



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Orcemys, a new genus of arvicolid rodent from the early Pleistocene of the Guadix–Baza Basin, southern Spain



Orcemys, un nouveau genre de rongeur arvicolidé du Pléistocène inférieur du bassin de Cadix–Baza, Espagne méridionale

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ABSTRACT

A new arhizodont arvicoline rodent is described from early Pleistocene deposits of Barranco de los Conejos and Barranco del Paso in the Guadix–Baza Basin of southern Spain. The molars of *Orcemys* appear to represent a pedomorphic origination from a large rhizodont *Mimomys*. A few dental characters of *Orcemys* are superficially similar to those of the lagurines, but the presence of sparse cementum in reentrant folds and a *Mimomys*-kante formed opposite T5 on the first lower molar clearly identify *Orcemys* as an arvicoline. The character mosaic of *Orcemys* is unique among large early Pleistocene voles and the dentition of a potential ancestor probably resembled that of *Mimomys medasensis* with a tendency towards simplification. With *Tibericola vandermeuleni* and *Mimomys oswaldoreigi*, *Orcemys* represents one of the earliest experiments with arhizodonty among European voles. Including *Mimomys medasensis* at Barranco del Paso, this set of arvicolids redefines a previously recognized early Pleistocene MmQ1 biozone in Spain.

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R É S U M É

Un nouveau rongeur arvicoliné arhizodonte est décrit dans les dépôts du Pléistocène inférieur de Barranco de los Conejos et de Barranco del Paso dans le bassin de Cadix–Baza, en Espagne méridionale. Les molaires d'*Orcemys* semblent représenter une origine pédomorphique à partir d'un grand rhizodonte, *Mimomys*. Quelques caractéristiques dentaires d'*Orcemys* sont superficiellement similaires à ceux des laguriné, mais la présence de ciment épars dans les plis rentrants et un T5 formé à l'opposé de *Mimomys*-kante sur la première molaire inférieure identifient *Orcemys* comme un arvicoliné. La mosaïque de caractères d'*Orcemys* est unique parmi les

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grands campagnols du Pléistocène inférieur, et la dentition d'un potentiel ancêtre ressemble probablement à celle de *Mimomys medasensis*, avec une tendance à la simplification. Avec *Tibericola vandermeuleni* et *Mimomys oswaldoreigi*, *Orcemys* représente les essais les plus précoces d'arhizodontie parmi les campagnols européens. Si l'on inclut *Mimomys medasensis* dans Baqqranco del Paso, cet ensemble d'arvicolidés redéfinit une biozone MnQ1 reconnue antérieurement au Pléistocène inférieur en Espagne.

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1. Introduction

Although the first arhizodont arvicolid rodents are known from the Pliocene (the Lemminae and Pliophenacomyinae [Zakrzewski, 1984], [Fejfar and Repenning, 1998]), during the early Pleistocene about 2.0 Ma (million years ago) arvicoline rodents with rooted molars began experimenting with arhizodonty. This group included voles of the nascent tribes Arvicolini and Lagurini originating from a vast radiation of mimomyine voles, predominantly in the Old World, and the Dicrostonychini, probably originating in the New World.

Among the earliest well-dated representatives of this radiation is *Microtus (Allophaiomys)* from the Short Haul locality of Kansas, USA, currently morphologically inseparable from *M. pliocaenicus* from the Betfia 2 locality of Romania (Hir, 1998; Kormos, 1933; Martin, 2008). Short Haul is bounded below by the Huckleberry Ridge ash dated at 2.11 Ma and above by the base of the Olduvai subchron (Martin et al., 2008). The importance of the Short Haul record is that it documents an ancient age for the origination of *Microtus* and also suggests that early Pleistocene European *Microtus* are the result of a later dispersal, probably originating in Asia. Other arhizodont arvicoline genera appearing during the early Pleistocene include the Old World *Arvicola*, *Chionomys*, *Tibericola*, *Stenocranium* and *Victoriamys* (Agustí et al., 2013; Cuenca-Bescós et al., 2016; Martin, 2012). Early Pleistocene arhizodont voles also originating as end members of endemic mimomyine stems in East Asia include *Huanonomys* and *Heteromimomys* (Zhang et al., 2010; Zheng, 1992). Another evident descendant of the Old World mimomyine radiation that reached North America (Tesakov and Kolfshoten, 2011) is a relative of the North American sagebrush vole, *Lemmsicus curtatus*, recovered from early Pleistocene deposits (probably between 0.78–1.0 Ma) in Porcupine Cave, Wyoming (Bell and Barnosky, 2000). According to Koenigswald and Tesakov (1997), rootless lagurines, represented by the transition from rhizodont *Borsodia* to arhizodont *Prolagurus* (= *Lagurodon*), occurred in eastern Europe at a point subsequent to the arrival of *Allophaiomys* close to the Olduvai subchron (perhaps between 1.90–1.75 Ma). Another lineage of lagurines, *Kalymnomys*, endemic to the Aegean-Anatolian region of southeastern Europe and western Asia, developed arhizodont molars prior to the dispersal of *Allophaiomys*, possibly between 2.1–1.9 Ma (van den Hoek Ostende et al., 2015).

