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A new species of water vole from the Early Pleistocene of Southern Europe

GLORIA CUENCA-BESCÓS, JORDI AGUSTÍ, JAIME LIRA, MARIA MELERO RUBIO, and JUAN ROFES



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In the Early Pleistocene Red Lower Unit of the Sima del Elefante site (Sierra de Atapuerca karst complex, Burgos, Spain), levels TE9–TE13, dental and mandibular remains of an arvicoline are referred to as the new species *Arvicola jacobaeus* sp. nov. The new species has medium-sized hypselodont molars, with abundant cementum in the re-entrant folds, and thick enamel band with differentiation of the *Mimomys*-type. The occlusal morphology of M3 is simple. The dental morphology of the new species resembles that of *Arvicola sapidus*, though smaller. It is more derived, in size and morphology than the Middle Pleistocene species *Arvicola mosbachensis*. The morphologic affinities among *Arvicola jacobaeus*, *Arvicola terrestris*, and *A. sapidus* suggest a common ancestry. A preliminary phylogenetic analysis corroborates that *Mimomys savini* is the sister group of the *Arvicola* clade.

Key words: Mammalia, Rodentia, Arvicolinae, systematics, Pleistocene, Atapuerca, Spain.

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Introduction

The genus *Arvicola* Lacépède, 1799 is represented in the extant European fauna by two species: *Arvicola terrestris* (Linnaeus, 1758), the northern water vole; and *Arvicola sapidus* Miller, 1908, the southern water vole, which is larger and which is limited to the Iberian Peninsula and southern France (Díaz de la Guardia and Pretel 1978; Rekovets 1990; Abbassi and Desclaux 1996; Abbassi et al. 1998; Desclaux et al. 2000; Maul et al. 2000; Cubo et al. 2006; Román Sancho 2007; Centeno-Cuadros et al. 2009a, b). The morphological characters of the limbs of water voles are linked with their fossorial/aquatic adaptations; the aquatic or semiaquatic character probably represent the ancestral condition, as seen in *A. sapidus* (Cubo et al. 2006; Roman Sancho 2007). The related species, *Mimomys savini* Hinton, 1910, was probably a semiaquatic rodent that spread from Eastern to Western and Southern Europe along the wet plains of coast and fluvial environments (Cuenca-Bescós et al. 2001: fig. 2).

During the Pleistocene several species of the genus *Arvicola* have been recognized: *Arvicola mosbachensis* (Schmidtgen, 1911); *Arvicola cantianus* (Hinton, 1910); *Arvicola bactonensis* Hinton, 1926; *Arvicola grenii* Hinton, 1926; *Arvicola praeceptor* Hinton, 1926; *Arvicola sapidus aupsensis* Râdulescu, 1989; *Arvicola chosaricus* Alexandrova, 1976; *Arvicola kalmankensis* Zazhigin, 1980. These taxa were discussed in a number of papers, so we shall not touch upon them here (see Koby 1965; Râdulescu 1989; Rekovets 1990; Gromov and Polyakov 1992; Abbassi et al. 1998; Maul et al. 2000; Kalthoff et al. 2007; Markova 2007).

The large voles of the species *Mimomys savini* and its putative descendant, *Arvicola*, provide evidence for European biostratigraphy (Heinrich 1978; Kolfschoten 1993), not always coincident with the chronostratigraphic limits. More precisely, the *Mimomys–Arvicola* transition has been proposed as the biostratigraphic Early–Middle Pleistocene limit in Europe. The last appearance datum (LAD) of *Mimomys* and first appearance datum (FAD) of *Arvicola* is also used as the marker of the Cromer II–Cromer III boundary in England, Thuringia and the Rhine basin (Koenigswald and Kolfschoten 1996), dated around 600 Ka, while the chronostratigraphic limit of the Early–Middle Pleistocene is fixed in the Matuyama-Brunhes paleomagnetic reversal, at 780 Ka (Koci and Sibrava 1976; Kuiper et al. 2008).

Institutional abbreviations.—MPZ, Museo Paleontológico de Zaragoza, Zaragoza, Spain.

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Other abbreviations.—a, anteroconid complex length; ACC, anteroconid complex of m1; acd, anteroconid; AL, anterior loop; ATA, Atapuerca; BRA, buccal re-entrant angle; LRA, lingual re-entrant angle; m1, m2, m3, the lower molars; M1, M2, M3, the upper molars; p, posterior lobe length; PL, posterior loop; ROI, region of interest; SDQ, Schmelzband Differenzierungs Quotient (enamel thickness differentiation quotient); T1…T5, the dentine fields or triangles. The re-entrant angles and the triangles are numbered consecutively from PL towards ACC of the m1; TE, Sima del Elefante site; TE-LRU, Lower Red Unit of TE; Z, depth.

Evolutionary characters for the study of fossil arvicolines.—In arvicoline molars, characters such as the cementum in the re-entrant angles, the enamel-free areas in occlusal view (which form the occlusal intersection with the dentine tracts in lateral or medial views), and the enamel differentiation between the trailing and leading edges, as well as the arrangement of this differentiation, are unique among rodent molars. These characters are linked to hypsodonty, or the increase in height of the molar crowns, that resulted from adaptation to an herbivorous, distinctly abrasive diet entailing substantial dental wear. As an adaptation to abrasive grasses the hypsodont molars became hypselodont in some arvicoline lineages, acquiring the character of continuous growth. The biological advantage of this molar type and its continuous growth is the ability to process very abrasive food, because the tooth tissue lost through wear is continuously replaced (Kesner 1980; Koenigswald et al. 1994). The loss of roots in the molars of some arvicoline lineages during the Pleistocene can be described in terms of a heterochronic process of paedomorphosis, or neoteny (Agustí et al. 1993).

Continuous growth generally gives rise to crowns in the form of high columns or dentine prisms, with an osteodentine core and bordered by enamel (Hinton 1926). On the occlusal surface, the prisms form a certain number of folds that produce reentrant and salient angles of enamel on the buccal and lingual sides. These dentine fields or prisms bordered by enamel form a pattern of alternating polygons that may either be closed or confluent and are termed triangles by authors (Meulen 1973; Rabeder 1981; Martin 1987; Repenning 1992). The dentine fields are varyingly confluent with one another, and with the anteroconid complex (ACC). The confluence pattern is one of the most useful diagnostic characters in arvicolines (Meulen 1973; Rabeder 1981, Repenning 1992). Closed or confluent fields in combination with the ACC shape in the wearing surface of cheek teeth make identification possible even when fossil remains are limited or incomplete.

Enamel differentiation and Schmelzband Differenzierungs Quotient (SDQ).—There are arvicolines with almost uniformly thick enamel bordering the triangles (undifferentiated type), and with a differentiation in enamel thickness between the leading and trailing edges (Koenigswald et al. 1994). Thickness differentiation is observed in the clade *Mimomys* Forsyth-Major, 1902, where rooted molars have a thick trailing edge. This character evolves into a thin trailing edge in the extant lineages derived from *Mimomys*: the genus *Microtus* Schrank, 1798 and the species *Arvicola terrestris* (Linnaeus, 1758). The *Microtus*-type represents the apomorphic character state, while in the plesiomorphic stage the enamel band is thicker in the trailing edge: this is the *Mimomys*-type (Heinrich 1978; 1987; Koenigswald et al. 1994; Koenigswald and Kolfschoten 1996). In spite of that, in earlier representatives of the *Microtus*-type, in *Allophaiomys* Kormos, 1932, the enamel thickness is variable; it may be of the *Microtus*-type (Markova 2005), undifferentiated (Alcalde et al. 1981) or of the *Mimomys*-type (Meulen 1974). The enamel is undifferentiated or slightly *Mimomys*-type in the first representatives of the genus *Allophaiomys* (see Meulen 1974, Garapich and Nadachowski 1996; Tesakov 1998b). The examination of enamel differentiation is one of the parameters measured in the evolution and ontogeny of arvicolines (Heinrich 1978; Röttger 1987; Ventura and López Fuster 1989; Kalthoff et al. 2007).

Morphology of the molars.—Species of the genus *Mimomys* have a lower first molar (m1) with a simple and primitive occlusal morphology (Hinton 1926): from distal to mesial, the occlusal surface of the m1 comprises the posterior lobe, three distal triangles, and an anterior complex formed by two open triangles convergent with one another and with the anterior lobe or anteroconid complex (Meulen 1973; Repenning 1992). The three distal triangles are completely closed in the species of *Arvicola*, but in the species of *Mimomys* this character is more variable. The anteroconid complex of m1 also displays unique structures such as the *Mimomys*-kante, or ridge, and the enamel islet. The third upper molar (M3) is simple, with a single, closed triangle and a posterior complex with two salient angles, one buccal and one lingual. The posterior lobe varies from being rounded to triangular and is broadly connected to the two salient angles. In some species M3 has a simpler morphology, in which the triangles are broadly confluent both with one another (there is no closed triangle) and with the anterior and posterior lobes (Garapich and Nadachowski 1996). The more primitive species exhibit enamel islets in m1 and in M3 (Rabeder 1981).

