

First evidence of *Microdyromys* (Gliridae, Rodentia, Mammalia) in the Early Pliocene of the Balearic Islands and its bearing on the origin of the late Neogene insular dormice from the western Mediterranean

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Abstract

This paper reports the first occurrence of the dryomine dormouse *Microdyromys* in the Balearic Islands. *Microdyromys boveri* sp. nov. is characterized by lower molars with anterolophid, anterotropid, metalophid, centrolophid, mesolophid, posterotropid and posterolophid, and by upper molars with anteroloph, protoloph, metaloph and posteroloph as well as well-developed prototrope, precentroloph, centrotrope, postcentroloph, metatrope and posterotrope. In many cases this dental pattern is replaced by one formed of several small ridges and cuspules, in which the ridges cannot be identified. This dental pattern clearly differs from the much simpler one of *Eliomys*, which has been regarded as the direct ancestor of the endemic Balearic genus *Hypnomys*. The presence of *Microdyromys boveri* challenges this phylogenetic hypothesis, *Hypnomys* rooting in a late Miocene species of *Microdyromys*. This could have been also the case for other Plio-Pleistocene endemic genera from the western Mediterranean, such as *Thyrenoglis* (Sardinia) and *Maltamys* (Malta, Sicily). The closest affinities of *Microdyromys boveri* are with the species *Microdyromys chaabi* from Oued-Zra (Morocco), suggesting a North African origin. Its presence in Mallorca could therefore be linked to the regression caused by the Messinian salinity crisis.

Introduction

The Balearic Islands form an insular system in the western Mediterranean Sea and are divided into two main archipelagos: the Gymnesics, comprising Mallorca, Menorca, and their surrounding islets, and the Pityusics, including Eivissa, Formentera, and associated islets (Fig. 1). The establishment of their current insular configuration dates to the end of the Messinian salinity crisis, when the Mediterranean basin was reflooded during the early Pliocene, at 5.33 Ma (Krijgsman et al., 2024).

The Neogene fossil record of the Balearic Islands documents two major insular faunal episodes (e.g. Agustí, 1986; Agustí and Moyà-Solà, 1990; Mas et al., 2018). The earlier episode is restricted to the middle Miocene and has only been identified in the Gymnesic Islands (Mein and Adrover, 1982; Adrover et al., 1985; Quintana and Agustí, 2007). In contrast, the second faunal episode is recorded across all the main islands of the archipelago. In Mallorca, this episode is represented by the *Myotragus* fauna, which spans from the early Pliocene to the Holocene (Alcover et al., 1981). In Menorca, the Pliocene record is characterized by the *Nuralagus rex* fauna (Agustí et al., 1982; Quintana et al., 2011), which was replaced by *Myotragus* assemblages by at least the early Pleistocene (Bover et al., 2008). In the Pityusic Islands, the earliest phase of this second episode is documented in Eivissa by an early Pliocene assemblage dominated by the bovid *Ebusia moralesi* (Moyà-Solà et al., 2022; Agustí et al., 2026).

In Mallorca, the oldest known Pliocene localities include Caló den Rafelino, Na Burguesa-1, and the recently discovered Na Burguesa-2. These sites record faunal assemblages belonging to the second insular episode, with Caló den Rafelino being younger than the Na Burguesa deposits (Agustí et al., 2012; Bover et al., 2007). Compared with post-Pliocene Mallorcan sites, these early Pliocene localities display a higher taxonomic diversity (Bover et al., 2014; Torres-Roig, 2021; Torres-Roig and Alcover, 2024).

Rodent remains from these deposits have been essential for establishing the relative chronology of the faunal assemblages and represent one of the main sources of information for reconstructing the earliest phases of insular evolution in the Balearic Islands. Although insular evolutionary patterns are well documented in large mammals such as *Myotragus*, their expression in small rodents remains less thoroughly explored.

Within this context, the *Microdyromys* material from Na Burguesa-1 constitutes a rare and informative record. The presence of complex dental features combined with incipient derived traits makes this taxon particularly valuable for investigating the initial stages of insular differentiation within the *Hypnomys* lineage in the Balearic Islands during the earliest Pliocene.

Geographical and geological setting

The Na Burguesa-1 (NB-1) site is in the south-western sector of the Serra de Tramuntana, close to Palma (Mallorca, Balearic Islands), at approximately 160 m a.s.l., halfway along the road leading to the monument situated at the summit of Puig des Caragol (Fig. 1). The deposit consists of a fossil-rich breccia infilling a paleocave or karstic fissure excavated in Lower Lias grey limestones. At present, the original cavity is completely eroded, and only the infilling sediments are preserved.

The breccia is composed of angular limestone clasts embedded in a red-brown silty matrix, strongly cemented by calcite, and includes levels with a high concentration of small-vertebrate remains. The fossil assemblage consists of disarticulated bones recovered from a series of karstic breccia blocks extracted from the deposit. These blocks were prepared in the IMEDEA laboratory located at the UIB campus using a cyclic acetic-acid treatment (Torres-Roig et al., 2017a; 2017b).

The first recoveries of fossil vertebrates have revealed an excellent state of preservation, as well as a high richness in both taxa and skeletal elements. The clear predominance of small mammals with a marked size selection, together with the presence of remains attributable to a large barn owl (*Tyto* sp.) and other elements assignable to a smaller strigiform, indicate that the deposit was formed mainly through bioaccumulative processes (Torres-Roig et al., 2019a).

All evidence suggests that the deposit originated within a relatively closed cavity, which favoured both sediment accumulation and the concentration of bone remains derived from strigiform predatory activity. The age of the deposit, as well as that of other earlier Balearic sites, has been estimated indirectly through comparison of the morphological characters of some recovered taxa with those from other well-dated localities, since no absolute dating is currently available for these deposits. In the case of NB-1, both *Apocricetus darder*i and *Paraethomys balearicus* exhibit clearly archaic characters, allowing the site to be placed between the Messinian and the earliest Pliocene (Bover et al., 2014; Torres-Roig et al., 2017b; Torres-Roig et al., 2019b). Moreover, the pronounced gigantism displayed by the cricetid suggests a very early Pliocene age as the most probable chronology for the deposit.

Materials and methods

The material used to characterize *Microdyromys boveri* sp. nov. comprises a total of 618 isolated teeth (14 dP4, 58 P4, 77 M1, 72 M2, 71 M3, 10 dp4, 63 p4, 91 m1, 3 m1/m2, 75 m2, and 84 m3). All specimens were individually catalogued and curated at the Institut Mediterrani d'Estudis Avançats, Esporles, Mallorca (collection acronym: IMEDEA). This material was compared with newly studied material of *Hypnomys morpheus* from Cova de sa Bassa Blanca (Mallorca), comprising 55 isolated teeth (5 P4, 14 M1/M2, 6 M3, 6 p4, 16 m1/m2, and 8 m3), as well as with published type material of *H. waldreni* from Cap Farrutx, Mallorca (Reumer, 1979); *H. eliomyoides* from Binigaus, Menorca (Agustí, 1980); *H. onicensis* from Pedrera de s'Ònix, Mallorca (Reumer, 1981); and the scarce material of *Hypnomys* sp. from Caló den Rafelino, Mallorca (Bover et al., 2014). In addition, comparisons were made with published type material of continental *Microdyromys* species (*M. sinuosus* from Ampudia 3, Álvarez-Sierra and García-Moreno, 1986; *M. chaabi* from Oued Zra, Jaeger, 1977; *M. remmertii* from Vargas 7, García-Paredes et al., 2010; *M. koenigswaldi* from Valdemoros 3B, De Bruijn, 1966; *M. complicatus* from Armantes 7, De Bruijn, 1966; and *M. "miocaenicus"* from Sansan, De Bruijn, 1966).

Dental nomenclature and measurement protocols follow Freudenthal (2004). Tooth measurements were obtained using an Edge AM7915MZT Dino-Lite digital microscope, and values are expressed in millimeters. Fossil illustrations were produced from scanning electron microscopy micrographs obtained with a Hitachi S-3400N at the Scientific and Technical Services of the Universitat de les Illes Balears (UIB, Mallorca, Balearic Islands). Lower teeth are referred to as dp4, p4, and m1–3, and upper teeth as dP4, P4, and M1–3. Only the best-preserved specimens were included in the detailed morphological description, whereas all specimens, including those partially eroded or showing advanced occlusal wear, were measured. Measurements for each specimen, as well as measurement data obtained from the literature, are provided in the Supplementary Online Material.

Institutional abbreviations: IMEDEA, Institut Mediterrani d'Estudis Avançats, Mallorca, Spain

Measurements abbreviations: L, length; W, width; n, number of specimens; min, minimum; max, maximum; mean, mean value.

Systematic Palaeontology

Order Rodentia Bowdich, 1821

Family Gliridae Thomas, 1827

Genus *Microdyromys* de Bruijn, 1966

Type species: *Microdyromys koenigswaldide* Bruijn, 1966; Valdemoros 3B, Zaragoza. Spain; MN4B. Middle Miocene

Type locality: Na Burguesa-1, Palma, Mallorca, Illes Balears, western Mediterranean (Bover et al., 2014).

Microdyromys boveri sp. nov.

LSID urn: lsid:zoobak.org:act:

Holotype: Isolated left M1 (IMEDEA 107481).