One of the regions in Eurasia with a very dense Late Cenozoic fossil record is the Iberian Peninsula. This region documents the evolution of rhizodont mimomyine vole

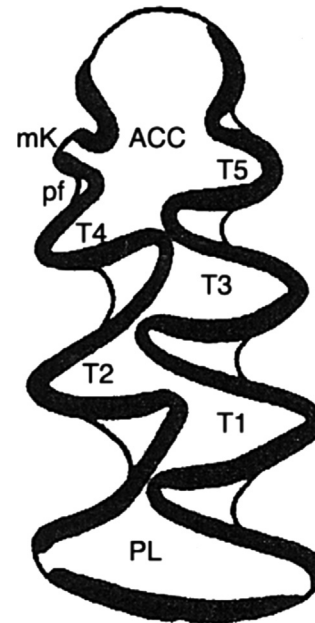


Fig. 1. Generalized *Mimomys* left m1 with a high mimosinuide on the *Mimomys*-kante (mK) breaking through the occlusal surface. Pf: prism fold; PL: posterior loop; T: triangle; ACC: anteroconid complex.

Fig. 1. M1 gauche de *Mimomys* avec une mimosinuide élevée sur la brisure de *Mimomys*-kante au travers de la surface occlusale. Pf : pli de prisme ; PL : boucle postérieure ; T : triangle ; ACC : complexe antéroconide.

assemblages of the Villanyian into arhizodont arvicoline voles of the Biharian with several lineages representing a combination of autochthonous evolution and dispersal from the Eurasian mainland. In 2005, J. Gibert (Institut Paleontologia Crusafont) provided R. Martin with arvicolid fossils recovered from Barranco (B.) del Paso in the Guadix–Baza Basin. Among the material were a number of molars from a large, arhizodont species with a high dentine tract at the position of the *Mimomys*-kante (ridge) (Fig. 1). Thinking that the taxon might be a large Iberian relative of *Borsodia* (Tesakov, 1993), Martin sent illustrations to A. Tesakov, at which point Tesakov suggested the taxon was an arvicoline and likely new. Unknown to Martin and Tesakov, J. Agustí (IPHES) had found a few molars of the same taxon at B. de los Conejos. Agustí et al. (2013) published an illustration of a first lower molar (m1) of the new taxon from B. de los Conejos and tentatively concluded it represented rootless *Mimomys medasensis*. At a recent workshop on arvicolid rodents held in Berlin, Germany as

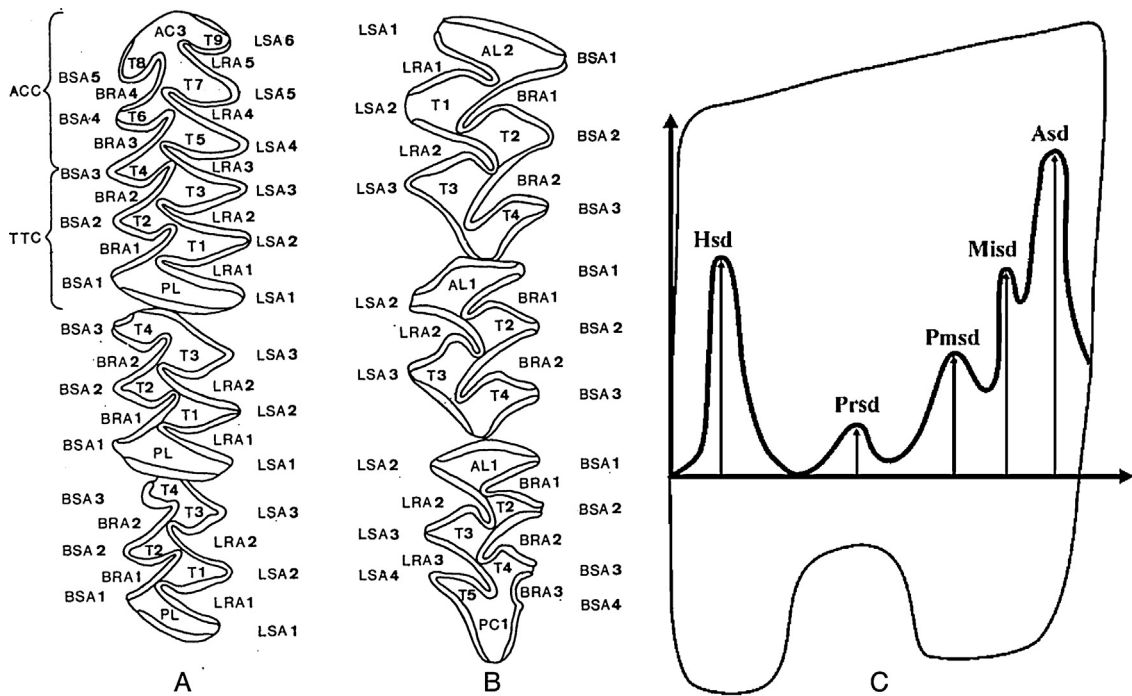


Fig. 2. A, Left lower and B, left upper, arvicolid molars with labeled topography. ACC: anteroconid complex; TTC: talonid-trigonid complex; AC: anteroconid; PL: posterior loop; AL: anterior loop; PC: posterior cap; T: triangle; BSA: buccal salient angle; LSA: lingual salient angle. C. Sinuoids (dentine tracts; or “enamel-free areas”) on labial side of m1. Asd: anterosinuoid; Misd: mimosinuoid; Pmsd: prismosinuoid; Prsd: protosinuoid; Hsd: hyposinuoid.