Morphology of the mandible.—The mandible, which is scarcely represented in the fossil record, plays an important part in the systematics of arvicoline rodents (Hinton 1926; Repenning 1968; Kesner 1980). The diagnostic characters are: the ascending ramus and the double crest for the insertion of the masseter, which is divided into the upper or dorsal crest and the lower or ventral crest, the masseteric crests (upper and lower) originating at m1, the arvicoline groove, the deep and long internal temporal fossa separating the second and third lower molars (m2, m3) from the ascending ramus, the symphyseal eminence for the insertion of the digastric muscle. The eminence of the alveolus of the lower incisor is large and is visible on the lateral side of the mandible (capsule for base of incisor in Repenning 1968); in medial view it reaches up to the mandibular foramen in the ascending ramus, which has a high position. In this paper we also note the strong genial tubercle on the medial side of the water vole

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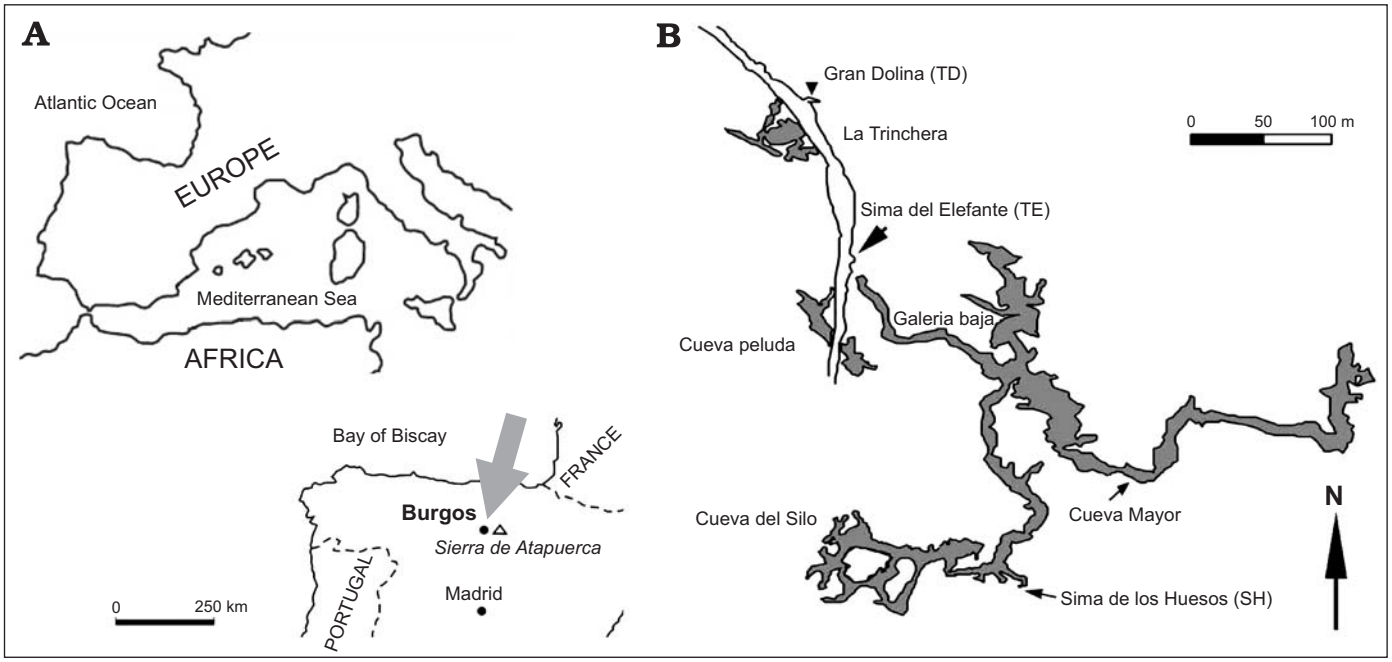


Fig. 1. **A**. General situation of the Atapuerca localities in the Iberian Peninsula. **B**. A map depitcing the main karstic system of the Atapuerca Hill, and the main two sets of localities: the Trinchera del Ferrocarril or La Trinchera localities, where the Sima del Elefante belongs; and the Cueva Mayor-Sima de los Huesos system. Note that Sima del Elefante could be an ancient opening to the Cueva Mayor-Galería Baja karstic tunnel.

mandible. This is considerably larger in *Arvicola* than in *Terricola* or *Microtus*.

Origin of hypselodont taxa derived from *Mimomys*.—The genus *Mimomys* was widely distributed across the Northern Hemisphere during the Pliocene (Chaline et al. 1999, Repenning 2003), but at the beginning of the Pleistocene its specific diversity diminished considerably. This was accompanied by an important evolutionary change: various lines became more hypsodont, eventually leading to hypselodont genera such as *Allophaiomys* (Kormos 1932) and *Arvicola* (Agustí 1991; Agustí et al. 1993; Maul et al. 1998; Maul 2001). The first genus with hypselodont molars, presumed to be a descendant from a species of *Mimomys*, was *Allophaiomys*, small in size and with enamel that was undifferentiated or of the *Microtus*-type, which first appeared at the beginning of the Early Pleistocene, circa 1.7 Ma (Repenning 1992; Garapich and Nadachowski 1996). Less well-known is the appearance of hypselodont forms such as *Mimomys oswaldoreigi* Agustí, Castillo, and Galobart, 1993 in Spain (Agustí et al. 1993), likewise at the beginning of the Early Pleistocene. Much later on, at the beginning of the Middle Pleistocene (around 600 Ka), other groups of medium-sized to large arvicolines that lose their roots are *Arvicola mosbachensis*, *Arvicola cantianus*, and *Arvicola terrestris* in central Europe and the Pannonian Basin (Heinrich 1987; Kolfschoten 1993; Maul et al. 2000).

Origin of *Arvicola* derived from *Mimomys*.—*Arvicola* is alleged to be a descendant of *Mimomys* because of the great similarity in the morphology of the occlusal surface of the molars (Koenigswald and Kolfschoten 1996), the loosening of roots and the complexity of the third upper molar (M3) being the evolutionary differences. The extant species of *Arvicola* share the rootless molars, and the M3 more complex, although they differ in their enamel differentiation: it is of the *Mimomys*-type in *Arvicola sapidus*, while of the *Microtus*-type in *Arvicola terrestris*. The SDQ values of the *Mimomys*-type were also present in the species *Arvicola cantianus* and *Arvicola mosbachensis* of the Middle Pleistocene.

While the origin of *Arvicola terrestris* as a gradual evolution of the phyletic lineage *Mimomys savini–Arvicola cantianus* (or *Arvicola mosbachensis*, see Maul et al. 2000)— *A. terrestris,* seems to have some consensus (Rekovets 1990; Kolfschoten 1993), the origin of *A. sapidus* is more doubtful. The first appearance of the most primitive representative of the lineage of *A. terrestris* seems to be well-established as having occurred during the second half of the "Cromerian Complex" (Kolfschoten 1993). Transitional forms are known from several sites (Râdulescu and Samson 1993; Kolfschoten 1990; Koenigswald and Kolfschoten 1996; Heinrich 1987).

For the origin of *A. sapidus* and its relationship to *A. terrestris* as well as to *M. savini* different models have been discussed. Rabeder (1981) postulates two lineages: one leading to *A. sapidus* and the other to *A. terrestris*; according to this model, the lineages became separated long before the beginning of the middle Pleistocene. Molecular genetic studies have dated the split of *A. terrestris* and *A. sapidus* around 250 Ka (Centeno-Cuadros et al. 2009b) and the genetic distance between *A. terrestris* and *A. sapidus* confirms their specific independence (Diaz de la Guardia and Pretel 1978; Rekovets 1990).

The aim of this paper is to present a new species of a large vole of early Pleistocene age, related to *Mimomys* and to

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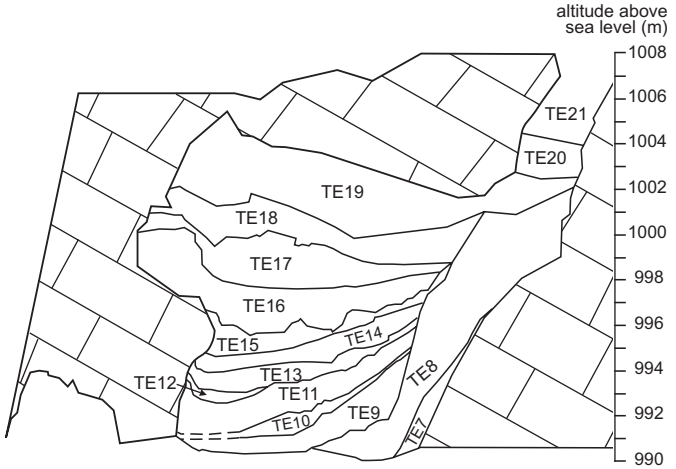


Fig. 2. Geologic profile and lithostratigraphic units (TE7 to TE21) of the cave deposits of the Sima del Elefante locality, in the Trinchera del Ferrocarril of Sierra de Atapuerca Hill. Below the trench (Trinchera) level there are nearly 6 m of unearthed sediments, though levels TE8 and TE7 were sampled in the north trench perforation during the field campaign of 1996. The floor of the cave was identified by the presence of a 40-cm thick limestone layer in the north drill. Underneath the limestone layer, a distinct set of sediments was found, which was interpreted to represent the infill of a cavity from a lower karst floor. Two strata have been distinguished: the uppermost, composed of clay, small clasts (1–2 cm), and manganese oxide; the lowermost, with rounded quartzite pebbles, is interpreted as part of a terrace of the Arlanzón River left into the cave. Modified from Huguet Pàmies 2007.

Arvicola, in terms of size, morphology and enamel differentiation. So far it has only been found in the lower levels of the Sima del Elefante site from the Lower Pleistocene of the karstic complex of the Sierra de Atapuerca in Burgos (Spain).

Geological setting

The Sima del Elefante site (labelled TE in stratigraphic, palaeontological and archaeological samples) is a major cave infill located in an ancient railroad cut (Trinchera del Ferrocarril) of the Sierra de Atapuerca (Figs. 1–3). It corresponds to an ancient opening to Galería Baja in the Cueva Mayor Karst subsystem, and is completely full of sediments of allochthonous origin. The stratigraphic section of Sima del Elefante, including Lower and Middle Pleistocene deposits, is 25 m thick, 19 m of which were exposed during the construction of the railway (Figs. 2, 3). This section comprises 22 levels, the lowermost of these, known as the Sima del Elefante Lower Red Unit (TE-LRU), are Early Pleistocene in age (Cuenca-Bescós et al. 2001; Rosas et al. 2004; Cuenca-Bescós and García 2007; Carbonell et al. 2008). The sample of fossil voles analysed here comes from the Lower Red Unit of the Sima del Elefante Atapuerca site (Fig. 3).