Paratypes: 9 P4 (IMEDEA 107300, IMEDEA 107353, IMEDEA 107355, IMEDEA 107356, IMEDEA 107360, IMEDEA 107361, IMEDEA 107369, IMEDEA 107371, P4 IMEDEA 107372), 9 M1 (IMEDEA 107390, IMEDEA 107394, IMEDEA 107409, IMEDEA 107416, IMEDEA 107440, IMEDEA 107470, IMEDEA 107484, IMEDEA 107493, IMEDEA 107518), 16 M2 (IMEDEA 107374, IMEDEA 107382, IMEDEA 107424, IMEDEA 107427, IMEDEA 107429, IMEDEA 107431, IMEDEA 107454, IMEDEA 107464, IMEDEA 107465, IMEDEA 107466, IMEDEA 107474, IMEDEA 107489, IMEDEA 107496, IMEDEA 107504, IMEDEA 107514, IMEDEA 107515), 14 M3 (IMEDEA 107521, IMEDEA 107525, IMEDEA 107526, IMEDEA 107532, IMEDEA 107534, IMEDEA 107535, IMEDEA 107547, IMEDEA 107549, IMEDEA 107542, IMEDEA 107555, IMEDEA 107556, IMEDEA 107575, IMEDEA 107584, IMEDEA 107589), 7 p4 (IMEDEA 103984, IMEDEA 103996, IMEDEA 103998, IMEDEA 107021, IMEDEA 107035, IMEDEA 107039, IMEDEA 107041), 7 m1 (IMEDEA 107063, IMEDEA 107071, IMEDEA 107089, IMEDEA 107100, IMEDEA 107163, IMEDEA 107174, IMEDEA 107181), 12 m2 (IMEDEA 107051, IMEDEA 107072, IMEDEA 107104, IMEDEA 107124, IMEDEA 107127, IMEDEA 107180, IMEDEA 107193, IMEDEA 107194, IMEDEA 107205, IMEDEA 107210, IMEDEA 107211, IMEDEA 107212), 14 m3 (IMEDEA 107230, IMEDEA 107234, IMEDEA 107248, IMEDEA 107260, IMEDEA 107264, IMEDEA 107263, IMEDEA 107270, IMEDEA 107273, IMEDEA 107285, IMEDEA 107286, IMEDEA 107287, IMEDEA 107289, IMEDEA 107290, IMEDEA 107297).

Derivatio nominis: Named in honour of our colleague Pere Bover, for his significant contributions to the study of Balearic vertebrate palaeontology.

Measurements: See Table 1, Fig. 2 and Supplementary table S1.

Diagnosis: Species of *Microdyromys* with very complicated dental pattern. The lower molars are usually characterized by 7 main ridges (anterolophid, anterotrope, metalophid, centrolophid, mesolophid, posterotrope and posterolophid). However, the ridges between anterolophid and posterolophid can be decomposed in a number of small ridges and cuspules, performing a reticulated pattern. A continuous ectolophid is usually present. The basic design of the upper molars is composed of anteroloph, protoloph, metaloph and posteroloph, but most of the molars present also a well-developed prototrope, precentroloph, centrotrope, postcentroloph, metatrope and posterotrope. Again, in a high number of upper molars this complicated dental design derives in a reticulated pattern, composed of multiple small ridges and cuspules intersecting to form polygonal morphologies. A continuous endoloph is always present.

Differential diagnosis: *Microdyromys boveri* sp. nov. displays a larger size and a more complicated dental pattern than *Microdyromys praemurinus*, *Microdyromys legidensis* and *Microdyromys koegniswaldi*. It

differs from *Microdyromys complicatus* for its larger size and much more complicated dental pattern, including reticulation of ridges. *Microdyromys remmerti* and *Microdyromys sinuosus* are closer in size to *Microdyromys boveri* sp. nov. and display complicated molars, but a reticulated dental pattern is never observed. Finally, a similar reticulated pattern is observed at some molars of *Microdyromys chaabi*, but they never reach the level of reticulation of *Microdyromys boveri* sp. nov.

Microdyromys boveri sp. nov. also differs from other species with complex dental pattern such as *Vasseuromys* because of the absence of continuous endoloph in the upper molars. Only *V. tectus* Sinita & Nesin (2018) presents a continuous endoloph, but the upper molars of this species always present an anterotrope and, moreover, a reticulated pattern is never observed in its molars.

Description

dP4: The basic occlusal dental pattern is composed of 3 main ridges, all connected by a continuous endoloph: protoloph, metaloph and posteroloph. A small anteroloph can be recognized in 3 teeth. In 4 teeth a precentroloph and postcentroloph are present also. However, in other 4 teeth these ridges are discomposed in several small ridges and cuspules, performing a reticulate surface (Fig. 5).

P4: The basic occlusal dental pattern is composed of 3 main ridges, all connected by a continuous endoloph: In 24 teeth (50%), a small antheroloph can be recognized at the anterior wall (Fig. 5). A small entoloph is attached labial and lingually to the protoloph, in some cases forming a ring. A precentroloph is present in 30 teeth (62%). Between protoloph and precentroloph a small prototrope can be recognized in 16 teeth (33%). In 6 teeth (12%) the lingual end of the precentroloph connects directly to the precentroloph or the metaloph. A postcentroloph is present in 19 teeth (40%). However, in 9 teeth (19%), the ridges can be hardly recognized in the posterior part of the crown, being reduced to small, isolated ridges and cuspules. This reticulated pattern is extended to the whole crown in 5 other teeth (10%).

M1: Highly variable, complicated occlusal dental pattern. In its simplest version, it is composed of four main ridges: anteroloph, protoloph, metaloph and posteroloph (Fig. 6). However, the number of ridges can be extended up to 10 in most of the molars. Therefore, a well-developed prototrope can be observed in 15 molars (24%), while a small prototrope is present in 22 molars (35%). A well-developed precentroloph is present in 33 molars, while a small precentroloph is present in 12 molars (19%). A well-developed postcentroloph is present in 24 (38%) molars, while a small one is present 15 molars (24%). Between precentroloph and postcentroloph, a centrotrope is present in 15 molars (24%). Between the postcentroloph and the metaloph, a metatrope is present in 30 molars (48%). Finally, a posterotrope is present between the metaloph and the posteroloph in 12 molars (19%). However, in its most complicated version, only 4 main ridges can be recognized (anteroloph, protoloph, metaloph, posteroloph), the other ridges being decomposed into multiple small, isolated ridges and cuspules, performing a reticulated pattern, which is present in 33 molars (52%). In any case, a continuous lingual endoloph is always present.

M2: As in the case of M1, the occlusal pattern is again very complex, with the number of ridges reaching up to 10 in most molars (Fig. 7). A well-developed prototrope can be observed at 12 molars (20%), while a small prototrope is present in 14 molars (24%). A well-developed precentroloph is present in 31 molars (53%), while a small precentroloph is present in 9 molars (15%). A well-developed postcentroloph is present in 24 molars (41%), while a small one is present in 17 molars (29%). Between precentroloph and postcentroloph, a centrotrope is present in 13 molars (22%). Between the postcentroloph and the metaloph, a metatrope is present in 35 molars (60%). Again, as in the case of M1, a reticulated dental pattern is recognized in 22 molars (38%), the ridges inside the trigone being discomposed in multiple small ridges and cuspules. A continuous lingual endoloph is always present.

M3: A well-developed anterotrope between the anteroloph and the protoloph is present in 6 molars (17%). A prototrope can be observed in 6 molars (17%). A well-developed precentroloph is present in 15 molars (42%), while a small one is present at 18 molars. A well-developed postcentroloph is present in 28 molars (78%), while a small one is present in 11 molars (30%). Between precentroloph and postcentroloph, a centrotrope is present in 10 molars (28%). Between the postcentroloph and the metaloph, a metatrope is present in 30 molars (83%). A well-developed posterotrope is present in 10 molars (28%), while a small one can be recognized in 4 molars (11%). The proportion of reticulated dental pattern is restricted to 7 molars (19%). A continuous lingual endoloph is always present (Fig. 8).

dp4: All the teeth display a reticulated crown surface, formed of small cuspules, where no ridge can be distinguished. A continuous endolophid-ectolophid surrounds the walls of the teeth (Fig. 9).

p4: The basic dental pattern is formed of anterolophid, mesolophid and posterolophid. A well-developed posterotropid is always present (Fig. 9). The anterior part of the teeth are usually decomposed in several cuspules, although the metalophid can be recognized in some cases. Anterolophid, mesolophid, posterotropid and posterolophid are usually connected by a continuous ectolophid. Moreover, a continuous endolophid is also observed in some teeth.

m1: The basic occlusal dental pattern is composed of 7 main ridges: anterolophid, anterotropid, metalophid, centrolophid, mesolophid, posterotropid and posterolophid (Fig. 10). The anterolophid is long in all cases. An anterotropid is always present, being large in 35 cases (55%) and small or very small in 33 cases (52%). The metalophid is long in all cases. In some cases, the anterolophid is connected to the anterotropid and the metalophid by a continuous endolophid. A long centrolophid is present in 34 cases (53%), while it is small in 11 (17%). The centrolophid is connected to the metalophid by a continuous endolophid in 15 cases (23%). A small anterior extra ridge between the metalophid and the centrolophid can be observed in 4 cases (6%). In a similar way a posterior extra ridge between the centrolophid and the mesolophid is observed in 8 cases (12%). Mesolophid, posterotropid and posterolophid are always long. The three ridges are connected by a continuous endolophid in 22 cases (34%). A continuous ectolophid can be also observed in 47 cases (73%). A reticulated pattern inside the trigone is observed in 10 cases (16%).

m2: As in the m1, the basic occlusal dental pattern is composed of 7 main ridges: anterolophid, anterotropid, metalophid, centrolophid, mesolophid, posterotropid and posterolophid (Fig. 11). The anterolophid is connected to the metalophid and eventually to the anterotropid by a continuous endolophid long in 4 cases (7%). A small anterotropid is present in 16 teeth (30%), while a large one occurs in 4 other teeth (7%). The metalophid is present in 43 teeth (80%). A long centrolophid is present in 50 cases (93%). A small anterior extra ridge between the metalophid and the centrolophid can be observed in 8 cases (15%). The centrolophid is connected to the mesolophid by a continuous endolophid in 22 cases (41%). A posterior extra ridge between the centrolophid and the mesolophid is observed in 8 cases (15%). Mesolophid, posterotropid and posterolophid are always long. The three ridges are connected by a continuous endolophid in 9 cases (17%). A continuous ectolophid can be also observed in 21 cases (39%). A reticulated pattern inside the trigone is observed in 6 cases (11%).

m3: As in the former molars, the occlusal pattern is composed of anterolophid, metalophid, centrolophid, mesolophid, posterotropid and posterolophid (Fig. 12). The anterolophid is connected to the metalophid by a continuous endolophid in 28 cases (49%). An anterotropid between anterolophid and metalophid is present in 11 cases (19%). A long centrolophid is always present. Mesolophid and posterolophid are always long, while a small posterotropid is present in 41 teeth (72%). Mesolophid and posterolophid are connected by a continuous endolophid in 40 teeth (70%). A fully developed continuous ectolophid is observed in 8 teeth (14%), while an incomplete one is observed in 40 teeth (70%).