Fig. 2. A, molaires d’arvicolidés inférieures gauches, B, supérieures gauches, avec topographie marquée. ACC : complexe antéroconide ; TTC : complexe talonide-trigonide ; AC : antéroconide ; PL : boucle postérieure ; AL : boucle antérieure ; PC : couronne postérieure ; T : triangle ; BSA : angle buccal saillant ; LSA : angle lingual saillant. C. Sinuïdes (zones de dentine ou « zones ne comportant pas d’émail » sur le côté labial de m1. Asd : antérosinuïde ; Misd : mimosinuïde ; Pmsd : prismosinuïde ; Hsd : hyposinuïde.

part of the 2014 annual meeting of the Society of Vertebrate Paleontology, Tesakov and Martin examined the B. del Paso arvicolid material and concluded that enough specimens were available to define and justify a new taxon separate from *M. medasensis*. They invited Agustí to join them in the description of this taxon, resulting in the contents that follow.

2. Dental terminology and measurements

Arvicolid molar occlusal morphology and terminology of the crown-root junction, the linea sinuosa (Fig. 2), follow Meulen (1973) and Rabeder (1981). Lower molars are designated by lower case, uppers by upper case letters; acc = anteroconid complex, acd = anteroconid of first lower molar (m1). Anterior and posterior enamel edges of triangles, as seen in occlusal morphology under the dissecting microscope, may display distinct differences in thickness (be differentiated). The term negative enamel differentiation applies if the posterior (trailing) edges in the lowers are thicker than the anterior (leading) edges (opposite in the uppers – anterior edges thicker). Most *Mimomys* dentitions display negative differentiation. Positive enamel differentiation describes the condition in which the posterior edges are thinner than the anterior edges in the lowers (opposite in the uppers). Most *Microtus* species have positive differentiation. A few extinct and extant arhizodont voles display the undifferentiated condition, in which anterior and

posterior edges are of equal thickness. As shown by Martin et al. (2006), molars that appear undifferentiated under the light or dissecting microscope may actually be slightly differentiated if edges are measured more accurately under the electron microscope. Rhizodont molars possess roots; arhizodont molars are rootless and evergrowing. Hypsodont = high-crowned, hypselodont = high-crowned and rootless. The m1 in some archaic arvicoline genera, including *Mimomys*, is characterized by the presence of a unique structure named the *Mimomys*-kante. This is an enamel projection from the anterior border of T4 that breaks the standard third buccal (labial) reentrant fold (BRA3) of arvicolid m1s into two new folds. The fold posterior to the *Mimomys*-kante is referred to as the *prism fold* (Fig. 1).

All measurements are greatest measurements on the occlusal surface. The BTQ, or Basic Triangle Quotient, of Tesakov (1998) was used to quantify enamel differentiation of the m1 as follows:

$$\text{BTQ m1} = 100 \times \frac{(\text{SDQ1} + \text{SDQ2} + \text{SDQ3})}{3},$$

where SDQ_n = thickness of anterior (leading) enamel edge / thickness of posterior (trailing) edges in the first three primary triangles (T1–T3). Differentiation categories are recognized as $\text{BTQ} > 100$ = positive differentiation, $\text{BTQ} = 100$ = undifferentiated, $\text{BTQ} < 100$ = negative differentiation.

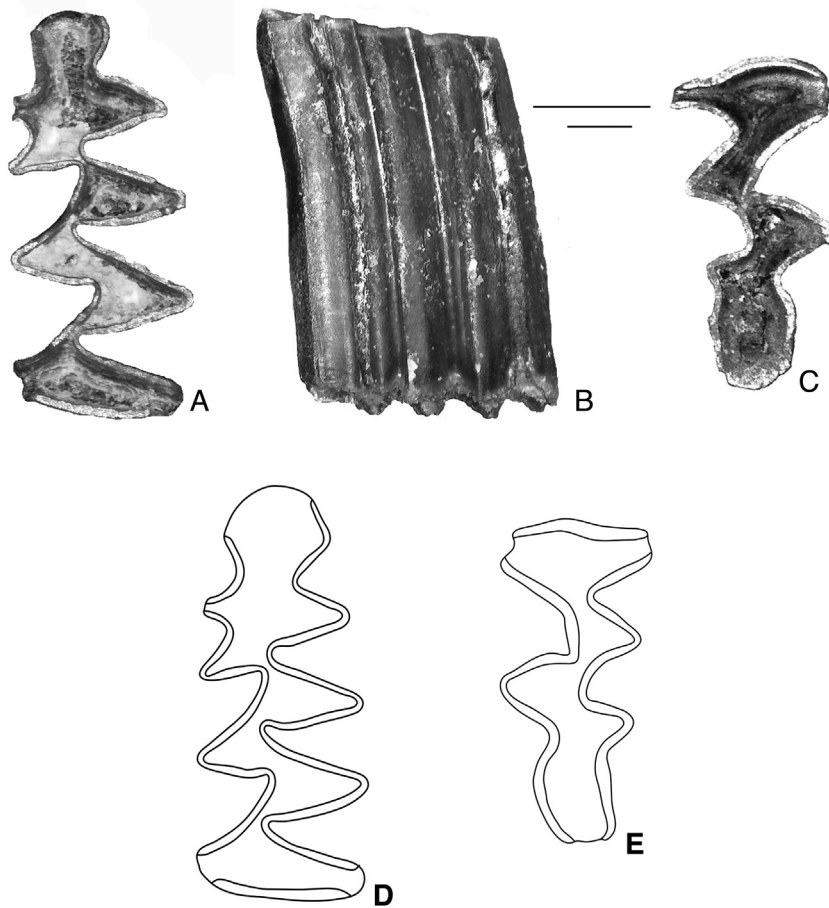


Fig. 3. *Orcemys giberti* from the Guadix–Baza basin, Spain. Occlusal (A) and labial (B) views of holotype Lm1, IPHES BC-030 and occlusal view (C) of paratype LM3, IPHES BC-036, B. de los Conejos. Occlusal view (D) of Lm1, OM-BP 0101 and RM3, OM-BP 0111, B. del Paso. Lines: 1 mm, top for A, C, D, E; bottom for B.