TE-LRU comprises levels TE7 to TE14 and is extremely rich in faunal remains, most of which are very well preserved. The TE-LRU represents the Atapuerca Faunal Unit 1 of Cuenca-Bescós and García 2007 and Cuenca-Bescós et al. 2010). The faunal assemblage of TE-LRU is given in Table 1. Small mammals proved to be crucial in dating the Lower Red Unit of the Sima del Elefante site as the oldest one in Atapuerca (i.e., pre-Jaramillo faunas; Laplana and Cuenca-Bescós 2000; Rofes and Cuenca-Bescós 2006, 2009, in press; Cuenca-Bescós and García 2007). Moreover, the Lower Red Unit of the Sima del Elefante site is below a normal polarised zone in the stratigraphic sequence as indicated in Fig. 3. The arvicoline and insectivore associations, in particular, showed that this unit indicates an Early Pleistocene age, similar to the localities of Fuente Nueva 3 and Barranco León in the Granada basin (ca. 1.2–1.5 Ma, Cuenca-Bescós and García 2007; Carbonell et al. 2008; Cuenca-Bescós et al. 2010). This is consistent with the presence of the large-sized mustelid *Pannonictis nestii*, referable to the Early Pleistocene (García et al. 2008). Recent cosmogenic nuclide analysis dated the Sima del Elefante TE9 level to ~1.2 Ma (Carbonell et al. 2008), thus confirming the biostratigraphically-inferred chronology (Table 1).

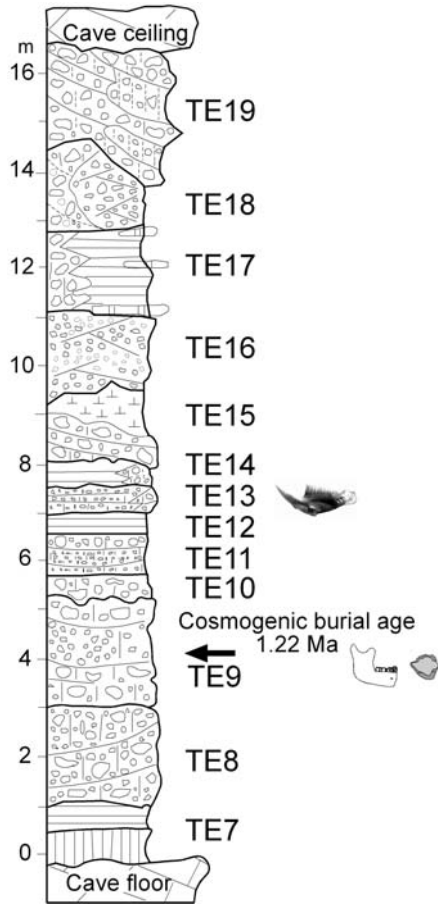


Fig. 3. Synthetic column showing the lithostratigraphic units of the north section of the Sima del Elefante site, labelled TE (levels TE7 to TE19). Levels that correspond to the Lower Red Unit, TE-LRU are TE7 to TE14. Units TE20 to TE22 do not outcrop here, but in the southern section (see Fig. 2). Black arrow points to level TE9 from which the recently discovered human remains were retrieved, and where the burial dating, based on the radioactive decay of cosmogenics, has been calculated (Carbonell et al. 2008). The small arvicoline mandible points to the level (TE13) where the holotype of *Arvicola jacobaeus* sp. nov. was found. The figure has been modified from Carbonell et al. (2008).

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Table 1. Early Pleistocene vertebrates of the lower levels or Lower Red Unit of the Sima del Elefante site, Atapuerca, Burgos, Spain.

Fishes, amphibians, and reptiles	Salmonidae indet., *Salamandra salamandra*, *Alytes obstetricans*, *Pelobates cultripe*, *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Hyla arborea*, *Rana* (*temporaria*) sp., *Pelophylax* (*ridibunda*) sp., Lacerticae indet., *Anguis fragilis*, *Natrix* cf. *natrix*, *Natrix maura*, *Coronella girondica*, and Chelonia indet.
Aves	*Carduelis chloris*, *Perdix paleoperdix*, *Coturnix coturnix*, *Columba livia*, *Haliaetus albicilla*, *Circaetus gallicus*, *Falco tinunculus*, *Falco* sp., *Turdus* sp., Alaudidae indet., *Anas* sp.
Primates	*Macaca* sp., *Homo* sp.
Eulipotyphla (Insectivores)	*Asoriculus gibberodon*, *Beremendia fissidens*, *Crocidura kornfeldi*, *Sorex* sp., *Erinaceus praeglacialis*, *Galemys kormosi*, *Talpa europaea*
Chiroptera	*Myotis* spp., *Rhinolophus* spp.
Carnivora	*Canis* cf. *arnensis/mosbachensis*, *Vulpes* cf. *alopecoides*, *Ursus* cf. *dolinensis*, cf. *Baranogale antiqua*, *Mustela* cf. *palerminea/praenivalis*, *Pannonictis nestii*, *Panthera gombaszoegensis*, *Lynx* cf. *issidorensis, Mustela* cf. *palerminea/praenivalis*
Perissodactyla	*Stephanorhinus etruscus*, *Equus* sp. (stenonian type)
Artiodactyla	*Eucladoceros giulii*, *Megaloceros savini*, *Dama nestii* cf. *vallonnetensis*, *Bison* sp., Bovidae indet, *Sus* sp.
Rodentia	*Sciurus* sp., *Eliomys quercinus*, *Castor fiber*, *Ungaromys nanus*, *Pliomys* cf. *simplicior*, *Allophaiomys lavocati*, *Allophaiomys burgondiae*, *Allophaiomys nutiensis*, *Arvicola jacobaeus* sp. nov. (this work), *Castillomys rivas*, *Apodemus* sp.
Lagomorpha	cf. *Lepus* and *Oryctolagus* cf. *giberti*

Noteworthy is that the Lower Red Unit from Sima del Elefante, from where the new fossil vole was retrieved, yielded, during the field campaign of 2007, a hominin mandible that, together with Mode 1 lithic tools and faunal remains bearing traces of hominin processing, represents the oldest and most accurately dated record of human presence in Europe (Carbonell et al. 2008).

Material, methods, and terminology

A total of 121 dental and mandibular elements have been analysed. Some of the teeth, like those of the holotype, are still associated with the dentary (Figs. 4, 5, 6), although the majority consist of isolated teeth (Appendix 1, Fig. 7). The specimens were obtained by concentrating the sediment after a process of washing and sieving, with 0.5 mm mesh-size, the sediments excavated from Sima del Elefante during the course of the Atapuerca campaigns between 1999 and 2007, plus two previous sample pits in 1995–96. The fossil remains of small vertebrates are then packed in plastic sacs, labelled with an abbreviation indicating the year of the field campaign, the site, stratigraphic level, the excavation grid unit, and the depth (Z) in cm where appropriate, (e.g., ATA 04 TE-13 H-31 Z: 1150–1160), enabling us to maintain stratigraphic control throughout. Afterwards, in the Laboratory of Palaeontology of the University of Zaragoza, the small fossil remains are picked and sorted using a hand-held or binocular magnifying glass, and a preliminary classification of the fossils is recorded in the data base of the Atapuerca small vertebrates sampling record. The fossils are stored in the Palaeontology section of the Department of Earth Sciences of the University of Zaragoza, Spain. For the measurements and study in detail of the molars and mandible we use a binocular microscope with 7×, 16×, 20×, and 40× of magnification. The details and photographs of Figs. 4, 5, 7, were made with a Scanning Electron Microscope. The specimens studied for this paper are kept in the MPZ.

The nomenclature and measurements for the various parts of the occlusal surface of the arvicoline molars follows the proposal put forward by Meulen (1973), with certain modifications (Fig. 4), derived mainly from the works of Rabeder (1981), Repenning (1992), and our own studies. We here apply a new way of measuring the occlusal surface of the molars of arvicolines by the use of an image-capturing programme that allows one to measure different parameters in objects inscribed within a particular region of interest

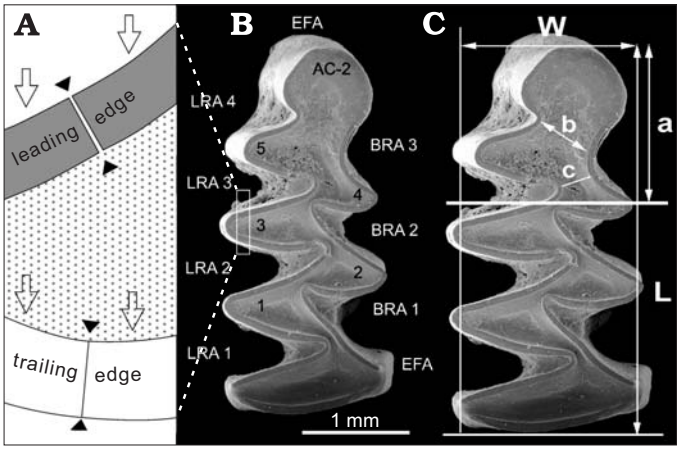


Fig. 4. Dental terminology and measurements taken on the occlusal surface of the m1 of arvicoline molars from Heinrich (1978) and Meulen (1973), modified. **A**. Leading and trailing edges of a dentine field or triangle. **B**. The occlusal surface of a lower first molar of *Arvicola jacobaeus* sp. nov., with the triangles (T) labelled from distal to mesial (T1–T5). **C**. Measurements taken on the occlusal surface of the molar. Abbreviations: a, anteroconid length (AC-2+T4–T5); AC-2, anteroconid complex; b, width of the anteroconid complex; BRA 1–3, buccal re-entrant angles; c, opening or separation of the T4 and T5 triangles; EFA, enamel free areas; L, total length; LRA 1–4, lingual re-entrant angles; W, total width.