Remarks

The classically so-called Plio-Pleistocene *Myotragus* faunas from Mallorca and Menorca are characterized by the presence of a single lineage of rodent, the dormouse *Hypnomys*, until the discovery of the site of Caló d'en Rafelino, which yielded the endemic cricetid *Tragomys* (Agustí et al., 2012), and Na Burguesa-1, which has yielded a basal species of this cricetid together with the endemic murid *Paraethomys* (Torres-Roig et al., 2017b, Torres-Roig et al., 2019b). *Hypnomys* has been classically related to the continental genus *Eliomys* (Agustí, 1981; Zammit Maempel and de Bruijn, 1982; Bover et al., 2019). The late Turolian glirid faunas of Europe are dominated by the species *Eliomys truci*, which displays a simple dental pattern.

However, the presence of the new glirid species at the site of Na Burguesa-1 suggests that this hypothesis should be reconsidered. Thus, the new species from Na Burguesa-1 presents a very complex dental pattern, with several features, such as the presence of long centrotropes and metatropes, the occasional presence of posterotrope, long mesolophids, centrolophids and posterolophids, that are absent at *Eliomys*. Since after the Zanclean flood the Balearics remained isolated from the continent, the new species from Na Burguesa-1 should be considered the direct ancestor of *Hypnomys*. The oldest record of *Hypnomys* is found at the site of Caló den Rafelino, represented by an upper and a lower molar which were referred to *Hypnomys* sp. (Bover et al., 2014). The dental pattern is typical of the genus, with the upper molar characterized by the presence of anteroloph, protoloph, prototrope, precentroloph, postcentroloph and posteroloph, while the lower molar present anterolophid, metalophid, centrolophid,

mesolophid, posterotropid and posterolophid. Given the limited amount of available material, the biometric data suggest that it may represent the smallest taxon of the genus (Fig. 3).

At the late Miocene, prior to the Messinian salinity crisis, several genera with complex dental pattern appear as potential ancestors for the new species of Na Burguesa-1 and the *Hypnomys* lineage. This is the case of *Vasseuromys*, a genus which is present from the early to the late Miocene (Turolian) in Europe. As *Microdyromys boveri* sp. nov., some of the species assigned to this genus present a very complex dental pattern, with high number of ridges including anterotrope, prototrope, centrotrope, metatrope and posterotrope. Most of them differ from *Microdyromys boveri* sp. nov. in lacking a continuous endoloph in the upper molars, except for the last species of the genus, *V. tectus* (Sinitza & Nesin, 2018). However, this species differs from *Microdyromys boveri* sp. nov. by the presence of anterotrope in the upper molars. Moreover, the reticulated pattern observed in *Microdyromys boveri* sp. nov. is never observed in *V. tectus*. In contrast, the species from Na Burguesa-1 shows clear affinities with the living *Dryomys nitedula*, in which the upper molars are characterized by the presence of a continuous endoloph, and long precentroloph, prototrope, centrotrope and posterotrope. In the case of the lower molars this species presents an anterotropid, a posterotropid and a continuous endolophid (Daams, 1981).

Before *Dryomys*, a *Dryomys*-like dental pattern is already present at some species of the Miocene genus *Microdyromys*, particularly within the middle Miocene species *M. complicatus* and *M. remmertii*, in which the upper molars display a complicated dental pattern including anterotrope, prototrope, centrotrope, metatrope and posterotrope (Daams, 1981; García Paredes et al., 2010).

The late Miocene record of this genus is very scarce. One of the latest records of *Microdyromys* is *Microdyromys sinuosus* Alvarez-Sierra, 1986, from the late Vallesian of the Duero Basin (Spain), which was previously assigned to the new genus *Myolidus*. *Microdyromys sinuosus* presents a complicated dental pattern, with anterotrope, prototrope, centrotrope, metatrope and posterotrope.

The youngest record of *Microdyromys* is practically restricted to the early Turolian site of Dorn-Dürkheim (Germany), where Franzen & Storch (1975) described two upper molars of *Microdyromys* sp. The pattern of these molars is quite simple, comparable to the middle Miocene species *Microdyromys koegniswaldi*. Out of Europe, one of the latest records of *Microdyromys* is that of *Microdyromys* (= *Afrodyromys*) *chaabi* Jaeger, 1977, from the latest Vallesian of Oued-Zra. Curiously some upper molars of this African species share with the species from Na Burguesa-1 a reticulated pattern inside the trigone (Jaeger, 1977; Pl. V, fig. 18).

Biometric comparison

The biometric comparison of the dental measurements (Figs. 3-4) shows that *Microdyromys boveri* sp. nov. occupies an intermediate size between continental species of *Microdyromys* and the insular genus *Hypnomys* (Supplementary Tables S1–S3). The teeth of *Microdyromys boveri* sp. nov. are clearly smaller than those of all known species of *Hypnomys*, including *H. morpheus* (Cova de sa Bassa Blanca,

Mallorca; this paper), *H. onicensis* (Pedrera de s'Ònix, Mallorca; Reumer, 1981), *H. waldreni* (Cap Farrutx, Mallorca; Reumer, 1979) and *H. eliomyoides* (Binigaus, Menorca; Agustí, 1980), as well as the material referred to *Hypnomys* sp. from Caló d'en Rafelino (Mallorca; Bover et al., 2014). Conversely, *Microdyromys boveri* sp. nov. is noticeably larger than the continental representatives of *Microdyromys*, such as *M. complicatus* and *M. "miocaenicus"* (De Bruijn, 1966), *M. remmerti* (García-Paredes et al., 2010), *M. sinuosus* (Álvarez-Sierra, 1986), *M. koenigswaldi* (De Bruijn, 1966) and *M. chaabi* (Jaeger, 1977).

In the bivariate plots of tooth length and width, the measurements of *Microdyromys boveri* sp. nov. define a distinct cluster that falls between those of continental *Microdyromys* and the considerably larger Plio-Pleistocene representatives of *Hypnomys*. The ranges of the continental species are consistently smaller, whereas those of *Hypnomys* show markedly larger values for both variables. Consequently, the biometric distribution of *Microdyromys boveri* sp. nov. bridges the gap between these two groups. This intermediate position suggests that *Microdyromys boveri* sp. nov. represents an early stage in the size increase that characterizes the insular lineage leading to *Hypnomys*, preceding the pronounced enlargement observed in the later representatives of this endemic Balearic genus.

Discussion

Besides *Hypnomys*, a number of endemic glirids have been described from the late Neogene insular faunas from the western Mediterranean, such as *Stertomyx* (Gargano, southern Italy; Daams & Freudenthal, 1985), *Anthracoqlis* (Maremma, northern Italy; Engesser, 1983), *Thyrrhenoglis* (Capo Figari, Sardinia, Engesser, 1976), *Maltamys* (Malta and Sicily; Zammit-Maempel & de Bruijn, 1982; Thaler, 1972) and *Leithia* (Malta; Adams, 1863). As happened with *Hypnomys*, some of them (*Thyrrhenoglis*, *Maltamys*) have been closely related to the continental *Eliomys* by Zammit-Maempel & de Bruijn (1982). However, the presence of *Microdyromys boveri* sp. nov. at the Early Pliocene of Mallorca shed new light on the origin of these endemic glirids from the western Mediterranean islands and, as in the case of *Hypnomys*, suggests that this affiliation should be reconsidered. Biometrically, *Microdyromys boveri* sp. nov. occupies an intermediate position between the continental species of *Microdyromys* and the considerably larger Plio-Pleistocene representatives of *Hypnomys* (Figs. 3–4; Tables S1–S3), supporting its interpretation as an early member of the insular lineage that later gave rise to the genus *Hypnomys*. In the case of *Thyrrhenoglis*, the affinities with *Microdyromys* are evident. The oldest representative of the genus, *Thyrrhenoglis figarensis*, presents a dental pattern that more closely resembles that of *Microdyromys* more than that *Eliomys*, characterized by: upper molars with prototrope, precentroloph, postcentroloph and frequent posterotrope, lower molars with occasional anterotropid, long centrolophid and posterotropid. The dental pattern of *Maltamys* is even more complicated, with constant presence of anterotrope and posterotrope in the upper molars, and anterotropid and posterotropid in the lower molars, suggesting again a relationship with *Microdyromys* more than with *Eliomys*. The case of *Stertomyx* and *Anthracoqlis* seems different, since these genera lack the presence of a continuous endoloph as it is the case of *Hypnomys*, *Thyrrhenoglis* or *Maltamys*. However, their dental pattern is still very complicated, suggesting in this case a direct relationship with late Miocene species of

Vasseuromys. The chronology of these genera is also different, ranging from the late Vallesian to the Turolian, but not reaching the Pliocene.

In contrast, the cases of *Hypnomys*, *Tyrrhenoglis* and *Maltamys* seem to be clearly related to the Messinian salinity crisis, which enabled terrestrial connections between southern Europe, northern Africa and western Eurasia. This is best illustrated by the presence of African taxa such as ctenodactylids in some insular faunas, as in the case of *Pellegrinia panormensis* (associated to *Maltamys* cf. *gollcheri*) in Sicily (Thaler, 1972) and an undetermined ctenodactylid in Sardinia, initially assigned to Gerbillidae indet. by Abbazi et al. (2004). In the case of Na Burguesa-1, as we have seen, *Microdyromys boveri* sp. nov. shows the closest affinities with *Microdyromys* (or *Afrodyromys*) *chaabi* from the latest Vallesian of Oued-Zra. This therefore indicates that the late Neogene representatives of *Microdyromys* could have been restricted to northern Africa, dispersing into Europe during the Messinian salinity crisis, as happened with other African species.