Fig. 3. *Orcemys giberti* du bassin de Cadix–Baza, Espagne. Vues occlusale (A) et labiale (B) de l'holotype Lm1, IPHES BC-030 et vue occlusale du paratype LM3, IPHES BC-036, bassin de los Conejos. Vue occlusale (D) de Lm1, OM-BP 0101 et RM3, OM-BP 0111, B. del Paso. Lignes : 1 mm, sommet pour A, C, D, E, base pour B.

The microhistological enamel banding pattern of the occlusal molar surface as seen under the scanning electron microscope (SEM) is known as the schmelzmuster (Koenigswald, 1980). L=lamellar enamel, T=tangential enamel, R=radial enamel. Incipient tangential enamel (IT) is intermediate between radial and well-developed tangential enamel, in which enamel prisms are bent at a 45° angle and the edges are not flat and feathered. A L–R pattern on the anterior (leading) edges of a triangle on the lower molars implies that the inner band was composed of lamellar enamel and the outer of radial enamel. Further definition of these terms can be found in Martin et al. (2003, 2006). Schmelzmuster photos were taken with an FEI Quanta 600 ESEM.

A phylogenetic analysis was done with MacClade 4.06 (Maddison and Maddison, 2001) including *Orcemys* and select arvicolid. Characters and a data matrix are found in Appendix I. *Promimomys insuliferus* was chosen as the outgroup. The comparison was made only with large *Mimomys* species (mean m1 length ≥ 3.30 mm), as it was assumed

that the arhizodont dentition of *O. giberti* originated as a pedomorphic population from a large rhizodont ancestor.

OM=Orce Museum (Centro Interpretación Primeros Probladores Jose Gibert), BP=Barranco del Paso, IPHES=Catalan Institute of Human Palaeoecology and Social Evolution.

Systematic Paleontology

Class Mammalia Linnaeus, 1758

Order Rodentia Bowdich, 1821

Family Arvicolidae Gray, 1821

Subfamily Arvicolinae Gray, 1821

Orcemys, nov. gen.

Orcemys giberti, nov. sp.

(Fig. 3)

Holotype–B. de los Conejos: IPHES-BC-030, Lm1.

Paratype–IPHES BC-036, LM3.

Referred specimens–B. del Paso: OM-BP 0101, Lm1, OM-BP 0100, broken Lm1; OM-BP 0102, broken Lm1; OM-BP 0103, partly eroded Lm1; OM-BP 0105, broken LM1 or M2; OM-BP 0106, broken Rm2; OM-BP 0107, broken Lm2;

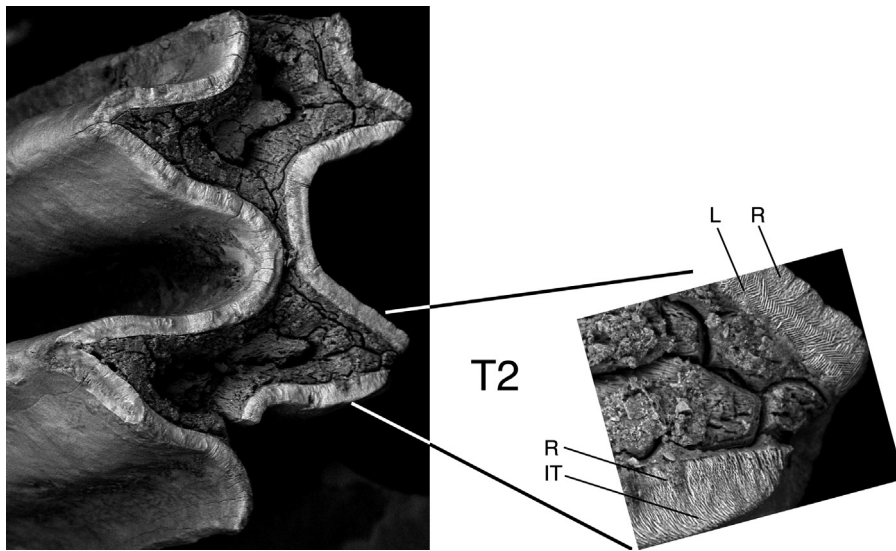


Fig. 4. Scanning electron microscope image of Rm2 (61 ×), OM-BP 0106 of *O. giberti* from B. del Paso, Baza Basin, Spain. Exploded image (492 ×) is of tip of T2 showing LR-RIT schmelzmuster (enamel banding pattern). L: lamellar; R: radial; IT: incipient tangential.

