormice were accompanied by the evolutionary divergence of feeding adaptations. This complements other evidence of ecological divergence in these taxa, which span predominantly faunivorous to herbivorous diets. Our findings suggest that insular gigantism involves context-dependent phenotypic modifications, underscoring the highly distinctive nature of island faunas.

1. Introduction

Insular gigantism is a widespread macroevolutionary pattern [1,2]. It occurred on many Mediterranean islands throughout the Neogene and Quaternary, and is known among small mammals including dormice, hamsters, murids, lagomorphs, shrews and moonrats [3–10]. Despite its prevalence, the ecological drivers of insular gigantism are rather complex, with climate, island area, availability of resources, and the presence of competitors and predators all proposed to play a part [2,11–18]. Similarly, the morphological consequences of gigantism are not well understood, and it is not clear whether giant island species have attained large size via similar evolutionary pathways. This raises the possibility that insular gigantism does not represent a single well-defined process, but in fact reflects the outcomes of evolution in a broad set of distinct ecological contexts.

Shape changes associated with increasing body size (allometry) are suggested to either result from optimized functionality based on natural selection, or from constraints that impose fixed or slowly evolving allometric trajectories [19]. Allometric constraints will result in shared allometric patterns (common allometry) among related species, and provide an expectation that evolution will

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proceed along lines of least evolutionary resistance (or 'genetic lines of least evolutionary resistance') [20], represented by a multivariate factor of the genetic or phenotypic variation [21] (but see [22]). Deviation from these lines might be expected during adaptation to distinct ecological niches, resulting in functional modification in shape and size. However, the evolvability of allometric relationships, and therefore the ability of ecological adaptation to cause divergent patterns of phenotypic evolution, is variable [23,24]: divergence from allometric trajectories may be common on long macroevolutionary timescales but are rare on shorter timescales.

The Island Rule describes extensive variation in both shape and size [1], and suggests a graded trend from gigantism in small mammals to dwarfism in larger species [13]. The evolutionary timescales of adaptation to insularity are generally short [25], meaning that divergence from an ancestral allometric trajectory may be difficult to realize [24]. Nevertheless, the exceptional increase in body size associated with insular gigantism can result in unexpected morphologies, and evolutionary shifts to novel ecologies in the context of the island setting might also be a powerful driver of evolutionary changes in morphology via functional adaptation.

Dormice (Gliridae) are potent exemplars of the evolutionary 'island effect' of body size increase, having evolved extraordinary large sizes more frequently than other mammals—and on at least eight different islands since the beginning of the Miocene [26,27]. Furthermore, giant dormice are known from both the fossil record (e.g. *Hypnomys* spp. from the Balearic Islands and *Leithia* spp. from Sicily and Malta) and an extant population of *Eliomys quercinus* on the island of Formentera [28]. Dormice, therefore, provide an ideal study system for addressing key questions regarding insular gigantism.

The fossil giants *Hypnomys* and *Leithia* most likely evolved from a mainland ancestor related to the genus *Eliomys* (Leithiinae) [29–31]. Previous studies uncovered craniomandibular differences between extant *Eliomys* populations and fossil island genera [31–34]. The possibility that they were more than simply enlarged forms of their mainland relatives is further supported by the change in ecological niche displayed by the extant giant population on Formentera, which shows increased faunivory in its diet [28]. Furthermore, the morphological features of the extinct island giants imply alternative lifestyles such as increased terrestriality in *Hypnomys* [31] and herbivory in *Leithia* [32].

Here, the cranial and mandibular morphology in the extant giant *E. quercinus* from Formentera and the extinct giant genera *Leithia* and *Hypnomys* are investigated in the context of a large dataset of non-giant dormouse skulls. *E. quercinus* has a large geographical distribution across Europe, including several populations on Mediterranean islands. Alongside fossil giants and the extant giant population on Formentera, non-giant *E. quercinus* still display significant intraspecific size variations. We aim to understand the transformation of the cranial and mandibular form (size and shape) in giant dormice by investigating the allometric trajectory of non-giant dormice. Characterization of the common allometric trajectory within *E. quercinus* populations enables us to distinguish between morphological differences occurring due to size variations and those potentially related to other factors. We ask to what extent the cranial and mandibular morphologies of island giant dormice are predicted by extrapolation of the allometric trajectory for extant non-giant dormice, or whether additional morphological variation occurs during evolution of giant size—possibly driven by island-specific shifts in ecology.