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(ROI). Length, width, anteroconid length "a" and posterior complex "p" were measured in the rectangle (ROI) in which the outline of the tooth is inscribed (Figs. 4C, 7M). The parameter "p" is the length of the posterior complex in M2 and M3 measured from the mesial limit of T3 to the distal edge of the molar (Fig. 7). This parameter makes it possible to estimate the posterior elongation of both molars.

The enamel thickness is measured in accordance with the method devised by Heinrich (1978; 1987) and Koenigswald and Kolfshoten (1996), where the SDQ (enamel differentiation quotient) is the average quotient obtained by dividing the thickness of the trailing edge by that of the leading (see the meaning of trailing-leading edges in Kesner 1980) edge of the enamel fields of the first lower molar (m1). This method was modified by Kolfschoten (1990), applying the measurements to all the molars, both upper and lower (Fig. 4A). We calculate the SDQ with the formula proposed by Heinrich (1987), and Koenigswald and Kolfschoten (1996) slightly modified:

$$SDQ = [3\ (teet \times 100/leet)]/N$$

Where teet is the trailing edge enamel thickness of the dentine fields and leet is the leading edge enamel thickness of the dentine fields. The sum of the resulting index of each dentine field is divided by N, the number of total calculated indices of each tooth.

The study of the anatomical characters of the mandible is based on the work of Repenning (1968) and Kesner (1980).

Systematic palaeontology

Order Rodentia Bowdich 1821

Superfamily Muroidea Illiger, 1811

Family Cricetidae Fischer, 1817

Subfamily Arvicolinae Gray, 1821

Genus *Arvicola* Lacépède, 1799

Arvicola jacobaeus sp. nov.

Figs. 4–7.

Etymology: From St. James or Santi Jacobi, the pilgrims' road to Santiago de Compostela that traverses the Sierra de Atapuerca and the symbol of the pilgrims (the scallop *Pectem jacobaeus*).

Holotype: Right mandible, with the complete horizontal ramus, the incisor and the three molars (m1, m2, m3). Catalogue number: ATA04 TE 13 H31 z1150-1160, MPZ 2008/380.

Type locality: Sima del Elefante site, Atapuerca, Burgos, Spain.

Type horizon: Lower Red Unit (TE-LRU), levels TE8–TE13, of Sima del Elefante site, pre-Jaramillo faunas, Early Pleistocene.

Material.—121 dental elements MPZ 2008/342–2008/462 (Appendix 1).

Diagnosis.—Medium-sized hypselodont *Arvicola* species with abundant cementum in the re-entrant folds, and thick enamel band with differentiation of the *Mimomys*-type. The enamel-free areas are present in both the salient angles of the posterior lobes of the lower molars (m1, m2, m3), as well as in both sides of the anterior lobe and in the T1 of the M1 and in the lingual side of the anterior lobes of M2 and M3. The occlusal surface of m1 is characterised by the absence of the enamel islet and *Mimomys*-kante. The distal triangles are closed to slightly confluent. The occlusal surfaces of m2 and m3 are of the *Mimomys*-type, with triangles that are slightly (in m2) to broadly (in m3) convergent; M1 has the anterior lobe and T1 slightly confluent, while T2 may or may not be connected with T1; M2 and M3 are of the *Mimomys*-type. The occlusal surface of M3 shows two to three fields, the anterior lobe 1(AL1), the T2 and the rest of the molar, where budding T3 and T4 are variable in size. The M3, in basal view, has a thick enamel wall.

Differential diagnosis.—*Arvicola jacobaeus* sp. nov. is somewhat smaller (length and width) than the extant species of *Arvicola*; the occlusal surface of the m1 is derived, similar to that in *Arvicola sapidus*, though the M3 is primitive, similar to that in *Mimomys savini*; the enamel thickness is of the *Mimomys*-type, though fairly thick all around the enamel wall; the roots have disappear though in M3 the base of the crown is slightly close, and the enamel thicker in basal view.



Fig. 5. Occlusal view of the right mandible with m1, m2, m3 of the cricetid rodent *Arvicola jacobaeus* sp. nov. from Sima del Elefante level TE 13. Holotype (ATA04 TE13 H31 1150-1160, MPZ 2008/380).

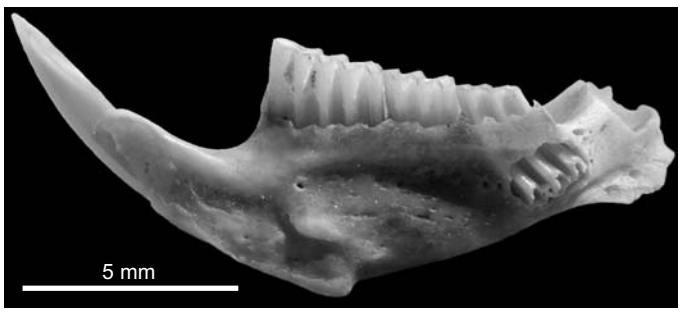


Fig. 6. Medial view of the right mandible with i1, m1, m2, m3 of the cricetid rodent *Arvicola jacobaeus* sp. nov. from Sima del Elefante level TE 13. Holotype (ATA04 TE13 H31 1150-1160, MPZ 2008/380). The photograph was made during the field campaign of 2005 by Javier Trueba.

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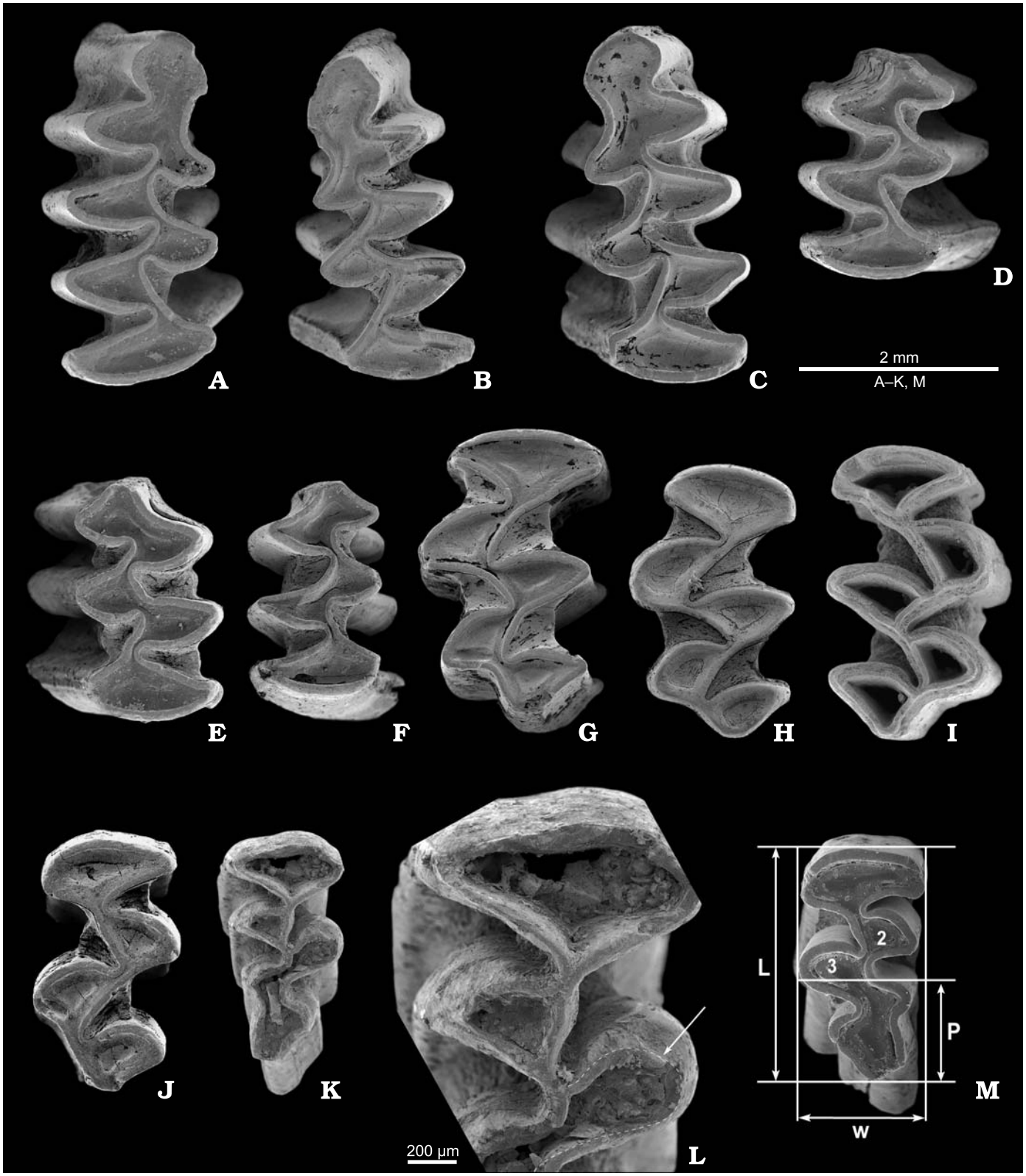


Fig. 7. Occlusal views (except some root or basal views) of isolated teeth of the cricetid rodent *Arvicola jacobaeus* sp. nov. from Sima del Elefante level TE9. **A**. Right m1 (TE9 1 1997 MPZ 2008/343). **B**. Left m1 (TE9 1 1998 MPZ 2008/344). **C**. Left m1 (TE9 s/n 1998 MPZ 2008/372). **D**. Right lower m2 (tooth in mandible with the m1 of A) **E**. Left lower m2 (tooth in mandible with the m1 of B). **F**. Right lower m3 (TE9 1 1998 MPZ 2008/345). **G**. Left M1 (TE9 s/n 1998 MPZ 2008/374) **H**. Left M1 (TE9 s/n 1998 MPZ 2008/376). **I**. Root view of left M1 (TE9 s/n 1998 MPZ 2008/375). **J**. Left M2 (TE9 s/n 1998 MPZ 2008/377). **K**. Root view of right M3 (TE9 1 1998 MPZ 2008/346). **L**. Detail of the incipient root development in the M3 in K. **M**. Left M3 (TE9 1 1997 MPZ 2008/342). Abbreviations: L, total length; W, total width; P, posterior length; 2,3, triangles 2,3. The arrow in L shows the thicker enamel and the closening of the crown in basal view.