Fig. 4. Image au microscope électronique à balayage de Rm2 (61 ×), OM-BP 0106 de *O. giberti* de B. del Paso, bassin de Baza, Espagne. Image en éclaté (492 ×) de l'extrémité de T2 montrant LR-RIT schmelzmuster (arrangement rubané de l'émail). L : lamellaire ; R : radial ; IT : tangentiel naissant.

OM-BP 0108, broken Rm3; OM-BP 0109, Lm3; OM-BP 0110, RM3; OM-BP 0111, RM3.

Locality and horizon—B. de los Conejos and B. del Paso, Guadix–Baza Basin, Granada, Spain; early Pleistocene, above Olduvai subchron, perhaps 1.5–1.7 Ma.

Etymology—*Orcemys*, after the area in the Guadix–Baza Basin that has produced a series of important paleontological localities; *giberti*, in honor of the late Josep Gibert y Clois, for his pioneering work with Pleistocene mammals in the Guadix–Baza Basin.

Diagnosis of genus and species—Size large (m1 > 3.30 mm); molars rootless and hypsodont; triangles with acute rather than rounded or bulbous tips, widest at bases; enamel negatively differentiated or undifferentiated; cement absent to minimal in reentrant folds; lingual reentrant folds on m1 horizontal to slightly provergent; schmelzmuster L-R on leading and R-IT on trailing edges (Fig. 4); *Mimomys*-kante narrow, somewhat elongated and located opposite base of T5; high dentine tract (the mimosinuid of Rabeder, 1981) on m1 at *Mimomys*-kante breaking through enamel on occlusal surface with minimal wear; BRA3 and LRA4 on m1 shallow, resulting in simple acid without pronounced lingual extension; T1–T2 on m1 widely confluent; T1–2 and T3–4 widely confluent on m2; T3–4 widely confluent on m3; T4 reduced on m3; enamel atolls absent from m1 and M3; M3 simple, with 2 labial and 2 lingual reentrant folds; anterior loop on M3 lingually narrowed and broadly confluent with T2; T3 widely confluent with posterior cap on M3; T4 on M3 minimally developed.

Differential diagnosis of the genus. Differs from *Mimomys* in having rootless molars, from genera of the Microtini in having sparse cement, nearly straight walls of occlusal triangles and simple M3.

Measurements—(length followed by width): holotype m1 (3.47 × 1.47 mm); m1 OM-BP0101 (3.78 × 1.58 mm);

m1 OM-PB0104 (3.32 × 1.52 mm); M3 IPHES BC–036 (2.69 × 1.39 mm); M3 OM-PB0110 (2.51 × 1.35 mm); M3 OM-PB111 (2.35 × 1.18 mm). BTQ of holotype m1 = 91; BTQ of m1 OM-BP0101 = 61.

Description of dentition—With the exception of the holotype m1 and paratype M3, the following description pertains primarily to the specimens from B. del Paso.

m1: The m1 is composed of three triangles and the anteroconid complex. A slim and relatively elongate *Mimomys*-kante is developed from the anterior enamel border of T4. A high mimosinuid breaks through the occlusal surface at the *Mimomys*-kante in the holotype from B. de los Conejos and two m1s from B. del Paso in which this area is preserved. Another, shallower fold forms the anterior border of the *Mimomys*-kante, leading to a small, simple, circular to oblong anterior cap. The enamel ranges from negatively differentiated to undifferentiated. An enamel atoll is absent in three adult m1s. In the holotype m1 and referred specimen OM-BP0101, thin dentine tracts connect the posterior loop with T1, T2–T3, and T3–acd. A relatively wide dentine isthmus connects T1–T2 in both specimens. In the m1 OM-BP0103, dentine tracts connect both T1–T2 and T2–T3, creating a relatively wide dentine field between these triangles. Differences in BTQ between the holotype and OM-BP0101 are well within the boundaries of individual variation for BTQ values (Martin et al., 2006).

m2: T1–T4 well developed. T1–T2 widely confluent (Fig. 4).

m3: Similar form to m2, except T4 is much reduced.

M1–M2: only one partial upper molar, probably a piece of M1, is available from B. del Paso. T3 is closed from T4, but nothing distinctive can be seen on this specimen.

M3: The M3 is simple, with an anterior loop, two triangles (T2 and T3) and a small, posteriorly extended posterior cap. BRA3 is negligibly developed and LRA3 is shallow. The