2. Material and methods

(a) Sample

We analysed the skulls and mandibles of 63 adult specimens (fully erupted third molar) of the extant species *E. quercinus*. Specimens were from the collections of the Senckenberg Museum, Frankfurt (SMF), the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Natural History Museum, London (NHMUK). Electronic supplementary material, table S1 includes a full list of all extant specimens used in this study and details of our μCT scanning methods are given in electronic supplementary material, Appendix S1. Because only adult individuals were analysed, our analyses (see below) describe patterns of static allometry.

Size variation in *Eliomys* was characterized among geographically separated extant populations and in fossil giants. We used centroid size (the square root of the summed squared distances between landmarks and the centroid [35]) derived from our landmark configurations as a size proxy. Our subsequent analyses focused on quantifying allometry within a single species, *E. quercinus*, the closest living relative of insular giant dormice lineages [29–31]. Ideally, we would compare the extinct giant dormice with their specific mainland ancestor populations. However, phylogenetic relationships among populations of *E. quercinus* are not currently known, let alone the relationships of mainland populations with extinct island giants.

Fossil specimens of the insular species *Hypnomys onicensis*, *H. morpheus* and *Leithia melitensis* were included in the analyses based on μCT models (electronic supplementary material, Appendix S1), with small missing portions reconstructed from photogrammetric models of other specimens. The fossil specimens include: a composite reconstruction of the skull of *L. melitensis* based on specimens present at the Museo Geologico Gemmellaro (mgupPS 78: 1–5) [32]; the reconstruction of an *L. melitensis* mandible located at the Museo Universitario di Scienze Della Terra, Rome (MUST R2s26); a well-preserved skull of *H. morpheus* from Cova des Coral·loides (unnumbered specimen, under the responsibility of the Heritage Authorities of the Consell Insular de Mallorca, Palma); and a mostly complete skull of the giant Balearic dormouse *H. onicensis* in the collection of the Institut Mediterrani d'Estudis Avançats, Esporles, Mallorca (IMEDEA 106855). Although this specimen is likely a sub-adult, based on size, dental wear and the unfused skull sutures, it is the most complete skull available of this species.

(b) Shape analyses of extant dormice

Anatomical landmarks were recorded from each cranium (42 landmarks) and mandible (19 landmarks) using Avizo Lite v. 9.2.0 (Thermo Fisher Scientific, Waltham, MA, USA). The *Arothron* package [36] was used to import the landmarks into R v. 3.5.3 [37]. We used three-dimensional geometric morphometrics to characterize shape variation among extant populations of *E. quercinus* and extinct giants. Generalized procrustes analysis (GPA) was performed, translating the landmark coordinates to the origin, scaling to unit centroid size and rotating them to a shared orientation, using a least-squares criterion [38,39]. This analysis separates variation in size (centroid sizes) from variation in shape (Procrustes coordinates) so they can be treated as individual variables. A principal component analysis (PCA) was performed using the geometric morphometric R package *Morpho* v. 2.6 [40], in order to evaluate the data in a lower-dimensional space and identify the largest variances in shape within the dataset.

(c) Allometry

Analysis of variance (ANOVA) was used to test the effect of size on adult shape variation (i.e. static allometry) in *E. quercinus* and the fossil giants. Using the procD.lm() function with 999 iterations in the R package *geomorph* v. 3.2.0 [41], the following linear model formula was evaluated: shape ∼log10(size), in which size is represented by centroid size. This analysis asks what changes in cranial or mandibular shape are associated with changes in cranial or mandibular size. Our initial analyses included a categorical variable differentiating between non-giant and giant dormice for both the extant dataset (including the extant Formentera giants), as well as the complete dataset (including the fossil giants). When used as a covariate, shape ∼log10(size) + giant, this variable asks whether giant dormice show specific differences in skull shape compared to non-giant dormice; when used as an interaction term, shape ∼log10(size) × giant, it asks whether the relationship between shape and size (i.e. its slope) differs between giant and non-giant dormice.