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Arvicola mosbachensis, described by Maul et al. (2000), presents morphological resemblances in the occlusal morphology of the molars with those of *A. jacobaeus*. The differences between *A. jacobaeus* and *A. mosbachensis* are: the smaller size of the m1 and the M3 of *A. mosbachensis*; the lack of *Mimomys*—fold in m1, the lack of T5, the high confluence between T3, T4 and PC1 in the M3, and the thicker, though highly variable enamel–thickness wall of *A. jacobaeus*. As in *A. jacobaeus*, some specimens of *A. mosbachensis* display incipient root development and thicker enamel wall in basal view, though *A. jacobaeus* presents this plesiomorphy only in the M3. On the other hand, by comparison with *Arvicola terrestris*, *A. sapidus*, and *Microtus*, the M3 of *A. jacobaeus* has an enamel wall markedly thick in the basal part, a stage prior to the initiation of the root formation (Fig. 7K, L). On the contrary, in *A. mosbachensis*, all the molars show the thick enamel wall in basal view (Maul et al. 2000).

Description.—The mandible has the typical arvicoline shape. The mandibular corpus is stout and deep, with a short diastema. A strong symphyseal, or digastric, eminence is its most remarkable feature. In medial view, a large mental spine or genial tubercle for the insertion of the genioglossus muscle is situated just above the posterior part of the symphyseal process, and thus above the digastric eminence and below m1 (Figs. 5, 6). The symphyseal area is caudally extended, indicating a strong fibrous joint (Fig. 6). In lateral aspect, the large mental foramen opens below the mesial border of m1. The lateral surface has an enlarged masseteric fossa of which the rostral end is situated below T4 of m1; its dorsal end is limited by the coronoid crest. The posterior part of the mandible is not preserved.

The molars of *A. jacobaeus* have abundant cementum in the re-entrant angles, and lack roots, folds and enamel islets. Moreover, the enamel differentiation is of the *Mimomys*-type and in general fairly thick throughout the perimeter of the tooth in its occlusal surface.

The lower first molar (m1): this has a posterior lobe; three alternating, closed to slightly open triangles, T1–T3; and an anteroconid complex with two open triangles, T4 and T5, broadly confluent with the anterior lobe (Fig. 7A–C).

The second and third molars (m2, m3): have similar occlusal surfaces to those of other species of *Mimomys* and *Arvicola* (Fig. 7D–F). In m3 the dentine fields vary from being broadly connected to slightly closed (Fig. 7F).

The upper first molar (M1): has an anterior lobe and four triangles, T1–T4, which are slightly interconnected. T1 has an enamel-free area in the lingual salient angle (Fig. 7G–I).

The second upper molar (M2): is of the general type in arvicolines.

The upper third molar (M3): this molar has three dentine fields: the anterior lobe, the T2, and a third one consisting of the rest of the molar, the T3 and T4 that comprise a single field together with the posterior lobe. There are two lingual and two buccal re-entrant angles (Fig. 7J–M) Two M3 present a thickening of the wall on their basal surface (Fig. 7K, L).

Discussion

Compared with the rest of the arvicolines of the Lower Red Unit of the Sima del Elefante (Atapuerca) site, *Arvicola jacobaeus* is the largest. The occlusal morphology of the m1 is simpler than that in *Allophaiomys lavocati*, with an elongated anteroconid and *Microtus*-type enamel differenciation (Laplana and Cuenca-Bescós 2000). The species *Allophaiomys nutiensis* and *Allophaiomys burgondiae* are also smaller and have the *Microtus*-type of enamel (Cuenca-Bescós et al. 2010).

Compared with other medium to large voles of the Early Pleistocene, *Arvicola jacobaeus* is similar in the occlusal surface of its molars to *Mimomys savini*, with a variable confluence between T3, T4, and the posterior lobe. The T4 is less developed than in *Mimomys savini.* The new species of Sima del Elefante lacks the enamel islet (which occurs mainly in rather young specimens in *M. savini* samples), the *Mimomys* fold, and the roots. In basal view, one M3 has a thick wall and a slight curvature which may be the stage prior to the formation of true roots (i.e., the sample of Mosbach 2, Maul et al. 2000) as in the M2 of *Mimomys intermedius* described by Râdulescu and Samson (1993). Note that *M. intermedius* is considered a synonymy of *M. savini* by most students (see i.e., Rekovets 1990; Gromov and Poliakov 1992; Maul et al. 2000).

During the Middle and Late Pleistocene appeared *Arvicola cantianus*, *Arvicola sapidus*, and *Arvicola terrestris*, as recorded in the introductory part. The three species are somewhat larger than *Arvicola jacobaeus*, both in length and in width, while *Arvicola mosbachensis* from Mosbach and their common ancestor (Maul et al. 2000), *Mimomys savini*, are somewhat smaller than *A. jacobaeus* (Fig. 8).

Arvicola jacobaeus has abundant cementum in the re-entrant angles, unlike the species of the genus *Borsodia* Jánossy

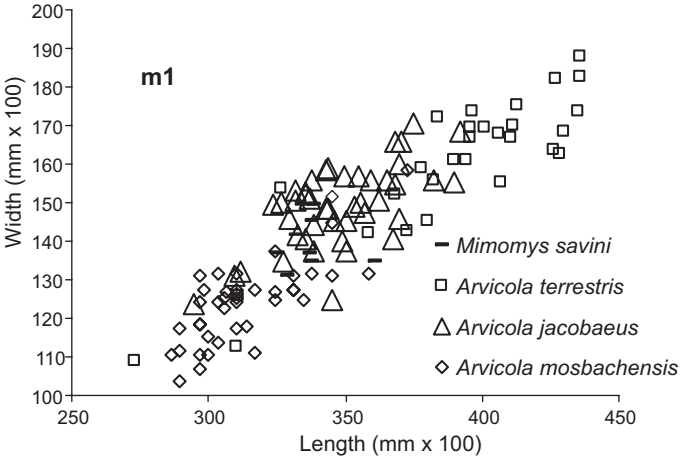


Fig. 8. Length–width scatter diagram of large arvicolinae rodents: *Mimomys savini* from the Lower Pleistocene levels of Gran Dolina, Atapuerca; *Arvicola terrestris* from the Upper Pleistocene levels of El Mirón, Cantabria; *Arvicola jacobaeus* sp. nov. from the Lower Pleistocene, Sima del Elefante levels TE9–TE13; *Arvicola mosbachensis* from Mosbach 2. Except the data from Mosbach 2, taken from Maul et al. (2000), the measurements were made by us.

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and Meulen, 1975, a small- to medium-sized lagurine vole, with an occlusal surface superficially similar to that of *Mimomys*, which lacks cementum (Jánossy and Meulen 1975; Popov 2001).

The genus *Kislangia* Kretzoi, 1954 has the m1 larger than 4 mm, and confluent dentine fields, especially in *Kislangia gusii* from the Late Pliocene of Almenara-Casablanca 1 and Galera 2 in Spain (Agustí et al. 1993). In *Arvicola jacobaeus* the dentine fields are closed or exhibit just slight confluence, in particular the three distal ones, T1–T3 (Kretzoi 1954; Agustí et al. 1993; Minwer-Barakat et al. 2004).

The species *Allophaiomys vandermeuleni* Agusti, 1991 is slightly smaller, the enamel is of the undifferentiated type (Agustí 1991), and lacks roots.

The species *Tibericola deucalion* (Kretzoi, 1969) is also smaller, the SDQ lower, the enamel of the *Mimomys*-type, and the roots are lacking (Meulen 1974; Garapich and Nadachowski 1996; Tesakov 1998a). Ruiz Bustos and Sesé (1985) proposed the re-assignation of *Allophaiomys deucalion* to *Arvicola deucalion*, and at the same time as the first representative of the *A. deucalion–Allophaiomys chalinei– Arvicola mosbachensis* lineage. We here want to remark that (i) the molars of the species *A. deucalion* has the *Mimomys*-type of differentiation of the enamel-thickness and lack roots, therefore it represents the most primitive species of the lineage *Allophaiomys–Microtus*; (ii) it cannot be the ancestor of *Arvicola mosbachensis* because the molars of this species exhibit incipient roots to different extent (Maul et al. 2000).

The molars of the species *Mimomys oswaldoreigi* Agustí, Castillo, and Galobart, 1993 are smaller, though similar to *Arvicola jacobaeus* in the derived occlusal characters such as the lack of the enamel islet and *Mimomys*-ridge in the m1 (Agustí et al. 1993). The lack of roots, except in the M3, is also mutually shared.

At this point, mention should also be made of the affinities of *Arvicola jacobaeus* with *Tibericola jordanica* Haas, 1966, from Ubeidiya (Koenigswald et al. 1992) and Yesher Benot Ya'aqov, Israel (Goren-Inbar et al. 2000). *T. jordanica* was initially classified within the genus *Arvicola* and described as a medium-sized to large species, lacking roots, with abundant cementum in the re-entrant angles and with T4–T5 separated to slightly confluent. Some specimens of *T. jordanica* display morphologies resembling *Chionomys* and not developed in *Arvicola jacobaeus.* The M3 is complex, with three well formed triangles. Another difference from *A. jacobaeus* is that the enamel thickness of *T. jordanica* is undifferentiated.