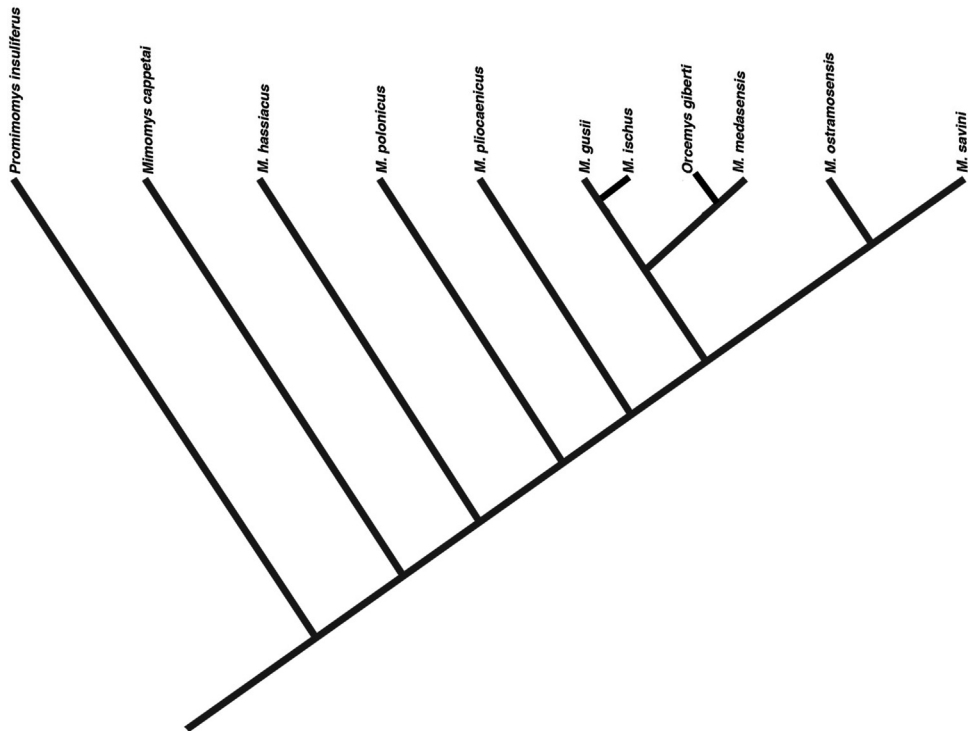


Fig. 5. Cladogram resolving relationships of *O. giberti* based on comparisons in Appendix I.
 Fig. 5. Cladogramme résolvant les relations de *O. giberti*, basé sur comparaisons (Appendice I).

anterior cap is widely confluent with T2 and T3 is widely confluent with the posterior cap. Enamel atolls are absent. The anterior loop is asymmetrical and can be considerably lingually narrowed. In general form, it somewhat resembles the M3 of the lagurines *Borsodia* and *Lagurodon*.

Cementum is mostly absent from the reentrant folds between triangles, but a slight bit of cementum can occasionally be seen adhering to the walls of reentrant folds. This feature discriminates *O. giberti* from contemporaneous *Mimomys medasensis* and *Tibericola vandermeuleni*, in which cementum is well-developed, and also from the lagurines, in which cementum is absent.

3. Discussion

3.1. Phylogenetic Relationships

The combination of characters expressed by *Orcemys* as shown by the cladogram in Fig. 5 is unique among Eurasian arvicolids. The unusual acc form of the m1, with a narrow, elongate *Mimomys*-kante associated with a high mimosinuid, is found in *Mimomys medasensis*, *M. malezi*, *Heteromimomys zhengi*, *Borsodia arankoides* and *Lagurodon arankae* in Eurasia and *Mimomys* (*Cromeromys*) species from Eurasia and North America, but only *L. arankae* is fully arhizodont. The M3 morphology of *O. giberti*, with an asymmetrical anterior loop and narrow, extended posterior cap, is decidedly lagurine in shape, as is the simple anteroconid shape of m1 anterior to the *Mimomys*-kante (Fig. 6). However, the presence of cementum in the reentrant folds and the position of the *Mimomys*-kante opposite T5 on m1

clearly demonstrate derivation from an ancestral arvicoline. Also, by the time advanced, occasionally arhizodont, *Lagurodon* appear in eastern Europe enamel differentiation is positive, unlike the condition in *Orcemys* in which differentiation is primarily negative to undifferentiated. Dental similarities of *O. giberti* molars to those of the lagurines are therefore convergent.

Agustí et al. (2013) suggested that the B. de los Conejos *O. giberti* represented rootless *Mimomys medasensis*, a species described initially by Michaux (1971) from Islas Medes off the northern coast of Spain. However, as shown by Michaux (1971), the juvenile morphology of *M. medasensis* m1s from the type locality differs from the morphology of *O. giberti*. Juvenile m1s of *M. medasensis* usually display an enamel atoll in the acd. Additionally, as in all other large *Mimomys* but not in *Orcemys*, juvenile *M. medasensis* display a bulbous lingual projection from the anterior end of the acd due to relatively deep penetration of LRA4 (Fig. 6). LRA4 shallows out in *M. medasensis* with later wear. BRA3 also tends to be relatively deep in juvenile *M. medasensis* m1s. In contrast, the m1 of *O. giberti* never displays deep LRA4 or BRA3, resulting in a simple and relatively narrow acc form at all wear stages. The M3 of *M. medasensis* is also typical for *Mimomys*, with a wide posterior cap enclosing an enamel atoll, whereas the M3 of *O. giberti* is more lagurine in its morphology. Thirty-six molars of *M. medasensis* in all wear stages were identified with *O. giberti* from B. del Paso. Root formation was observed in all specimens, including the least worn specimens with crown height comparable to molars of *O. giberti*. So, *O. giberti* molars are not juvenile *M. medasensis* molars.