Subsequent analyses aimed to quantify the allometric signal among non-giant populations and therefore used a more restricted sample, excluding giants. The independent effects of the population (defined by geographical location) and sex on shape were evaluated for non-giant *Eliomys* specimens using the model: shape ∼log10(size) + population + sex (electronic supplementary material, tables S2 and S3). We also asked whether the effect of allometry varies among populations (electronic supplementary material, table S1) using the model formula: shape ∼log10(size) ∗ population. The significance of coefficients and interaction terms in these models was assessed using ANOVA with permutation procedures.

(d) Predicted shape model

The allometric relationship defined above can be used to evaluate the extent to which the morphology of (giant) specimens is explained by their size. A multivariate regression for allometry shape ∼ size can be expressed as $Y = C + BX + E$ [42], in which Y is the shape vector, C is the intercept, B is the vector of the regression coefficients for size and represents the angle of the slope of the multivariate regression line, X represents centroid size and E explains the error term. When using Procrustes coordinates, the size component X can be evaluated as the difference between the centroid size of each specimen and the mean centroid size across all specimens. This procedure renders the intercept term C redundant with the mean shape from Procrustes superimposition.

Our analyses of allometry among non-giant dormice demonstrated a small, but significant, contribution of the population (i.e. geographical location) to cranial and mandibular shape variation (electronic supplementary material, tables S2 and S3). Therefore, we used the allometric relationships derived from the model shape ∼log10(size) + population among non-giant dormice for the allometric base model in the subsequent analyses.

(e) Predicting shape from size

The base allometric model provides a predicted shape for each specimen based on its size. The Procrustes coordinates of individual specimens can be projected on to an axis described by the vector of size coefficients, B, from the multivariate regression [43]. This vector defines an axis in multivariate space and is equivalent to the common allometric component (CAC) [44]. The orthogonal projection of specimens onto this axis gives a regression (or CAC) score. The plot of the regression score against size provides a two-dimensional representation of the allometric model. Shape residuals describe how the true shape of each specimen differs from its predicted shape and are represented in the plot as the vertical (i.e. shape) deviation of each specimen from the regression line.

(f) Predicting size from the shape

The base allometric model can also be used to infer a 'predicted size' for each specimen based on its shape (Procrustes coordinates). Predicted sizes identify whether the shape of a specific specimen resembles that of a smaller or a larger specimen. They also allow us to infer a best-fit shape based on predicted size, representing the shape a specimen would have if it only deviated from allometric expectations by modification of the position on the allometry line (under the assumption that all shape variation between specimens is associated with allometry).

Predicted sizes were inferred using a custom-written R function: predict.size() (electronic supplementary material, Appendix S2). This function uses the regression vector from the base allometric model to generate a series of predicted shapes representing individuals of different sizes. These predicted shapes are calculated using a $2 \times n$ matrix in which the first row comprises the vector of intercept values and the second row comprises the coefficients of size in the base allometric model. This was multiplied by an $\boldsymbol{m} \times 2$ matrix, in which the first column consists solely of ones and the second column contains an ascending sequence of size values of length $\boldsymbol{m}$. Our predict.size() function by default sets the upper size limit to 1.5 times the size of the largest individual within the dataset. The resulting matrix is transformed to an array based on the number of landmarks within the configuration and its dimensionality, creating a dataset comprising a sequence of shape coordinate data associated with the allometric trajectory per increment of size. This approach can be used to generate predicted sizes of external specimens that were not included in the base allometric model, provided they are superimposed on the consensus shape of this model.

The extent to which specimen shapes differ from the shapes predicted by allometry, given their predicted sizes, provides a measure of the amount of shape difference between specimen shapes and their deviation from allometric expectations (given actual sizes) that cannot be explained simply by modification of position on the allometry line. It, therefore, allows us to quantify the amount of non-allometric shape deviation exhibited by a specimen, which might, for example, reflect individual-, population- or species-specific variation. This is calculated as the orthogonal projection of specimen shapes on the regression vector. Our predict.size() function estimates this by evaluating the Procrustes distances between the actual specimen shape and every proposed shape on the regression vector. The proposed shape with the shortest Procrustes distances is the indicator for predicted size.