Finally, the presence of *Microdyromys boveri* n. sp. at Mallorca can also shed light on the origin of the insular faunas from Eivissa. On this island, Alcover & Agustí (1985) described a new glirid species, *Eliomys* (*Eivissia*) *canarreiensis*, from the Pleistocene site of Ca Na Reia. As with *Hypnomys* and other insular forms, *E. (Eivissia) canarreiensis* displayed very large dimensions. However, as a difference with *Hypnomys*, in this case the affinities with *Eliomys* were clear and this is why Alcover & Agustí (1985) considered *Eivissia* as subgenus. However, together with *Eliomys* (*Eivissia*) a second glirid species was also present, only represented by a right m1. The size of this second species is extraordinarily large (3.03 x 2.99 mm), only comparable to that of *Leithia* and *Stertomyx*. This very large species was referred to Gliridae sp. 2 by Alcover & Agustí (1985) or *Hypnomys* sp. by Moyà-Solà et al. (1984). Agustí et al. (2021) tentatively referred it as cf. *Hypnomys* sp., pointing out the differences with that genus. The main feature that distinguished the Eivissan form from *Hypnomys* was the presence of an anterotripid, a character which is not present in the former genus. However, as we have seen, an anterotripid is always present in the m1 of *Microdyromys boveri* sp. nov. from Na Burguesa-1, suggesting that this second large endemic species from Eivissa could have been originated also as an endemic variant of *Microdyromys*, as it was the case for *Hypnomys*, *Tyrrhenoglis* and *Maltamys*.

Conclusions

Until the finding at Na Burguesa-1, the origin of the endemic genus *Hypnomys* from Mallorca and Menorca was related to the continental genus *Eliomys*, the late Miocene species *E. truci* being widely present at several sites from western Europe (Agustí, 1981; Zammit Maempel and de Bruijn, 1982; Bover et al., 2019). This was also the case of other endemic genera from other western Mediterranean islands, such as *Tyrrhenoglis* and *Maltamys* (Zammit Maempel and de Bruijn, 1982). However, the presence of *Microdyromys boveri* sp. nov. in the Early Pliocene of Mallorca suggests that this scenario should be reconsidered. Therefore, the cheek teeth of the new species from Na Burguesa-1 display a much more complicated dental pattern than any species of *Eliomys*, including the presence of long centropres and metapres, occasional presence of posteropres, long mesolophids, centrolophids and posterolophids.

Such a *Dryomys*-like morphology fits the one of some Miocene representatives of the genus *Microdyromys*. Since Mallorca remained isolated after the Zanclean flood, *Microdyromys boveri* is regarded as the direct ancestor of *Hypnomys*. The evolutionary process leading to this last genus involved an increase in size and hypsodonty as well as a simplification of the dental morphology. Other western Mediterranean endemic genera such as *Maltamys* and *Tyrrhenoglis* also present a *Dryomys*-like dental pattern comparable to that of *Microdyromys boveri*, suggesting a similar origin. Moreover, the presence of molars with a reticulated pattern, formed by numerous small ridges and cuspules, is also observed in the African species *Microdyromys chaabi* from the late Miocene of Oued-Zra (Jaeger, 1977), thus suggesting an African origin for *Microdyromys boveri*. In such a case, its presence in Mallorca could be related to the Messinian salinity crisis and the opening of new gateways between Europe and northern Africa. Similar cases of African rodents have been described on other western Mediterranean islands, such as the large gerbil from the site of Ses Fontanelles in Eivissa (Agustí, 1989; Agustí et al, 2026), the murid *Paraethomys balearicus* from Na Burguesa-1 in Mallorca (Torres-Roig et al, 2021), the ctenodactylid *Pellegrinia panormensis* from Monte Pellegrino in Sicily (Thaler, 1972), and the undescribed ctenodactylid from Sardinia.

Declarations

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Author contributions

The study is based on fieldwork by ETR and JAA. The fossil material and the data collection were carried out by ETR. The systematic study was performed by JA, JAA and ETR. The manuscript was prepared by JA with contributions from all co-authors. All authors reviewed, contributed to, and approved the final version of the manuscript.

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Data availability statement

All data generated or analysed during this study are included in this published article.

Competing interests

The authors have no relevant financial or non-financial interests to disclose

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Tables

Table 1 is available in the Supplementary Files section.

Figures

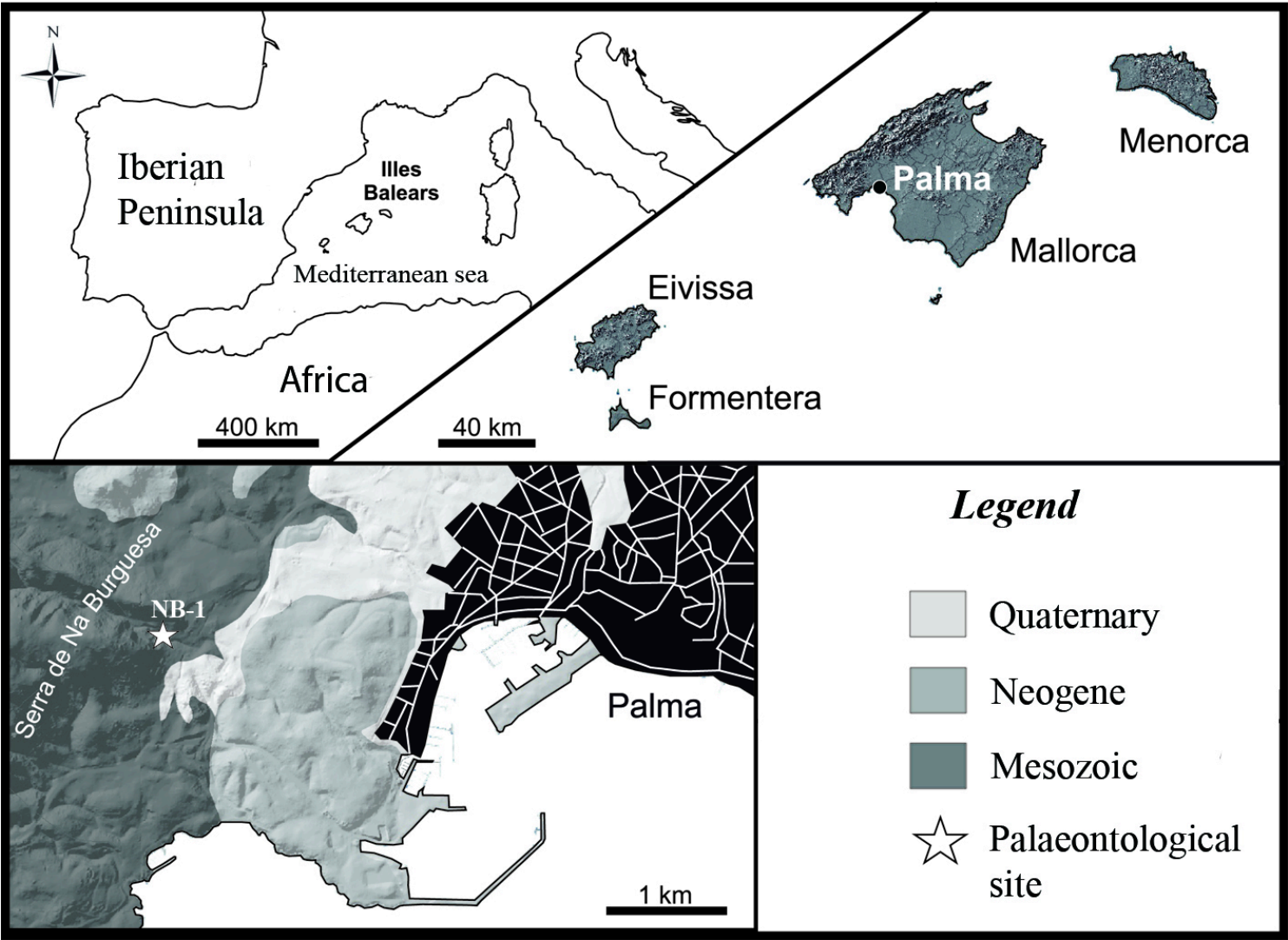


Figure 1

Geological and geographic location of the early Pliocene deposit of Na Burguesa-1(NB-1).