A less derived species of *Tibericola*, *Tibericola vandermeuleni*, was described by Agustí (1991) from the Guadix-Baza basin (Granada, southern Spain), and originally assigned to the genus *Allophaiomys*. *Tibericola vandermeuleni* shares with *Arvicola jacobaeus* the ever-growing molars and a relatively simple and short anteroconid complex. However, the species are clearly different in many other respects. *Arvicola jacobaeus* is larger than *T. vandermeuleni* and shows *Mimomys*-type differentiated enamel, while the latter species has undifferentiated or slightly *Mimomys*-type enamel. Moreover, *A. jacobaeus* has larger B values and much larger C values (sensu Meulen 1973; Agustí 1991). As in other derived hypselodont microtine species, the M3 of *T. vandermeuleni* is more complicated than this of *A. jacobaeus,* which in this way is more comparable to M3 of *Mimomys.*

Arvicola jacobaeus also differs from some large species of *Allophaiomys*, such as *Allophaiomys chalinei* Alcalde, Agustí, and Villalta, 1981. Again, *A. jacobaeus* shares with the latter species the presence of hypselodont molars and its relatively short, simple anteroconid complex. However, the species from Sima del Elefante is considerably larger and presents much larger B values (Tables 2, 3). While in *A. jacobaeus* the enamel is always of the *Mimomys*-type differentiated, in *Allophaiomys chalinei* it varies, being even of the *Microtus*-type differentiated in the more recent populations (such as Gran Dolina levels TD5 and TD6; Cuenca-Bescós et al. 1995, 1999b, 2001). As with *Tibericola*, the occlusal mor-

Table 2. Measurements of the upper molars of *Arvicola jacobaeus* sp. nov. from Sima del Elefante, Atapuerca, Burgos, Spain, levels TE9–TE13.

	M1 sup			M2 sup				M3 sup			
	L [mm]	W [mm]	SDQ	L [mm]	W [mm]	p/L	SDQ	L [mm]	W [mm]	p/L	SDQ
Mean	3.02	1.80	1.39	2.41	1.44	1.35	1.32	2.21	1.14	0.60	1.28
Min	2.82	1.58	1.11	2.24	1.32	1.13	1.02	2.01	1.02	0.56	1.03
Max	3.31	2.38	2.01	2.60	1.59	1.78	1.69	2.43	1.26	0.64	1.72
N	24	24	22	18	18	15	18	13	13	7	13
Typical error	0.03	0.03	0.05	0.03	0.02	0.05	0.04	0.04	0.02	0.11	0.06
Median	2.97	1.77	1.29	2.41	1.43	1.27	1.32	2.18	1.14	0.64	1.20
Mode	2.96	1.66		2.49	1.44	1.28		2.34	1.11		
Standard deviation	0.15	0.17	0.24	0.11	0.07	0.21	0.15	0.14	0.07	0.39	0.21
Variance	0.02	0.03	0.06	0.01	0.01	0.04	0.02	0.02	0.01	0.15	0.04
Kurtosis	-0.88	4.69	1.75	-0.98	0.20	-0.11	1.01	-1.30	-0.79	-2.03	-0.02
Asymmetry coefficient	0.57	1.77	1.38	0.13	0.57	1.17	0.38	0.02	0.20	0.32	0.86
Range	0.49	0.79	0.90	0.36	0.27	0.65	0.66	0.42	0.24	0.90	0.69
Σ	72.37	43.18	30.52	43.33	25.83	20.23	23.81	28.67	14.78	12.17	16.59
CI (95%)	0.06	0.07	0.10	0.06	0.04	0.12	0.07	0.08	0.04	0.23	0.13

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Table 3. Measurements of the lower molars of *Arvicola jacobaeus* sp. nov. from Sima del Elefante, Atapuerca, Burgos, Spain, levels TE9–TE13.

	m1 inf				m2 inf			m3 inf		
	L [mm]	W [mm]	A/L	SDQ	L [mm]	W [mm]	SDQ	L [mm]	W [mm]	SDQ
Mean	3.48	1.49	0.40	1.32	2.34	1.37	1.36	2.14	1.33	1.36
Min	2.95	1.24	0.36	0.86	2.01	1.20	0.95	1.77	0.99	0.93
Max	3.92	1.70	0.50	1.70	3.01	1.73	1.76	2.40	2.08	2.01
N	44	45	44	45	22	22	22	12	13	13
Standard error	0.03	0.02	0.01	0.02	0.06	0.03	0.04	0.06	0.08	0.08
Median	3.46	1.50	0.39	1.30	2.27	1.33	1.32	2.20	1.38	1.31
Mode	3.36	1.56			2.34	1.32			1.44	
Standard deviation	0.21	0.10	0.03	0.15	0.29	0.13	0.19	0.21	0.28	0.30
Variance	0.04	0.01	0.00	0.02	0.08	0.02	0.04	0.05	0.08	0.09
Kurtosis	0.21	0.20	2.21	2.05	0.68	2.00	0.20	-0.97	3.69	0.62
Asymmetry coefficient	-0.05	-0.32	1.74	-0.02	1.21	1.48	0.07	-0.58	1.52	0.79
Range	0.97	0.47	0.14	0.84	0.99	0.53	0.82	0.63	1.08	1.08
Σ	152.98	67.01	17.60	59.44	51.53	30.24	29.98	25.65	17.32	17.68
CI (95%)	0.06	0.03	0.01	0.04	0.13	0.06	0.08	0.14	0.17	0.18

phology of the M3 of *Allophaiomys chalinei* is more complicated than this of *A. jacobaeus* and in basal view it lacks any trace of roots.

Comparison of the enamel thickness of *Arvicola jacobaeus* with that in other large voles of the Pleistocene of Europe.—The separation between the species of the genus *Mimomys* and those of the genus *Arvicola* is based exclusively on the presence or absence of roots. For this reason it is particularly important to analyse the evolution of enamel thickness (SDQ) in the European large voles (Fig. 9, Table 4). The enamel differentiation of *A. jacobaeus* is of the *Mimomys*-type; see this work and descriptions in Röttger (1987) and Ventura and López-Fuster (1989).

In 1978 and subsequently, Heinrich observed that the enamel of *Arvicola* evolved from a differentiated enamel of the *Mimomys*-type to a differentiated enamel of the *Microtus*-type, thicker in the leading edge (mesial in the lower molars and distal in the upper molars) (Heinrich 1978). *Arvicola jacobaeus* retains the *Mimomys* conditions, both in terms of enamel thickness and the form of the anterior lobe of m1. However, it lacks (through presumed loss) three of the features that characterise *Mimomys*, the fold, the islet, and the roots. On the other hand, the enamel differentiation of *A. jacobaeus* shows great resemblance to that of *Mimomys savini, Arvicola cantianus*, and *Arvicola sapidus* (Fig. 9). What is more, the enamel of *A. jacobaeus* tends to be uniformly thicker throughout the enamel wall (Fig. 7A–H, J) in comparison to *Mimomys*, *Allophaiomys*, and other *Arvicola* species.

The origin of the southern water vole *Arvicola sapidus*

In agreement with the above discussions we can conclude that both extant species of *Arvicola* share a common ancestor, with some authors implicating *Mimomys savini* (Kolfschoten 1990, 1993; Râdulescu and Samson 1993; Koenigswald and Kolfschoten 1996; Heinrich 1978; Maul 2001). However, some authors, such as Rabeder (1981), postulate two different lineages leading to the extant *Arvicola sapidus* and *Arvicola terrestris*, which became separated before the beginning of the Pleistocene. Ruiz Bustos and Sesé (1985) also postulated a different origin (from the species *Allophaiomys deucalion*) for the lineage *Arvicola mosbachensis–Arvicola sapidus*.

The species *Arvicola sapidus* is morphologically more primitive than the species *Arvicola terrestris* (Cubo et al. 2006, this work), and also in its karyotype (Díaz de la Guardia and Pretel 1978). The new species *Arvicola jacobaeus* displays a mosaic of primitive, mimomyan and derived microtian character states. This is not unusual in the Iberian Peninsular, where other species of Arvicolinae exhibiting mixed characteristics have been described, such as *Mimomys oswaldoreigi* of the Early Pleistocene and *Tibericola vandermeuleni* of the middle Early Pleistocene. A morphological affinity with the species *Mimomys savini* is indicated by the size and the mor-

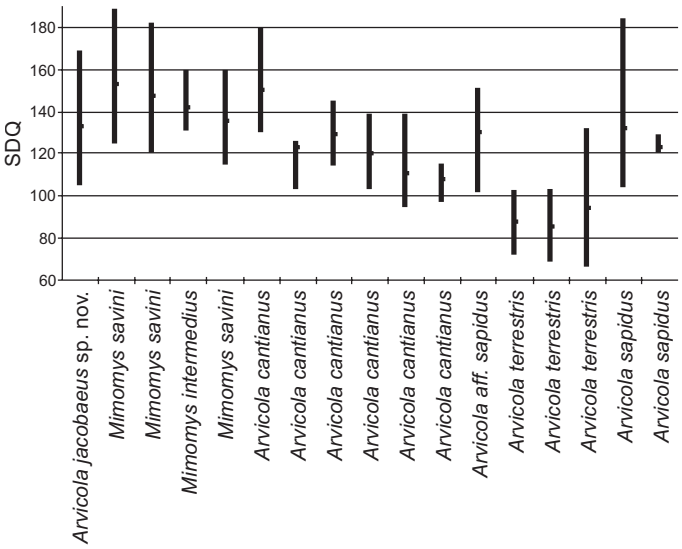


Fig. 9. Comparison of the SDQ values of large arvicoline rodents from selected literature (see text) as well as extant *Arvicola sapidus* from Spain (localities and ages listed in the same order as they appear in Table 4).