The relationship between predicted and actual size for each specimen was displayed graphically via a 'predicted size versus actual size', or PSvAS, plot. This method is complementary to existing allometric methods, and allows for the evaluation of the shape of individual specimens with respect to the base allometric model. A line with intercept = 0 and slope = 1 on this plot represents shapes with predicted sizes that match their actual sizes. This identity line divides the graph into two sections, the lower-right indicating specimens with a centroid size exceeding the predicted centroid size based on shape, and the upper-left including specimens with larger predicted sizes than the actual centroid size.

(g) Application of PSvAS to the dormouse dataset

The PSvAS method was used for analysing the shape of giant dormice, based on an allometric base model including non-giant, extant *E. quercinus* specimens. The fit of the fossil and extant giants within the model was analysed to determine whether certain morphological features are in line with the allometric predictions, or can be considered distinct characteristics for giants. Because the giant dormice are considerably different in size and shape compared to non-giant *Eliomys*, including such

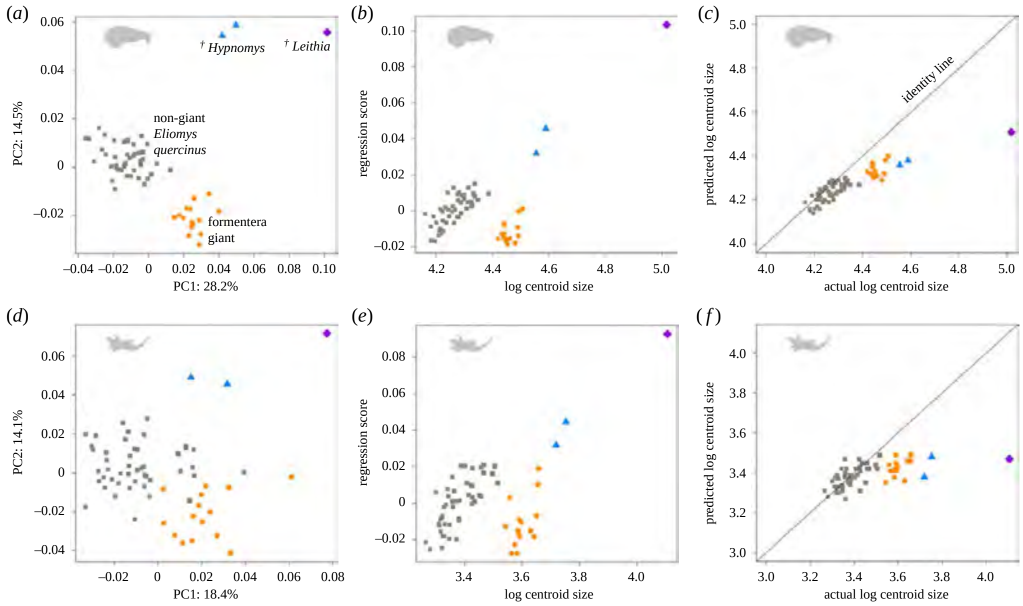

Figure 1. Cranial (top) and mandibular (bottom) shape differentiation in extant *Eliomys quercinus* specimens and fossil giants on the first two principal components (*a*,*d*); the common allometric component versus log centroid size with grouping (*b*,*e*); and the predicted size versus actual size analyses based on a non-giant base model including the predicted sizes for the giant Formentera population and fossil giants (*c*,*f*). (Online version in colour.)

specimens will affect the GPA and therefore influence the inferred allometric component. Instead, these specimens were superimposed to the consensus shape of the base model rather than being included in the original GPA.

3. Results

(a) Shape variation in dormice

Principal component ordinations for both the cranial and mandibular dataset depict a clear signal related to the distinctive morphology of giant species (figure 1*a*,*d*). The first principal component is correlated with size variation of extant, non-giant populations, with more positive values being associated with larger individuals. The second principal component appears to distinguish between extant (negative values) and fossil (positive values) giants. Overall, these patterns are more defined in the cranial analyses.