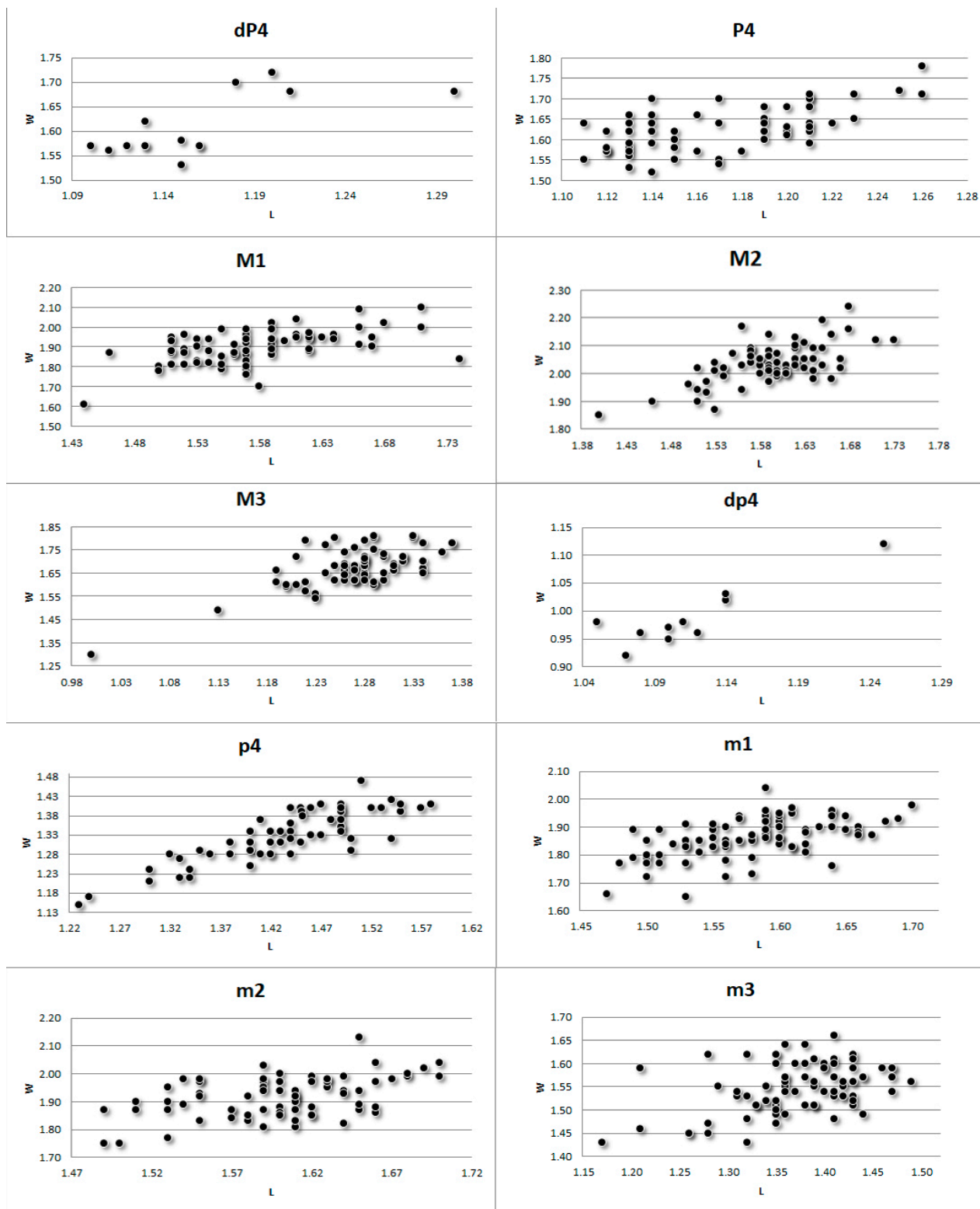


Figure 2

Plot of length versus width for premolars and molars of *Microdyromys boveri* sp. nov. from Na Burguesa

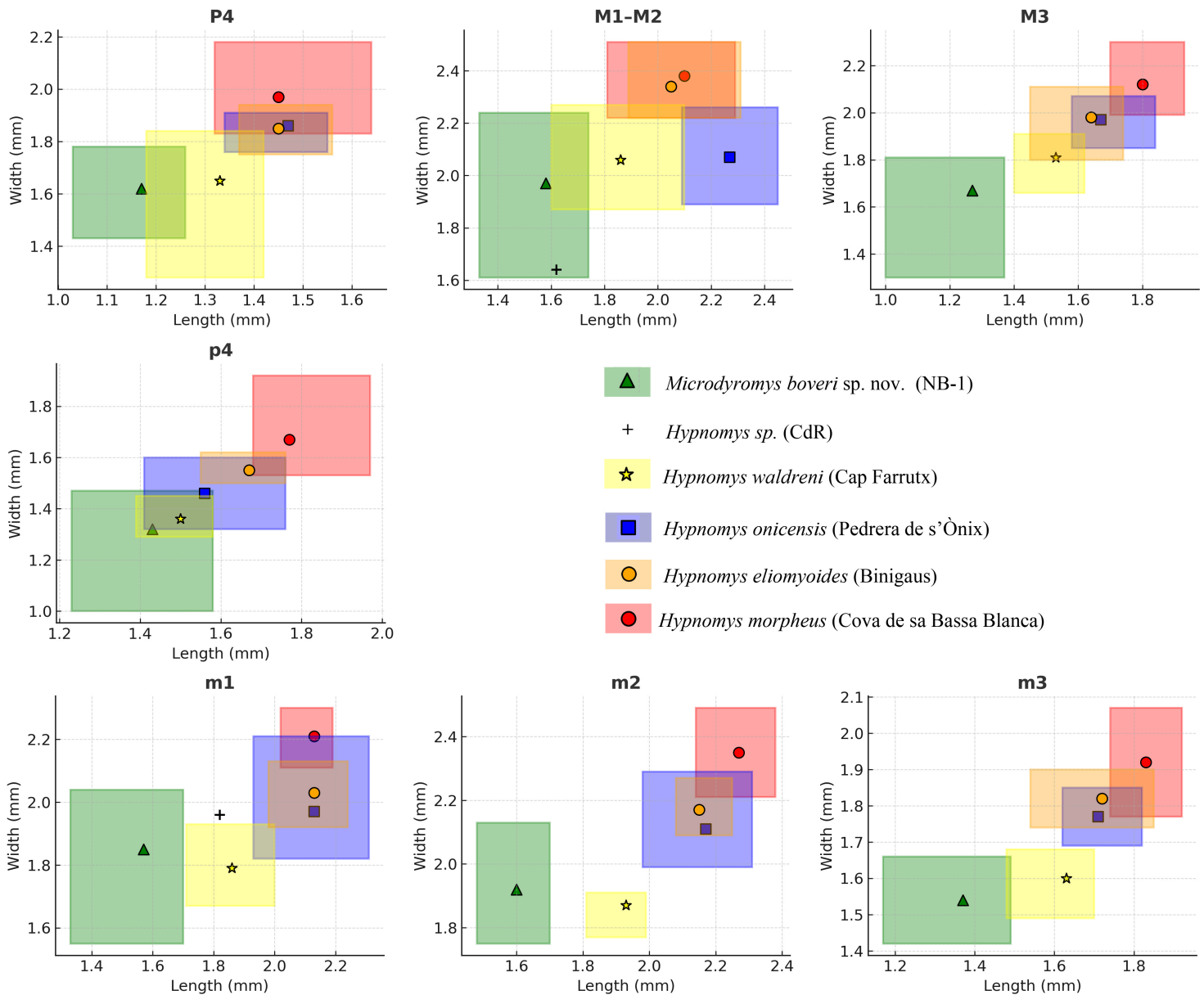


Figure 3

Ranges of size variation (in mm) in the upper (P4, M1–M2, M3) and lower (p4, m1–m2, m3) teeth of *Microdyromys boveri* sp. nov. from Na Burguesa-1 (type locality; this paper), *Hypnomys waldreni* from Cap Farrutx (type locality; Reumer 1979), *Hypnomys morpheus* from Cova de sa Bassa Blanca (unpublished material; this paper), *Hypnomys onicensis* from Pedrera de s'Ònix (type locality; Reumer 1981), *Hypnomys eliomyoides* from Binigaus (type locality; Agustí 1980). Mean sizes are marked by symbols inside the boxes. *Hypnomys* sp. from Caló den Rafelino (type locality; Bover et al. 2014) are represented only by single specimens (symbols without boxes).