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phology of the occlusal surface in *Arvicola jacobaeus*, with enamel fields that are slightly confluent in some specimens, the general thickness of the enamel, the type of differentiation and the loss of roots in conjunction with the retention of the capacity to form them. This same morphology, the enamel differentiation and the loss of roots, also indicate an affinity with the species *A. sapidus*, which is nonetheless distinct from *A. terrestris*, in particular as regards the SDQ values (Fig. 9, Table 4) and the more advanced character of the occlusal morphology in m1 and M3.

The characterisation of the chromosomal complement, in number of chromosomes, shows that *A. terrestris* is a derived

Table 4. Enamel thickness (SDQ) values of large arvicoline rodents of Europe. Measurements: Gran Dolina, levels TD3-TD6, Cuenca-Bescós et al. 1995; Gura Dobrogei and Casian caves, Radulescu and Samson 1993; several Holsteinian, Eemian, Saalian, Weichselian, and Weimar-Ehringsdorf localities in the Pannonian basin and Central Europe in Heinrich 1982; Miessehheim 1, Kolfschoten 1990; two Recent populations of *Arvicola sapidus* in Röttger 1987; Untermassfeld, Voigtstedt in Maul et al. 1998. Extant *A. sapidus*, and the Pleistocene *A. sapidus* from L'Abric Romani together with *A.* aff. *sapidus* from Galeria, Atapuerca, and *A. terrestris* from El Mirón, were measured for this work.

Species	Localities	SDQ values			
		max	min	mean	N
Arvicola jacobaeus sp. nov.	TE-LRU Sima del Elefante, Atapuerca, Burgos	169	105	133	45
Mimomys savini	Untermassfeld	179	131	153	9
Mimomys savini	Gran Dolina, Atapuerca, Burgos	166	118	148	8
Mimomys intermedius	Gura Dobrogei and Casian caves	160	131	142	12
Mimomys savini	Voigstedt	160	115	135	108
Arvicola cantianus	Miessenheim I	180	130	150	29
Arvicola cantianus	several Holsteinian localities Pannonian Basin	126	103	123	9
Arvicola cantianus	several Holsteinian localities Central Europe	145	114	129	7
Arvicola cantianus	Weimar Ehringsdorf	139	103	120	6
Arvicola cantianus	several Saalian localities Pannonian Basin	139	95	111	53
Arvicola cantianus	several Eemian localities Central Europe	115	97	108	12
Arvicola aff. *sapidus*	Trinchera Galeria, Atapuerca, Burgos	151	102	130	7
Arvicola terrestris	several Weichselian localities Pannonian Basin	103	72	88	115
Arvicola terrestris	several Weichselian localities Central Europe	103	69	86	88
Arvicola terrestris	El Mirón, Cantabria	132	66	94	32
Arvicola sapidus	Abric Romani, Tarragona	184	104	132	37
Arvicola sapidus	Recent, Zaragoza	129	120	123	4

Table 5. Table of characters of the first lower molars (m1) and upper third molars (M3) of *Arvicola jacobaeus* sp. nov. from Sima del Elefante, Atapuerca, Burgos, Spain, levels TE9–TE13, and related arvicoline species used in the cladistic analysis.

Characters	Character states	outgroup	*Allophaiomys deucalion*	*Mimomys tornensis*	*Mimomys savini*	*Arvicola mosbachensis*	*Arvicola terrestris*	*Arvicola jacobaeus*	*Arvicola sapidus*
Cement in the reentrant angles	0, no; 1, yes	0	1	1	1	1	1	1	1
Enamel free areas in occlusal view	0, no; 1, yes	1	1	1	1	1	1	1	1
Enamel thickness	0, undifferenciated, 1 intermediate; 2, differenciated	0	1	2	2	2	2	2	2
Enamel differenciation	0, *Mimomys*-type; 1, undiferenciated; 2, *Microtus*-type	0	0	0	0	1	2	0	0
Hypsodonty/hypselodonty	0, roots; 1 in some elements; 2 lacking	0	2	0	0	1	2	1	2
m1 *Mimomys* islet	0, present; 1, absent	0	1	0	0	1	1	1	1
m1 *Mimomys* fold	0, present; 1, absent	0	0	0	1	0	0	1	1
m1 size	0, small (<3); 1, medium; 2, large (>4)	0	0	0	1	1	1	1	2
m1 A/L	0, 35–45; 1, 45–50; 2, >50	0	0	0	0	0	0	0	0
m1 confluent T 4–5	0, confluent, 1, closed	0	0	0	0	0	0	0	0
M3 P/L	0, <45; 1, > 45	0	0	0	0	0	1	1	0
M3 number closed triangles	0, 0; 1, 1; 2, 2–3; 3, >3	0	0	1	1	1	2	1	2
M3 confluent triangles	0, confluent, 1, closed	0	0	1	0	1	1	0	1
M3 *Mimomys* islet	0, present; 1, absent	0	1	1	1	1	1	1	1

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form (with more advanced chromosome number, 2n = 36), which split off the main lineage at an unknown time in the Pleistocene. There is an opinion that *A. sapidus*, with an ancestral karyotype (2n = 40) was present in most Eurasian faunas prior to the Late Pleistocene, whereas the chromosome speciation and a wide distribution of *A. terrestris* occurred in Late Pleistocene (Díaz de la Guardia and Pretel 1978; Kalthoff et al. 2007). Our own studies in Middle Pleistocene localities of Atapuerca such as Galería (Cuenca-Bescós et al. 1999a), as well as those by other authors based on materials from other sites in southern Europe (López Martínez and Ruiz Bustos 1977; López Martínez 1980; Râdulescu 1989), demonstrate that an ancestral form of *A. sapidus*, generally classified in the mentioned works as *A.* cf. *sapidus*, was already present during the Middle Pleistocene. Synaptic sex chromosomes, the ancestral condition of arvicolines, are present in *A. sapidus* (Megías-Nogales et al. 2003), reinforcing the idea of the primitive character of this species. Heterochronic evolution of the species *A. sapidus* also proves its primitive condition (Cubo et al. 2006).

Phylogenetic analysis

Morphologic affinity among *Arvicola sapidus* and *Arvicola terrestris* suggests a common ancestor; probably *Mimomys savini* as mentioned above. However, we know very little about the relationships among the extant species and their purported relatives of early, middle, and late Pleistocene age. Consequently we perform here a preliminary initial data exploration in a phylogenetic approach by analysing the characters discussed throughout the text in the m1 and the M3 (Table 5) using PAST (Hammer et al. 2001). Being well aware of its tentative quality the resulting cladistic analysis reveal that *M. savini* is probably the sister group of the *Arvicola* species, and that *A. sapidus* and *A. terrestris* are more closely related to each other than to other *Arvicola* species (Fig. 10) including the new species described here.

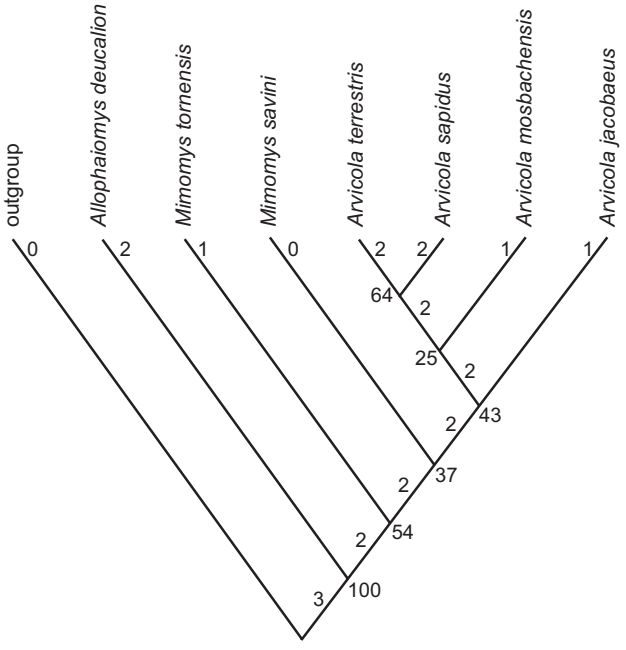


Fig. 10. Cladogram of fossil and extant arvicoline species related with *Arvicola jacobaeus* sp. nov. from the Lower Pleistocene, Sima del Elefante levels TE9–TE13. The cladistic analysis has been performed using PAST; to find the shortest tree we use the branch and bound algorithm and the Fitch character optimisation criteria, and 1000 bootstrap replicates (Hammer et al. 2001). The number of Most Parsimonious Tree is one, the tree length 22, the Consistency Index 0.7273, and the Retention Index 0.6. The Bremer support or Decay Index has not been analysed.

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Appendix 1

Arvicola jacobaeus sp. nov.