(b) Size-shape relationships

Our initial analyses of allometry demonstrate statistical significance for an independent variable distinguishing between giant and non-giant dormice both when including only extant populations, and for the complete dataset including fossil specimens (electronic supplementary material, tables S4 and S5). This indicates a role for non-allometric shape variation during the origin of giant dormouse cranial and mandibular morphology. The interaction term of this variable is non-significant for the extant dataset, but significant for the complete dataset including fossil specimens. This indicates that the relationship between shape and size among the living and extinct giants from multiple islands is different to that among non-giant populations (figure 1*b*,*e*). Our subsequent analyses further interrogate and characterize these differences.

(c) Allometric base model

ANOVAs demonstrate statistically significant effects of size and population on the allometric base models for both mandibular and cranial shape (electronic supplementary material, tables S2 and S3). The effect of sex (21 females; 24 males; 1 unknown) on mandibular and cranial shape is non-significant and sex was, therefore, was excluded from further analyses ($p = 0.188$; $p = 0.271$). The interaction term between size and population is also non-significant (mandible: $p = 0.548$; skull: $p = 0.346$), indicating that there is no evidence for population-specific allometric effects in non-giant dormice. Thus, the best model is: shape ~log10(size) + population; which explains 53% of the total variation in both the mandibular and cranial datasets (electronic supplementary material, tables S2 and S3). The PSvAS model was used to evaluate the shape of giant dormice crania and mandibles with respect to this allometric model, based solely on non-giant dormice (figure 1*c*,*f*).

(d) Predicted size versus actual size

The PSvAS plots describe the relationship between the size of each specimen and its predicted size based on shape in the context of the allometric model (figures 1*c*,*f* and 2). Giant specimens in these graphs are located firmly below the identity line, indicating that their shapes resemble the crania and mandibles of smaller individuals (electronic supplementary material, table S6). This effect is generally more pronounced for mandibles than for crania (figure 1). Furthermore, the larger fossil specimens deviate more from the identity line compared to the extant giants from Formentera.

(e) Predicted and actual morphology of giant dormice

Procrustes distances quantify the difference between the actual shape of giants and the predicted shapes based on