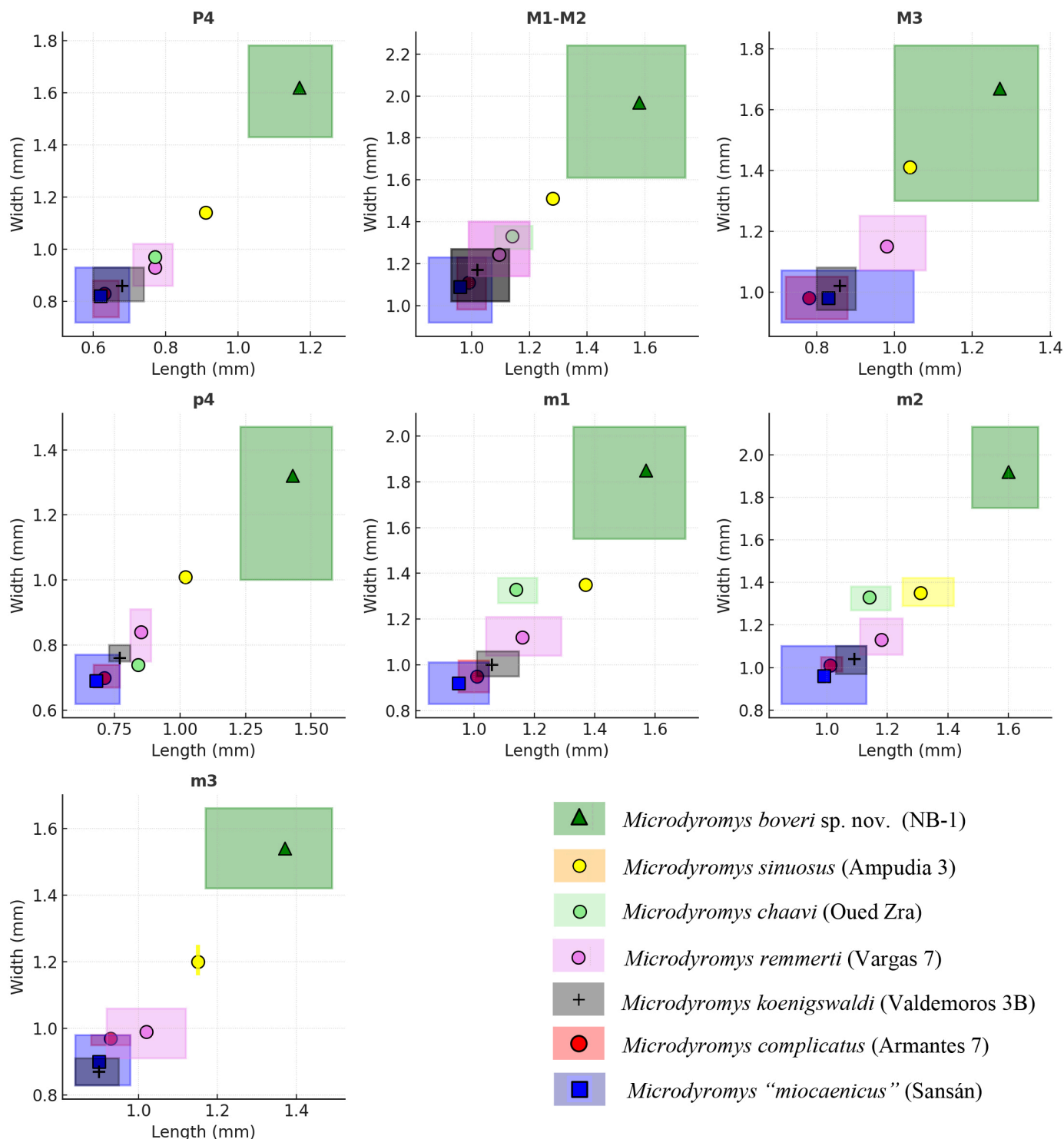


Figure 4

Ranges of size variation (in mm) in the upper (P4, M1–M2, M3) and lower (p4, m1–m2, m3) teeth of *Microdyromys boveri* sp. nov. from Na Burguesa-1 (type locality; this paper) compared with continental species of *Microdyromys*: *M. complicatus* (type locality Armantes 7; De Bruijn 1966), *M. "miocaenicus"* (type locality Sansan; De Bruijn 1966), *M. koenigswaldi* (type locality Valdemoros 3B; De Bruijn 1966), *M. remmertii* (type locality Vargas 7; García-Paredes et al. 2010), *M. sinuosus* (type locality Duero Basin;

Álvarez-Sierra 1986) and *M. chaabi* (type locality Oued Zra; Jaeger 1977). Mean sizes are marked by symbols inside the boxes.

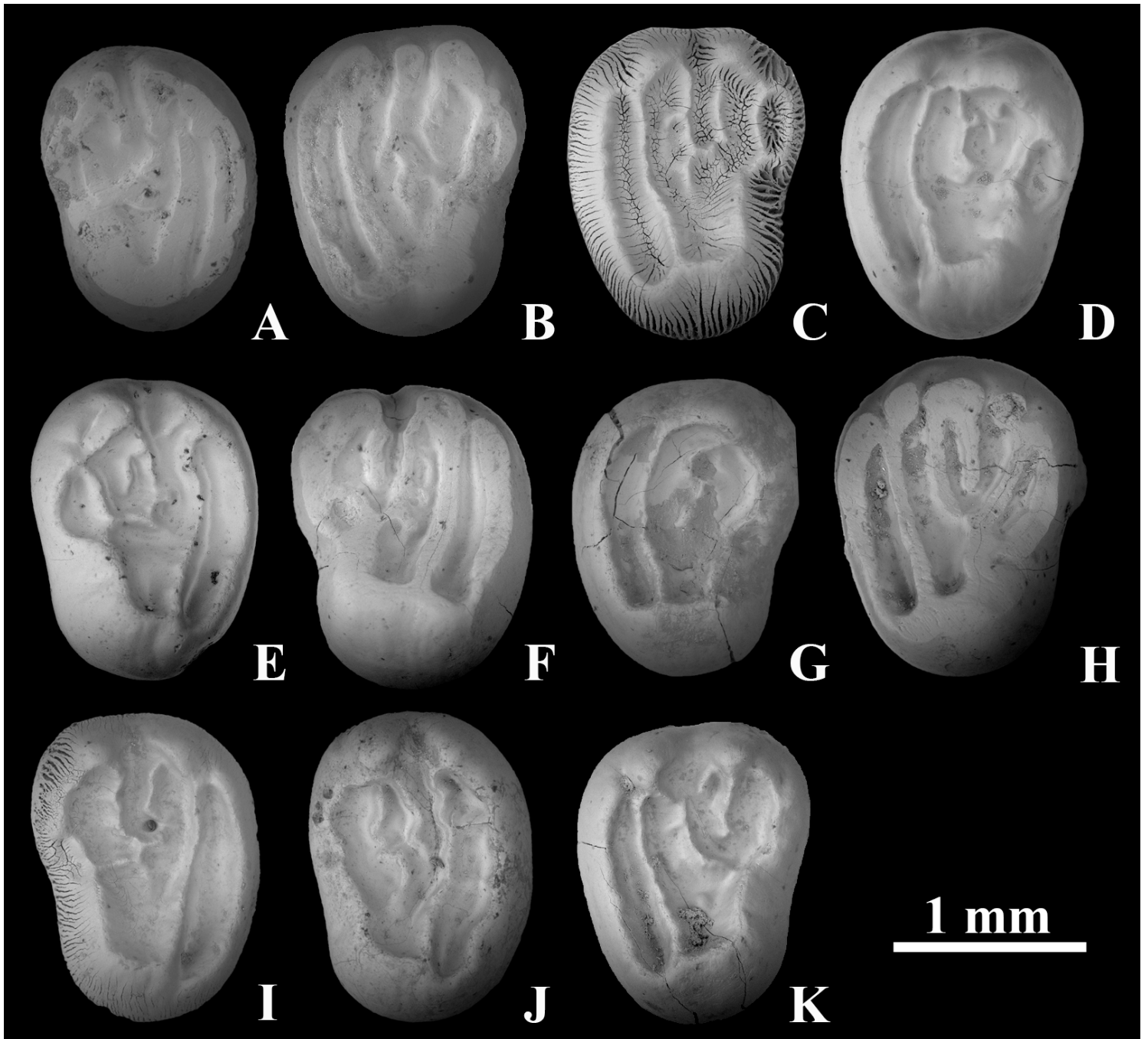


Figure 5

Upper premolars 4 in occlusal view of *Microdyromys boverisp.* nov. from NB-1, early Pliocene, Mallorca, Balearic Islands. A, left dP4 IMEDEA 107318; B, right dP4 IMEDEA 107333; C, right P4 IMEDEA 107300; D, right P4 IMEDEA 107353; E, left P4 IMEDEA 107355; F, left P4 IMEDEA 107356; G, right P4 IMEDEA 107360; H, right P4 IMEDEA 107361; I, left P4 IMEDEA 107369; J, left P4 IMEDEA 107371; K, right P4 IMEDEA 107372.

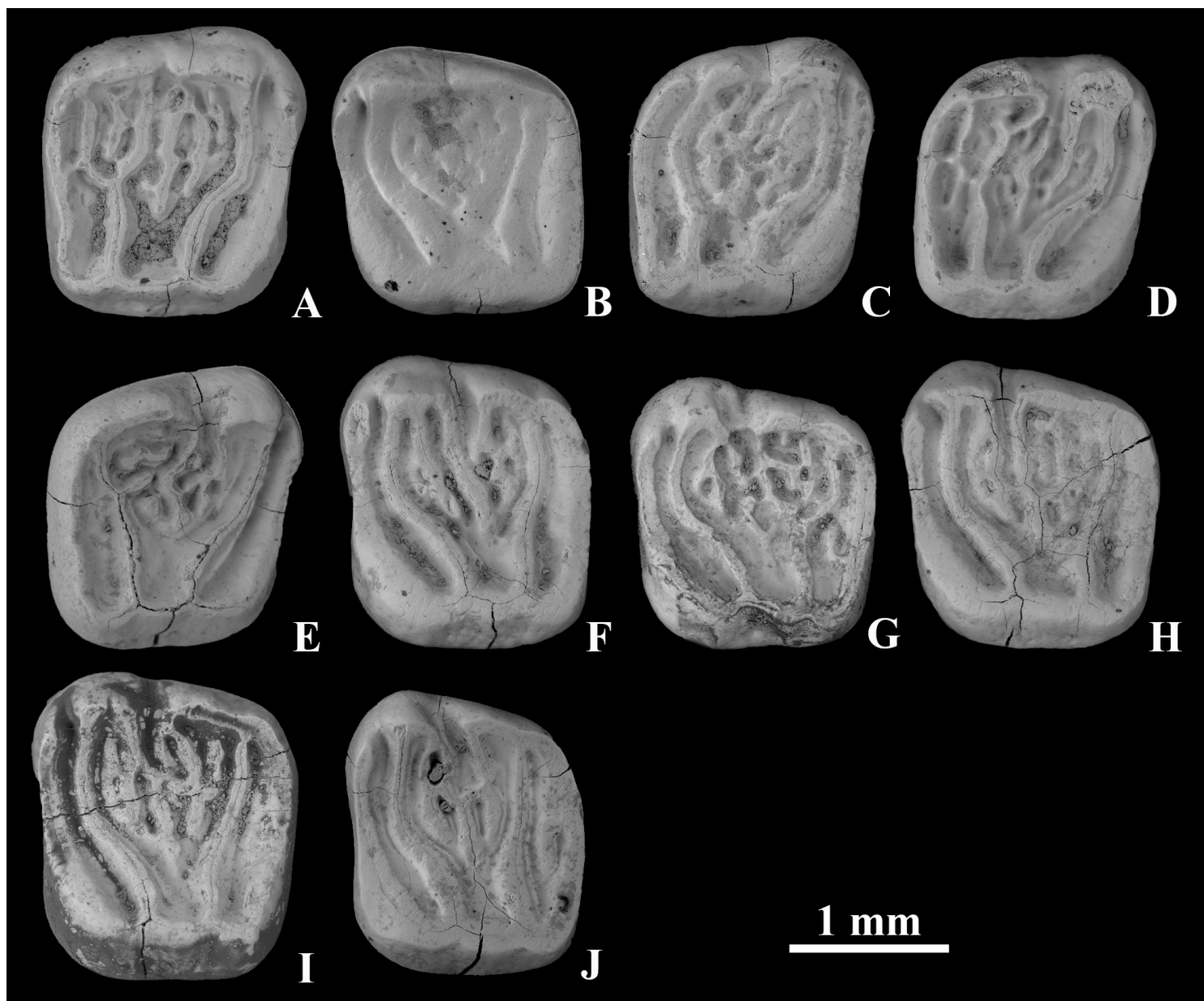


Figure 6

Upper molars 1 in occlusal view of *Microdyromys boverisp. nov.* from NB-1, early Pliocene, Mallorca, Balearic Islands. A, right M1 IMEDEA 107390; B, left M1 IMEDEA 107394; C, right M1 IMEDEA 107409; D, right M1 IMEDEA 107416; E, right M1 IMEDEA 107440; F, left M1 IMEDEA 107470; G, left M1 IMEDEA 107481 (**holotype**); H, left M1 IMEDEA 107484; I, left M1 IMEDEA 107493; J, left M1 IMEDEA 107518.