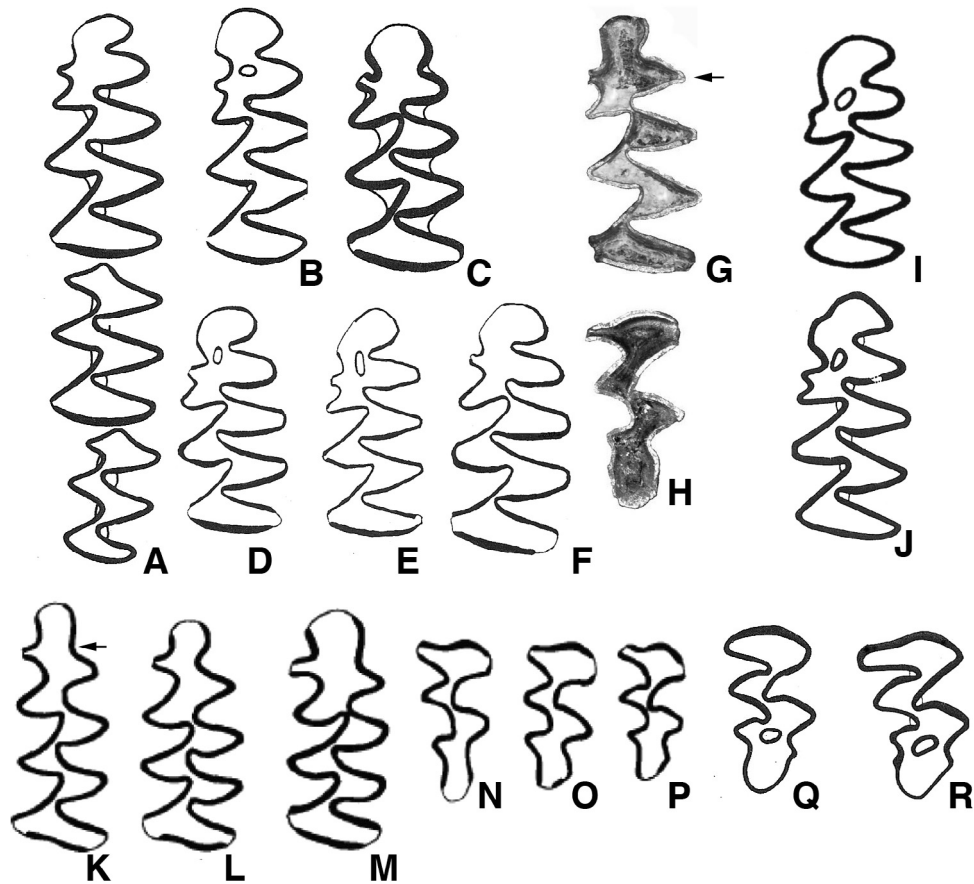


Fig. 6. Comparison of m1 and M3 morphologies between *O. giberti* and select species of *Mimomys* and *Borsodia*. A–C, Q: *Mimomys medasensis*, Medes Islands, Spain (from Michaux, 1971); D–F (E is juvenile): *M. ischus*, Almenara (Casablanca) 1, Spain (from Agustí et al., 1993); G–H: *O. giberti*, B. de los Conejos, Spain; I (reversed), *M. hassiacus* from Tollo de Chiclana 1B (from Minwer-Barakat et al., 2008); J, R (reversed); *M. cappelai*, Balaruc II, France (from Michaux, 1971); K–P (O–P reversed); *Borsodia arankoides*, Kryzhanovska 4, Ukraine (from Tesakov, 1998). Arrows identify position of *Mimomys*-kante relative to base of T5. Figures not to scale.

Fig. 6. Comparaison des morphologies de m1 et M3 entre *O. giberti* et des espèces sélectionnées de *Mimomys* et *Borsodia*. A–C, Q : *Mimomys medasensis*, îles Medes, Espagne (selon Michaux, 1971) ; D–F (E est juvénile) ; *M. ischus*, Almenara (Casablanca) 1 (selon Agustí et al., 1993) ; G–H : *O. giberti* los Conejos, Espagne ; I (retourné), *M. hassiacus* de Tollo de Chiclana 1B (selon Minwer-Barakat et al., 2008) ; J, R (retourné), *M. cappelai*, Balaruc II, France (selon Michaux, 1971) ; K–P (O–P (retourné)), *Borsodia arankoides*, Kryzhanovska 4, Ukraine (from Tesakov, 1998). Les flèches identifient la position de *Mimomys*-kante relative à la base de T5. Les figures ne sont pas à l'échelle.

However, a relationship with *M. medasensis* remains possible.

A number of the dental features of *O. giberti* are those that one would expect if *O. giberti* molars were paedomorphic forms inherited from an ancestral large rhizodont *Mimomys*, including absence of roots, minimal cementum in the reentrant folds and a more angular (prismatic) appearance of individual triangles. *Mimomys medasensis* and the earlier *M. ischus/gusii* complex occasionally display the high mimosinuid of *O. giberti* (Agustí et al., 2013; Esteban and Martínez-Salanova, 1987), but not the simple morphology of m1 and M3. Nevertheless, the ancestor of *O. giberti* must have possessed a dentition resembling that of *M. medasensis* in which juvenile m1 and M3 morphology tended towards simplification, and it is conceivable, perhaps even likely, that *O. giberti* evolved from a currently unrecovered population of *M. medasensis* or an Iberian *Mimomys* ancestral to both. In his original diagnosis of *M. medasensis*, Michaux (1971) noted that the

anterior cap of m1 was relatively narrow and the atoll on m1 was reduced in size relative to other *Mimomys* species.