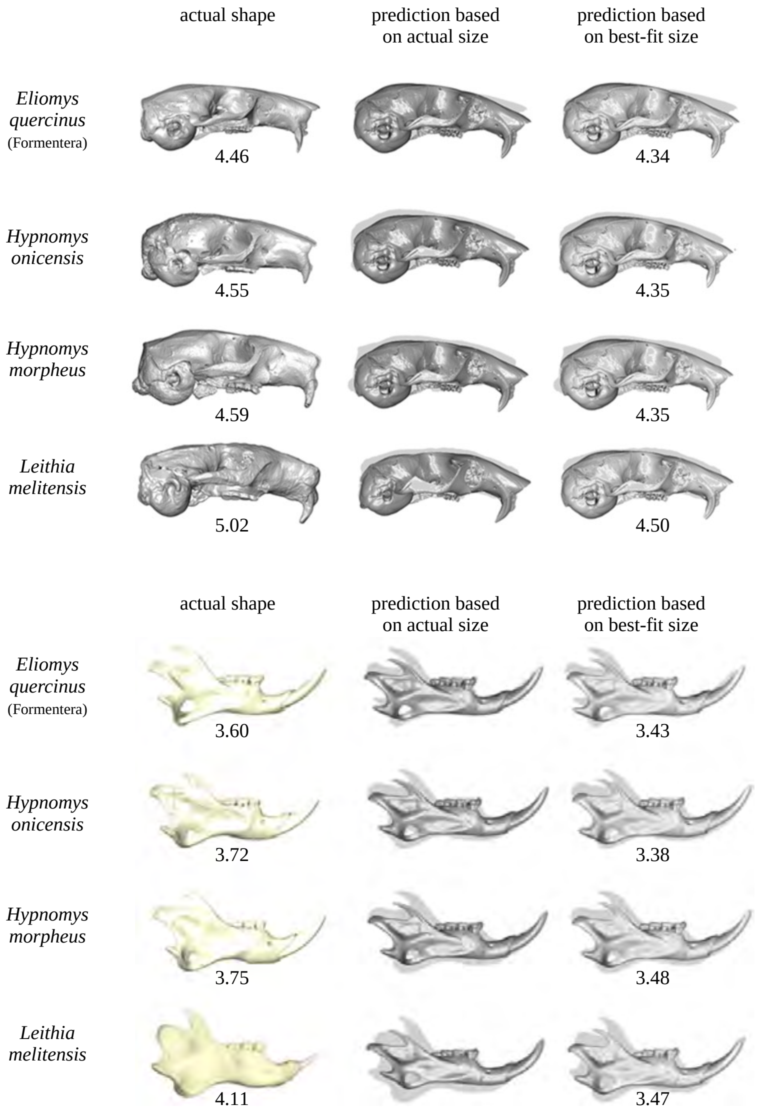

Figure 2. Predicted shapes of the fossil giants derived from the PSvAS model, using the shape predicted by the actual centroid size of the specimen and the shape presumed to be the best-fit with the actual shape of the specimen. (Online version in colour.)

the allometric model (electronic supplementary material, table S6). Differences between giant shapes and expectations under the allometric base model are relatively large (cranium: 0.07–0.18, mandible: 0.08–0.22), especially within the fossil genera *Hypnomys* and *Leithia*. These differences remain large even when using the predicted (best-fit) size given shape (electronic supplementary material, table S6; cranium: 0.07–0.13, mandible: 0.06–0.12), indicating that the actual morphology of giants is rather poorly predicted by the allometric model, suggesting that giant dormouse cranial and mandibular morphologies originated via largely non-allometric evolutionary processes.

Based on both their actual and predicted sizes, the crania of larger dormice are expected to have upper incisors that curve more posteriorly, an inferiorly angled rostrum, an increased maximum width of the zygomatic arch and a relative narrowing of the auditory meatus (figure 2). The predicted relative narrowing of the auditory meatus is seen in the fossil taxa, but other aspects of the actual shapes of the giants deviate from these predicted shapes: none show the predicted curvature in the incisors, and the proposed inferior angle of the rostrum is only evident in *L. melitensis*. The widening of the zygomatic arch is present within fossil giants, but is absent in the extant Formentera giants. Furthermore, the zygomatic widening in the fossil giants is located much more anteriorly than predicted.

The predicted mandibular morphology of giant dormice is also very different from their actual shapes. The predicted shapes show a very narrow and antero-posteriorly elongated structure, whereas the actual giants have robust mandibles, with the posterior part being greatly enlarged dorsoventrally. Although the PSvAS graph implies a best-fit for giant mandibular shapes similar to that of non-giant dormice, the large Procrustes distances between the fitted shape and the actual shape (electronic supplementary material, table S6) indicate this is not the result of isometric scaling. Instead, the giants exhibit some unique morphologies; e.g. distinct features in *L. melitensis* include a foreshortened and relatively straight lower incisor, an exceptionally large and unperforated angular process, a posteriorly located anterior margin of the masseteric ridge and a vertically oriented coronoid process.

As the cranial and mandibular warps were created using the respective landmark configurations, features not included in the configuration, such as the shape of the auditory bullae, cannot be reliably assessed using the warped images. Electronic supplementary material, figure S2 shows the positioning of the landmarks on the giants with regards to their predicted shapes. The width of the zygomatic plate, visible in lateral view, seems to increase with size in the fossil specimens. Furthermore, all giants appear to have a sharply angled cranial vault. Lastly, we noted a peculiar enlargement of the occipital condyle when observing the μCT scan of *H. morpheus*, not seen in other specimens.

4. Discussion

Extant giant Formentera dormice and fossil giant specimens of Sicily and Mallorca show substantial craniomandibular differences from their non-giant relatives (*E. quercinus*; figure 1 and electronic supplementary material, figure S3). Only a small portion of these morphological differences can be explained by the allometric trajectories of non-giant populations. Insular giant dormice, therefore, diverge substantially from allometric expectations. Additionally, we recognized that different species of giant dormice show distinctive deviations from their predicted shapes.