Figure 7

Upper molars 2 in occlusal view of *Microdyromys boveri* sp. nov. from NB-1, early Pliocene, Mallorca, Balearic Islands. A, right M2 IMEDEA 107374; B, left M2 IMEDEA 107382; C, right M2 IMEDEA 107424; D, right M2 IMEDEA 107427; E, left M2 IMEDEA 107429; F, right M2 IMEDEA 107431; G, left M2 IMEDEA 107454; H, right M2 IMEDEA 107464; I, left M2 IMEDEA 107465; J, right M2 IMEDEA 107466; K, right M2

IMEDEA 107474; L, left M2 IMEDEA 107489; M, right M2 IMEDEA 107496; N, right M2 IMEDEA 107504; O, left M2 IMEDEA 107514; P, right M2 IMEDEA 107515.

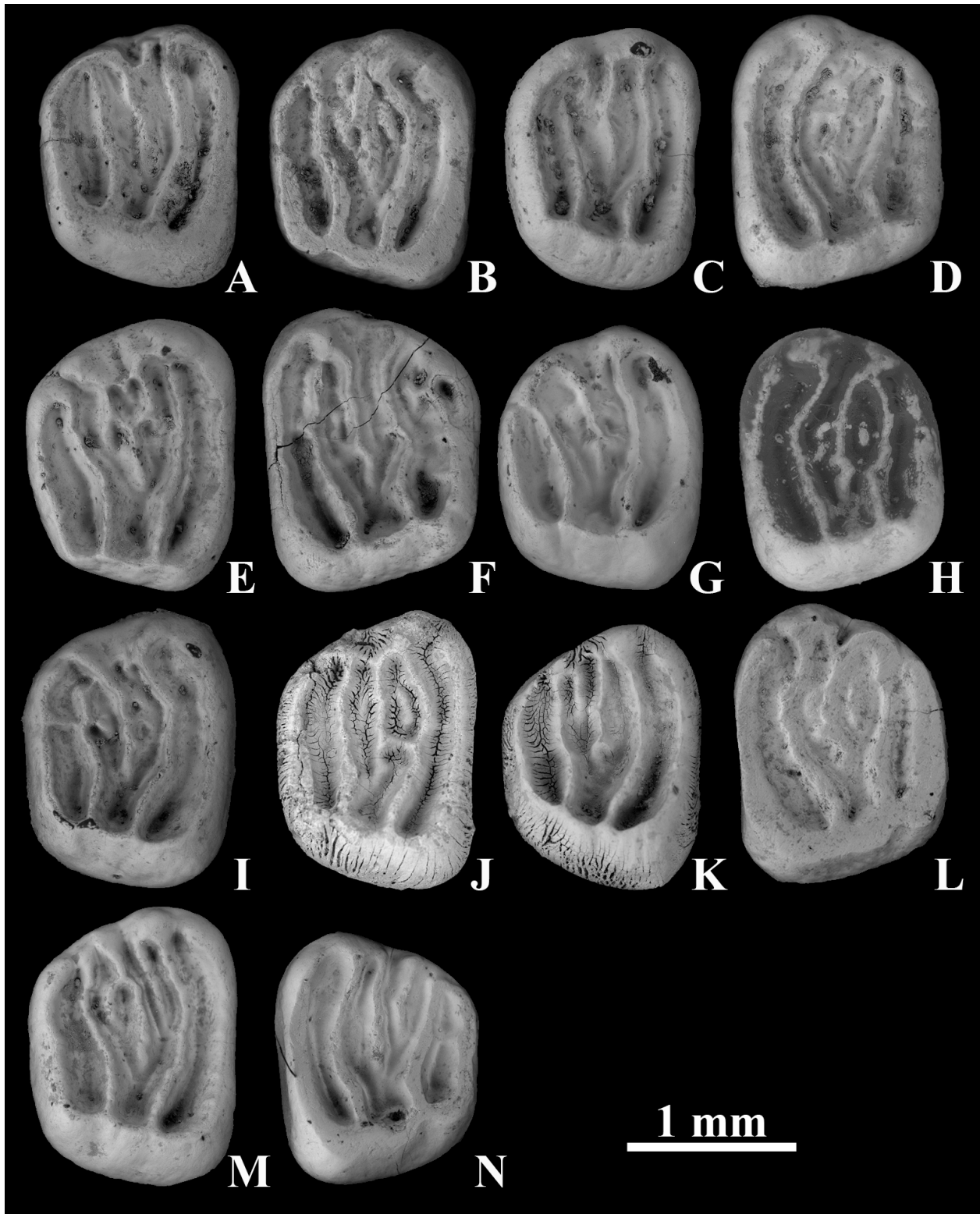


Figure 8

Upper molars 3 in occlusal view of *Microdyromys boveri* sp. nov. from NB-1, early Pliocene, Mallorca, Balearic Islands. A, right M3 IMEDEA 107521; B, right M3 IMEDEA 107525; C, right M3 IMEDEA 107526;

D, left M3 IMEDEA 107532; E, right M3 IMEDEA 107534; F, left M3 IMEDEA 107535; G, right M3 IMEDEA 107547; H, left M3 IMEDEA 107549; I, right M3 IMEDEA 107542; J, right M3 IMEDEA 107555; K, right M3 IMEDEA 107556; L, left M3 IMEDEA 107575; M, right M3 IMEDEA 107584; N, left M3 IMEDEA 107589.

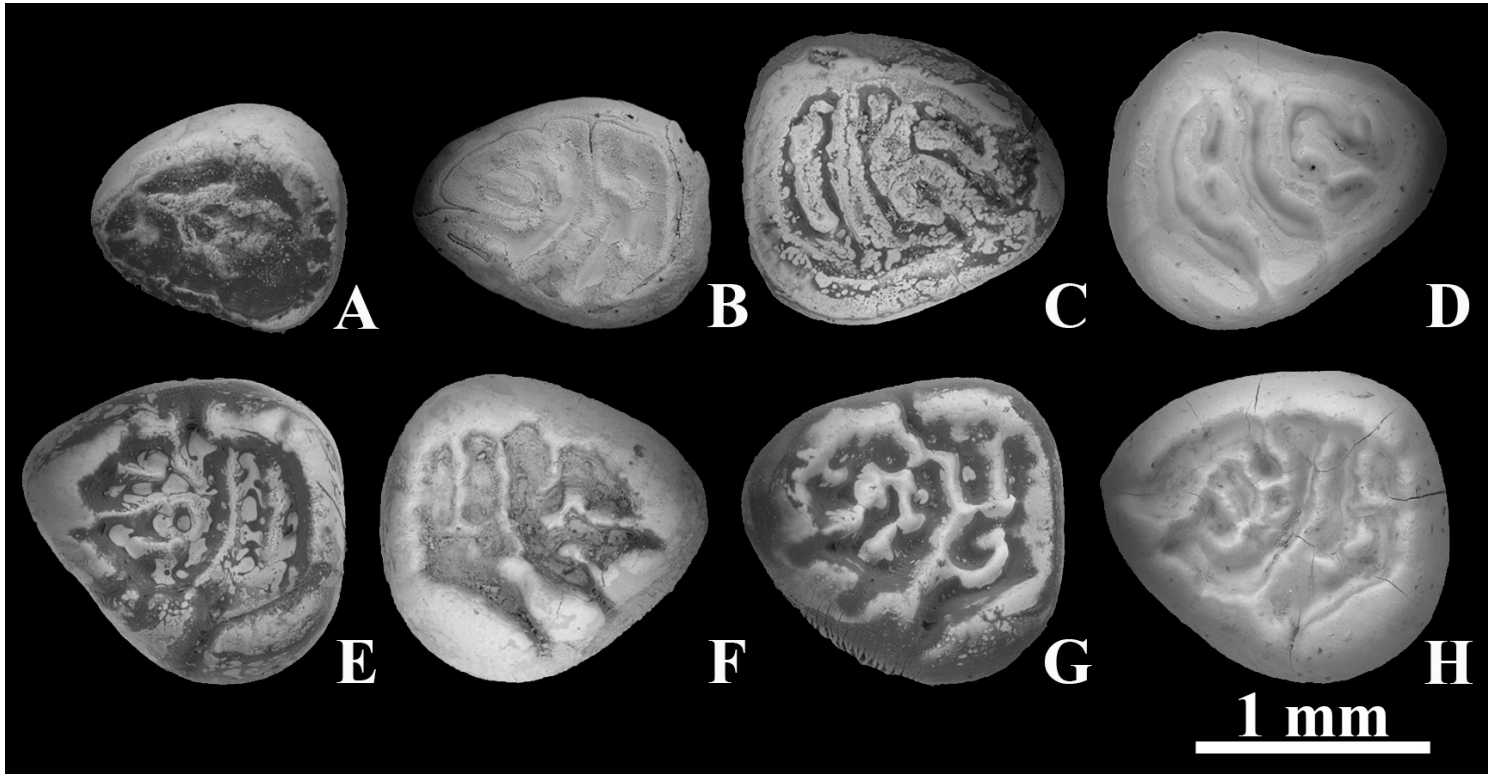


Figure 9

Lower premolars 4 in occlusal view of *Microdyromys boveri* sp. nov. from NB-1, early Pliocene, Mallorca, Balearic Islands. A, right dp4 IMEDEA 112097; B, left p4 IMEDEA 103984; C, right p4 IMEDEA 103996; D, right p4 IMEDEA 103998; E, left p4 IMEDEA 107021; F, right p4 IMEDEA 107035; G, left p4 IMEDEA 107039; H, left p4 IMEDEA 107041.