3.2. Biochronology

In their recent description of rodent biostratigraphy in the Guadix–Baza basin, Agustí et al. (2015) listed *Mimomys medasensis* as an associate of *Mimomys* (= *Kislangia*) *gusii* from their *Kislangia gusii* biozone, representing the MN (Mammal Neogene) 17 zone. *Mimomys medasensis* is present at B. del Paso but absent from B. de los Conejos. This difference in rodent faunal composition could therefore represent a difference in age between the latter sites. While there may be a temporal difference between the B. del Paso and B. de los Conejos localities, we suspect the difference is slight, and neither is likely to be as old as the sites of Galera 2 and Zújar 14 from the *K. gusii* biozone. The combination of *O. giberti*, (arhizodont) *Tibericola*

vandermeuleni and *Mimomys oswaldoreigi* defines the *Mimomys oswaldoreigi* biozone of Agustí et al. (2015) and Arvicolid Zone 1 of Martin (2012, 2016). In eastern Europe, this interval correlates with the early Tamaian (= Odessian) faunal horizon of the eastern European “Eopleistocene” (Rekovets and Nadachowski, 1995) and regional biochrons MQR 11–10, equivalent to the early Biharian of western Europe (Tesakov, 2004). The early Tamaian is characterized by the earliest arhizodont *Microtus*, *M. deucalion*. Known from a number of localities in the Black Sea region of the Ukraine and Russia, *M. deucalion* apparently ranges from just beneath the Olduvai subchron to about 1.6 Ma (Tesakov, 2004). No arhizodont arvicolids have been reported from European sites allocated to MN 17, the latter which is considered to be >2.0 Ma in age (Fejfar et al., 1998). Although *Mimomys medasensis* was tentatively recorded from MN 17 (Opdyke et al., 1997), this material has not been studied in detail and it is unclear if the second large *Mimomys* from Galera 2 and Zújar 14 (besides *M. gusii*) is the same species that we report here as *M. medasensis* from B. del Paso. Scott et al. (2007) also reported that B. del Paso was deposited in sediments above the Olduvai

subchron. The similarity of rodents, especially the arhizodont *O. giberti* and *T. vandermeuleni*, between B. del Paso and B. de los Conejos suggests that B. de los Conejos was also deposited after the Olduvai subchron. Agustí et al. (2013, 2015) provided a slightly older range for the *Mimomys oswaldoreigi* biozone, from about 2.0–1.6 Ma, but given all the available evidence we propose that B. del Paso and B. de los Conejos were deposited after Fuentenueva-1 during the period 1.5–1.7 Ma.

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Appendix I. Characters and matrix used for phylogenetic analysis.

	Differentiation ^a	Length m1 ^b	Roots ^c	M. kante ^d	Pos M. kante ^e	Atoll m1 ^f	Atolls M3 ^g	Cementum ^h	Form m1 ⁱ	Form M3 ^j	Mimosinuid ^k	Hyposinuid ^l
<i>Promimomys insuiliferus</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Mimomys cappelai</i>	1	2	1	2	2	1	1	3	2	1	1	2
<i>M. gusii</i>	2	2	1	2	2	2	2	3	2	1	3	3
<i>M. hassiacus</i>	2	2	1	2	2	2	2	2	2	1	3	2
<i>M. ischus</i>	2	2	1	2	2	2	2	3	2	1	3	3
<i>M. medasensis</i>	2	2	1	2	2	2	2	3	2	1	4	3
<i>M. pliocaenicus</i>	2	2	1	2	2	2	2	3	2	1	2	3
<i>M. polonicus</i>	2	2	1	2	2	1	2	3	2	1	2	2
<i>M. ostramosensis</i>	2	2	1	2	2	2	3	3	2	1	1	3
<i>M. savini</i>	2	2	1	1	1	3	3	3	4	1	1	4
<i>O. giberti</i>	2	2	2	2	2	3	3	2	3	2	4	3
<i>Arvicola sapidus</i>	2	2	2	1	1	3	3	3	4	1	1	3

^a Differentiation (ordered): 1 = undifferentiated; 2 = negatively differentiated; 3 = positively differentiated.

^b Length m1 (mean m1 length) (unordered): 1 = < 3.30 mm, 2 = > 3.30 mm.

^c Roots (irreversible): 1 = present, 2 = absent.

^d M. kante (*Mimomys*-kante) (ordered): 1 = absent, 2 = present.

^e Pos M. kante (position of *Mimomys*-kante) (unordered): 1 = absent, 2 = opposite T5, 3 = anterior to T5.

^f Atoll m1 (irreversible): 1 = persistent 2 = present or absent, 3 = absent.

^g Atolls M3 (irreversible): 1 = two, 2 = one, 3 = none.

^h Cementum (ordered): 1 = none, 2 = slight, 3 = well-developed.

ⁱ Form m1 (unordered): 1 = atoll present, 3 Ts, T4-5 undeveloped on acd; 2 = atoll present, 3 Ts + T4-5 incipient on acd, BRA3 & LRA4 relatively deep; 3 = atoll present or absent, anterior end acd narrow and simple; 4 = atoll absent, *Mimomys*-kante absent.

^j Form M3 (ordered): 1 = ant loop not distinctly asymmetrical, post loop relatively broad and short; 2 = ant loop asymmetrical, labially extended and narrow; post loop narrow and extended.

^k Mimosinuid (numbers refer to relative development from base of crown-root junction)(ordered): 1 = minimal development, 2 and 3 = more developed, 4 = breaks through occlusal surface with minimal wear.

^l Hyposinuid (numbers refer to relative development from base of crown-root junction)(ordered): 1 = minimal development, 2 and 3 = more developed, 4 = breaks through occlusal surface with minimal wear.

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