(a) Predicting giant size and shape

The cranial and mandibular morphologies of living and extinct island giants are different from those expected under an allometric model. Allometry-related aspects of the shapes of these giants are generally more similar to those of smaller dormice (although they also show substantial non-allometric shape differences), and this effect is more pronounced for the mandible than for the cranium (figure 1*c*,*f*). Although the craniomandibular shapes of giant dormice are more similar to smaller dormice than expected, this does not imply isometric scaling; the actual fit of the giants within the model is rather poor, and is worse for larger specimens (see Procrustes distances electronic supplementary material, table S6). Phylogenetically, the fossil specimens are more separated from the base model, potentially explaining the poor fit of these shapes within the model. The biologically implausible geometries that result from the extrapolation of the allometric model to giant sizes provide an alternative explanation. For example, the predicted skull shape based on the cranial size of *L. melitensis* (log centroid size = 5.02) has an unrealistically flexed cranial vault and occipital region, including a highly constricted foramen magnum. A similarly unlikely morphology is evident for mandibular geometry, with the expected shape at the size of *L. melitensis* (log centroid size = 4.11) being implausible owing to the very thin mediolateral width of the bone. Interestingly, the morphologies of smaller giants (Formentera population and *Hypnomys*) are not correctly predicted by the allometric base model either. These observations suggest that flattening or truncation of the allometric trajectory occurs at large size in order to maintain biological functionality.

Only part of the morphology of giant dormice can be explained by flattening of the allometric trajectory—large differences are also evident in comparison to their expected shapes based on (smaller) 'best-fit' centroid sizes (electronic supplementary material, table S6; and figure 2). This indicates the presence of population-specific morphological features within island giants, potentially reflecting adaptive variation due to island-specific environmental conditions or ecological shifts. For example, the extant giant population of Formentera is notably more faunivorous compared to other populations [28]. This suggests either that insular body size increases have resulted in a dietary niche shift, or that a shift towards carnivory reflects insular selective pressures on Formentera and is the driver of evolutionary increases in body size. Although this is not the classic explanation of large body size in small mammals on islands [1], it indicates that morphological variation among dormouse populations could represent allometry and dietary (or other ecological) adaptations.

(b) Morphological traits of giant dormice

Cranial morphology of island giants clearly deviates from the allometric expectations, even when compared to their 'predicted sizes' (i.e. best-fit sizes to the line of allometry; figure 2). The robust rostrum and narrowing of the infraorbital foramen within all fossil giants are not predicted by the allometric model at any cranial size. The model predicts the zygomatic arch in giants to become more enlarged posteriorly. In reality, the arch does get more robust, but its maximum width is located much more anteriorly. Larger dormice show a dorsoventral flattening of the skull and changes to the posterior part of the mandible, such as an elongated coronoid process and enlarged condylar and angular processes. These are areas associated with masticatory muscle attachment [45], and their modification suggests relative increases in molar bite force [46,47] or gape [48,49]. Multiple studies have already shown that small changes in cranial and mandibular size and shape can affect mechanical advantage and gape, both of which will impact the range of dietary items that can be processed. This effect has been shown in a number of mammalian groups [50–53] but is particularly well-studied in rodents [54–59]. The flattening of the skull is commonly seen in more rupicolous dormice [60], although it may also be a product of enlarged body size owing to negatively allometric scaling of brain size [61] and craniofacial evolutionary allometry (CREA) [62]. This pattern, which is seen in many mammalian groups, predicts relatively smaller braincases and longer rostra in larger species [63,64].

(c) Unique features of giant dormouse species

Significant modifications to shape and size can result from evolutionary adaptation to novel ecologies, including new diets [22]. We, therefore, interpret the unique morphological features identified in the giant dormouse populations as reflecting specific ecological adaptations to insular settings. As well as diverging from the non-giant allometric trajectory, giant dormice also differ morphologically from one another. Such differences can be the result of various factors, including variation in ecosystem composition, ecological niche occupation, as well as the duration of isolation on islands. The introduction of *E. quercinus* to Formentera is thought to have occurred roughly 4000 years ago, whereas both *Hypnomys* and *Leithia* were isolated for millions of years. Even though the morphology of Formentera dormice does not resemble an intermediate shape between an average-sized *E. quercinus* and the fossil giants, the differences in duration of isolation are substantial. Many population-specific aspects of giant dormouse cranial, and especially mandibular, structure complement previous evidence of divergent dietary and other ecological traits in these taxa.