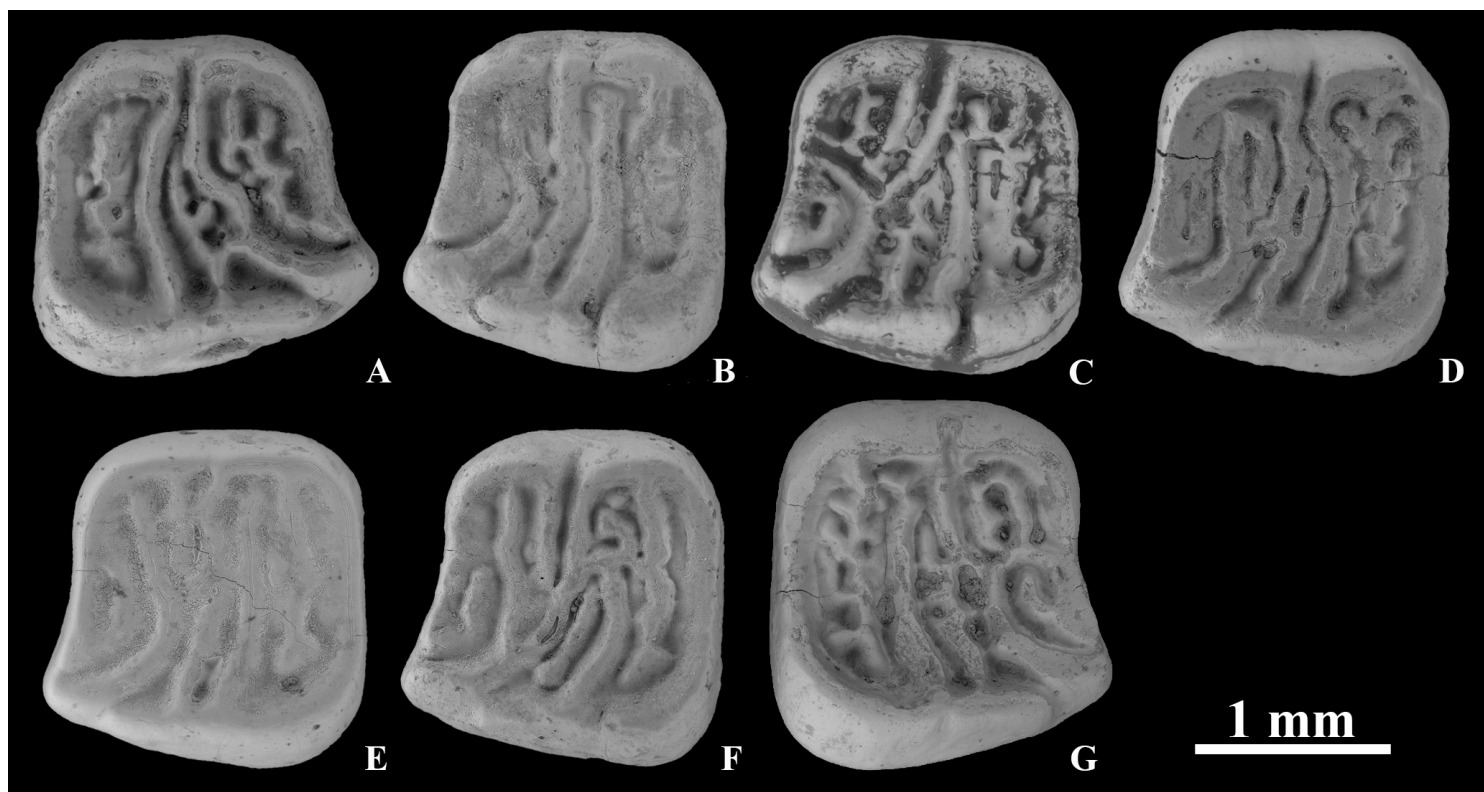


Figure 10

Lower molars 1 in occlusal view of *Microdyromys boveri* sp. nov. from NB-1, early Pliocene, Mallorca, Balearic Islands. A, right m1 IMEDEA 107063; B, left m1 IMEDEA 107071; C, left m1 IMEDEA 107089; D, left m1 IMEDEA 107100; E, left m1 IMEDEA 107163; F, left m1 IMEDEA 107174; G, right m1 IMEDEA 107181.



Figure 11

Lower molars 2 in occlusal view of *Microdyromys boveri* sp. nov. from NB-1, early Pliocene, Mallorca, Balearic Islands. A, left m2 IMEDEA 107051; B, right m2 IMEDEA 107072; C, right m2 IMEDEA 107104; D, right m2 IMEDEA 107124; E, left m2 IMEDEA 107127; F, right m2 IMEDEA 107180; G, right m2 IMEDEA 107193; H, right m2 IMEDEA 107194; I, left m2 IMEDEA 107205; J, right m2 IMEDEA 107210; K, left m2 IMEDEA 107211; L, right m2 IMEDEA 107212.

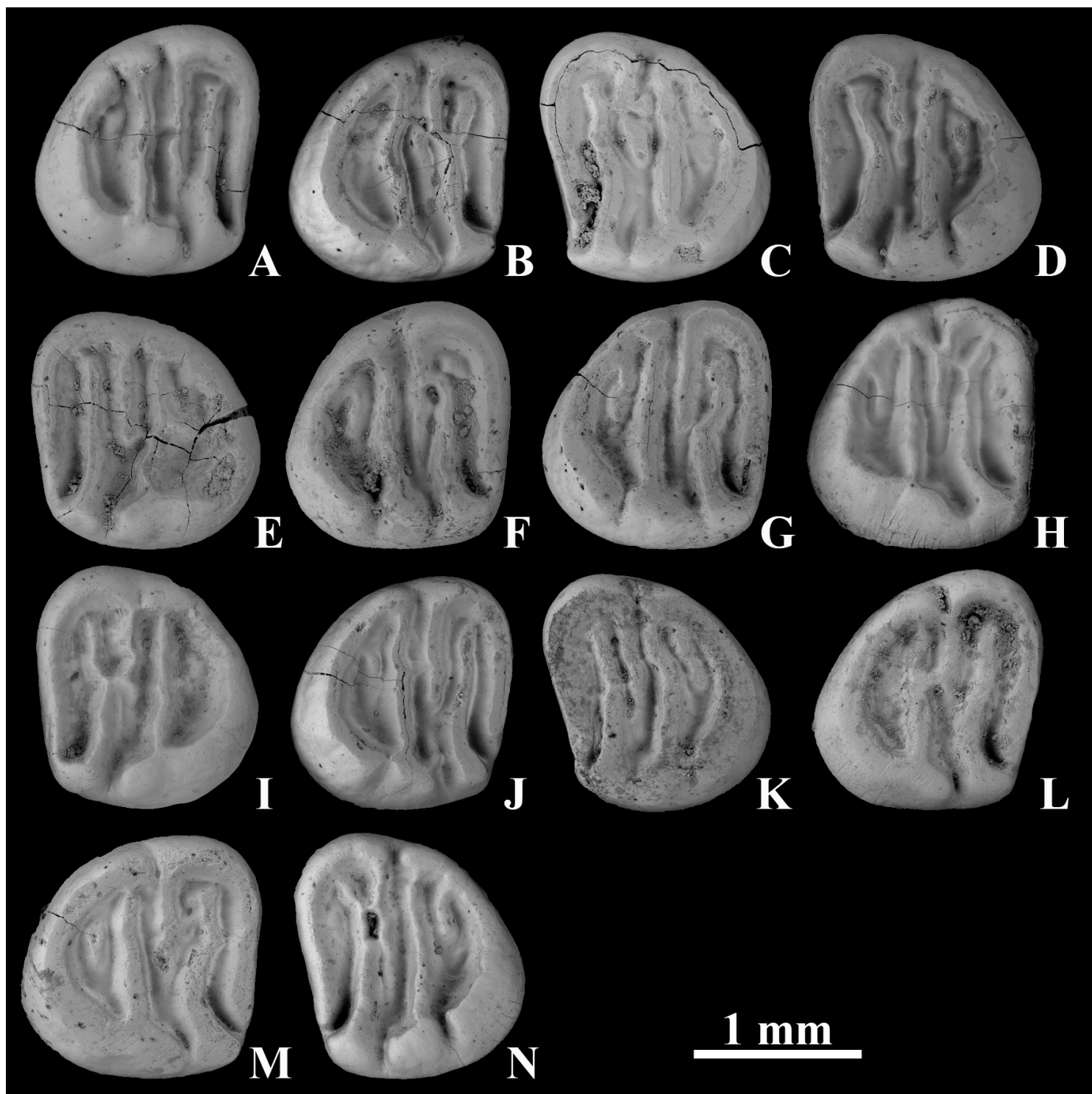


Figure 12

Lower molars 3 in occlusal view of *Microdyromys boveri* sp. nov. from NB-1, early Pliocene, Mallorca, Balearic Islands. A, right m3 IMEDEA 107230; B, right m3 IMEDEA 107234; C, left m3 IMEDEA 107248; D, left m3 IMEDEA 107260; E, left m3 IMEDEA 107264; F, right m3 IMEDEA 107263; G, right m3 IMEDEA 107270; H, right m3 IMEDEA 107273; I, left m3 IMEDEA 107285; J, right m3 IMEDEA 107286; K, left m3 IMEDEA 107287; L, right m3 IMEDEA 107289; M, right m3 IMEDEA 107290; N, left m3 IMEDEA 107297.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Table1.docx](#)
- [SupplemS1MeasurementsMboveriHypnomys.xlsx](#)
- [SupplemS2RangesMicrodyromys.xlsx](#)
- [SupplemS3RangesHypnomys.xlsx](#)