(d) Formentera

The Formentera dormice are the only extant giants and are morphologically different from the fossil giants. It is the only giant population retaining a large infraorbital foramen. Furthermore, the mandibular morphology of this population is characterized by a deep angular notch and relatively large coronoid process, in contrast to the fossil giants. This enlarged coronoid results in a larger attachment area for the temporalis muscle, suggesting an increased incisor bite force, which would be advantageous for the extensive faunivorous behaviour observed within the Formentera population [28]. Previous research has suggested that faunivory, more than other diets, places unique pressures on rodents, driving greater morphological change [58,65]. However, this is not the case in the dormice studied here, with the Formentera population resembling non-giant dormice more than the other giants, based on the relatively short Procrustes distances of the best-fit in the PSvAS model (cranium 0.07; mandible 0.06) (electronic supplementary material, table S6).

(e) Hypnomys

The *Hypnomys* material in our dataset is much more robust than other dormice, with the exception of *L. melitensis*. The PSvAS model indicates that the morphology of this genus is substantially different from extant dormice (cranium 0.10; mandible 0.08). The *H. onicensis* specimen examined here is considered a sub-adult and is less robust than *H. morpheus*. The latter is characterized by exceptionally pronounced occipital condyles. The robust morphology of the zygomatic area and mandible in the two *Hypnomys* specimens indicates well developed masseteric musculature, which suggests a diet including tough foods for this genus. A more abrasive plant-based diet has also been suggested based on molar microwear [66].

(f) Leithia

Leithia melitensis is the largest and most robust dormouse. *Hypnomys* and *Leithia* show similar morphological modifications, although these are often more pronounced within *Leithia* [32]. This also explains the relatively large Procrustes distances seen in the PSvAS model for this species (cranium 0.13; mandible 0.12). In particular, the width of the rostrum and the zygomatic plate is exceptional. The mandible within this giant has very large angular and condylar processes. It is the only giant in which there appears to be no fenestration of the angular process. However, the functional significance of this fenestra is unknown. The coronoid is deflected less posteriorly, resulting in a more upright position. The anterior margin of the masseteric ridge is positioned more posteriorly than in other dormice and the incisor is relatively short and curves less superiorly. The cranial and mandibular features seen in *L. melitensis*, in particular the exceptionally robust mandible, likely represent adaptations to a herbivorous diet [67], possibly explaining its extraordinary size. In addition, considerable variability in wear of the molar row is seen within the analysed fossil material of *L. melitensis* (electronic supplementary material, figure S4), indicating a relatively abrasive diet against which the molars were used extensively, also consistent with herbivory.

5. Conclusion

Multiple, independent dormice lineages achieved an exceptional large size in insular habitats since the end of the Messinian Salinity Crisis (5.33 Ma [68]). Extrapolation of common allometry as an evolutionary line of least resistance on short timescales predicts that island giants could have highly similar craniomandibular morphologies. Moreover, a graded trend to gigantism as proposed by the island rule suggests that the importance of selective pressures within an ecosystem varies in a predictable manner [13,14]. However, we find that the morphologies of giant dormice are not an extrapolation along the allometric gradient of non-giant populations. This indicates that insular gigantism may lead to a deviation from the otherwise strong allometric conservatism suggested to exist in rodents [69]. Furthermore, the cranial and mandibular features of giant dormice contain a prominent population-specific component, illustrating divergence and inherently non-predictable adaptations to various different ecological niches, on different islands. These differences in the evolutionary pathways of island giants may reflect differences in ecosystem composition among islands and through geological time. Our findings have implications that extend beyond the study of giant dormice, suggesting that island adaptation may commonly involve ecological shifts that are unique and context-dependent, resulting in a high diversity of evolutionary responses to insular habitats in mammals.

Data accessibility. The datasets supporting this article have been uploaded as part of the supplementary material. MicroCT scans are uploaded to the MorphoSource project 'Dormice (Gliridae)' (https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/941)

Authors' contributions. J.J.H. and P.G.C. conceived the study. R.B.J.B., N.J. and J.J.H. scanned the extant specimens. V.L.H., J.A.A., E.T.-R. and J.J.H. provided scans of fossil material. J.J.H. reconstructed and landmarked the dataset, and developed the applied methodology with R.B.J.B. J.J.H. drafted the manuscript. All authors contributed to the editing of the final manuscript and gave final approval before submission.

Competing interests. We declare we have no competing interests.

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