Field Label	anatomical element	Preservation	MPZ Label
ATA97 TE9 Toblerone 1	M3 sup	isolated tooth	MPZ 2008/342
ATA97 TE9 Toblerone 1	md m1m2	mandible	MPZ 2008/343
ATA97 TE9 Toblerone 1	md m1m2	mandible	MPZ 2008/344
ATA98 TE9 Toblerone 1	m3 inf	isolated tooth	MPZ 2008/345
ATA98 TE9 Toblerone 1	M3 sup	isolated tooth	MPZ 2008/346
ATA97 TE9 Toblerone 2	M3 sup	isolated tooth	MPZ 2008/347
ATA98 TE9 Toblerone 2	M3 sup	isolated tooth	MPZ 2008/348
ATA98 TE9 Toblerone 2	md m1m2	mandible	MPZ 2008/349
ATA98 TE9 Toblerone 3	M3 sup	isolated tooth	MPZ 2008/350
ATA98 TE9 Toblerone 3	md m1m2	mandible	MPZ 2008/351
ATA98 TE9 Toblerone 4	md m1m2	mandible	MPZ 2008/352
ATA98 TE9 Toblerone 5	md m1m2	mandible	MPZ 2008/353
ATA97 TE9 Toblerone 9	m1 inf	isolated tooth	MPZ 2008/354
ATA97 TE9 Toblerone 9	m2 inf	isolated tooth	MPZ 2008/355
ATA97 TE9 Toblerone 9	m3 inf	isolated tooth	MPZ 2008/356
ATA97 TE9 Toblerone 9	m3 inf	isolated tooth	MPZ 2008/357
ATA97 TE9 Toblerone 9	M1 sup	isolated tooth	MPZ 2008/358
ATA97 TE9 Toblerone 9	M2 sup	isolated tooth	MPZ 2008/359
ATA97 TE9 Toblerone 9	M2 sup	isolated tooth	MPZ 2008/360
ATA98 TE9 Toblerone 10	m1 inf	isolated tooth	MPZ 2008/361
ATA98 TE9 Toblerone 10	m2 inf	isolated tooth	MPZ 2008/362
ATA98 TE9 Toblerone 10	m3 inf	isolated tooth	MPZ 2008/363
ATA98 TE9 Toblerone 10	M1 sup	isolated tooth	MPZ 2008/364
ATA98 TE9 Toblerone 10	M1 sup	isolated tooth	MPZ 2008/365
ATA98 TE9 Toblerone 10	M2 sup	isolated tooth	MPZ 2008/366
ATA98 TE9 Toblerone 10	M2 sup	isolated tooth	MPZ 2008/367
ATA97 TE9 Toblerone s/n	M2 sup	isolated tooth	MPZ 2008/368
ATA97 TE9 Toblerone s/n	M1 sup	isolated tooth	MPZ 2008/369
ATA97 TE9 Toblerone s/n	m1 inf	isolated tooth	MPZ 2008/370
ATA97 TE9 Toblerone s/n	m2 inf	isolated tooth	MPZ 2008/371
ATA98 TE9 Toblerone s/n	m1 inf	isolated tooth	MPZ 2008/372
ATA98 TE9 Toblerone s/n	m2 inf	isolated tooth	MPZ 2008/373
ATA98 TE9 Toblerone s/n	M1 sup	isolated tooth	MPZ 2008/374
ATA98 TE9 Toblerone s/n	M1 sup	isolated tooth	MPZ 2008/375
ATA98 TE9 Toblerone s/n	M1 sup	isolated tooth	MPZ 2008/376
ATA98 TE9 Toblerone s/n	M2 sup	isolated tooth	MPZ 2008/377
ATA98 TE9 Toblerone s/n	M1 sup	isolated tooth	MPZ 2008/378
ATA98 TE9 Toblerone s/n	M1 sup	isolated tooth	MPZ 2008/379
ATA04 TE13 H31 1150-1160	Holotype md m1m2m3	mandible	MPZ 2008/380
ATA04 TE13 H31 1150-1160	md m1	mandible	MPZ 2008/381
ATA01 TE9a K31 630-650	M1 sup	isolated tooth	MPZ 2008/382
ATA01 TE9a K31 630-650	M1 sup	isolated tooth	MPZ 2008/383
ATA01 TE9a K31 630-650	M3 sup	isolated tooth	MPZ 2008/384
ATA02 TE9b-K30-600-620	m1 inf	isolated tooth	MPZ 2008/385
ATA02 TE9b I30 680-690	m1 inf	isolated tooth	MPZ 2008/386
ATA02TE9b I30 680-690	M3 sup	isolated tooth	MPZ 2008/387
ATA0405 TE12	M1 sup	isolated tooth	MPZ 2008/388
ATA0405 TE12	M2 sup	isolated tooth	MPZ 2008/389
ATA 02 TE9b 660-670	m1 inf	isolated tooth	MPZ 2008/390
ATA02 TE9b 640 650	M2 sup	isolated tooth	MPZ 2008/391
ATA00 TE9a	m1 inf	isolated tooth	MPZ 2008/392
ATA02 TE 9b L31 570-580	m1 inf	isolated tooth	MPZ 2008/393
ATA02 TE 9b J30 630-640	m1 inf	isolated tooth	MPZ 2008/394
ATA02 TE 9b L30 540-555	md m1m2	mandible	MPZ 2008/395
ATA02 TE 9b L30 540-555	md m1m2	mandible	MPZ 2008/396
ATA02 TE 9b I30 680-690	m1 inf	isolated tooth	MPZ 2008/397
ATA02 TE 9b K30 600-620	m1 inf	isolated tooth	MPZ 2008/398
ATA02 TE 9b K29 640-650	m1 inf	isolated tooth	MPZ 2008/399

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ATA02 TE 9b K29 640-650	m1 inf	isolated tooth	MPZ 2008/400
ATA02 TE 9b I30 670-680	m1 inf	isolated tooth	MPZ 2008/401
ATA02 TE 9b K31 620-630	m1 inf	isolated tooth	MPZ 2008/402
ATA02 TE 9b K31 620-630	m1 inf	isolated tooth	MPZ 2008/403
ATA02 TE 9b K31 620-630	m1 inf	isolated tooth	MPZ 2008/404
ATA02 TE 9b L30 600-610	m1 inf	isolated tooth	MPZ 2008/405
ATA02 TE 9b L29 660-670	m1 inf	isolated tooth	MPZ 2008/406
ATA02 TE 9b K30 590-600	m1 inf	isolated tooth	MPZ 2008/407
ATA03 TE 9b I31 1420-1430	m1 inf	isolated tooth	MPZ 2008/408
ATA02 TE 9b L30 580-590	md m1m2	mandible	MPZ 2008/409
ATA02 TE 9b L30 580-590	md m1m2	mandible	MPZ 2008/410
ATA02 TE 9b L30 580-590	md m1m2	mandible	MPZ 2008/411
ATA02 TE 9b K29 620-630	md m1m2m3	mandible	MPZ 2008/412
ATA02 TE 9b K29 620-630	m1 inf	isolated tooth	MPZ 2008/413
ATA03 TE 9c L30 L31 1290-1300	md m1m2	mandible	MPZ 2008/414
ATA03 TE 9c L30 L31 1290-1300	md m1	mandible	MPZ 2008/415
ATA03 TE 9c L30 L31 1290-1300	m1 inf	mandible	MPZ 2008/416
ATA02 TE 9b K30 580-590	md m1m2	mandible	MPZ 2008/417
ATA02 TE 9b J30 640-650	m1 inf	isolated tooth	MPZ 2008/418
ATA03 TE 9c K31/L31 1330-1340	m1 inf	isolated tooth	MPZ 2008/419
ATA02 TE 9c L30 1290-1300	m1 inf	isolated tooth	MPZ 2008/420
ATA01 TE 9a K30 610-620	m1 inf	isolated tooth	MPZ 2008/421
ATA02 TE9b K31 610-620	m2 inf	isolated tooth	MPZ 2008/422
ATA03 TE 9c L30/31 1350-1360	m2 inf	isolated tooth	MPZ 2008/423
ATA02 TE 9b L30 550-560	m2 inf	isolated tooth	MPZ 2008/424
ATA02 TE 9b J30 630-640	m3 inf	isolated tooth	MPZ 2008/425
ATA02 TE 9b J30 630-640	m3 inf	isolated tooth	MPZ 2008/426
ATA02 TE 9b I30 670-680	m3 inf	isolated tooth	MPZ 2008/427
ATA02 TE 9b k31 630-640	m3 inf	isolated tooth	MPZ 2008/428
ATA02 TE 9b k31 630-640	m3 inf	isolated tooth	MPZ 2008/429
ATA02 TE 9b K30 590-600	m3 inf	isolated tooth	MPZ 2008/430
ATA02 TE 9b I30 650-660	m3 inf	isolated tooth	MPZ 2008/431
ATA02 TE 9b L31 570-580	M1 sup	isolated tooth	MPZ 2008/432
ATA TE 9b L30 570-580	M1 sup	isolated tooth	MPZ 2008/433
ATA02 TE 9b J30 630-640	M1 sup	isolated tooth	MPZ 2008/434
ATA02 TE 9b J30 630-640	M1 sup	isolated tooth	MPZ 2008/435
ATA02 TE 9b K29 640-650	M1 sup	isolated tooth	MPZ 2008/436
ATA02 TE 9b K31 620-630	M1 sup	isolated tooth	MPZ 2008/437
ATA02 TE 9b K31 600-610	M1 sup	isolated tooth	MPZ 2008/438
ATA02 Te 9b J31 660-670	M1 sup	isolated tooth	MPZ 2008/439
ATA02 TE 9b K30 590-600	M1 sup	isolated tooth	MPZ 2008/440
ATA03 TE 9c L30 L31 1290-1300	M1 sup	isolated tooth	MPZ 2008/441
ATA01 TE 9a K30 610-620	M1 sup	isolated tooth	MPZ 2008/442
ATA03 TE 9c L29,30,31 1300-1310	M1 sup	isolated tooth	MPZ 2008/443
ATA03 TE 9c L29,30,31 1280-1290	M1 sup	isolated tooth	MPZ 2008/444
ATA02 TE 9c M31 1270-1280	M1 sup	isolated tooth	MPZ 2008/445
ATA02 TE 9c M31 1270-1280	M1 sup	isolated tooth	MPZ 2008/446
ATA02 TE 9b J30 630-640	M2 sup	isolated tooth	MPZ 2008/447
ATA02 TE 9b J30 630-640	M2 sup	isolated tooth	MPZ 2008/448
ATA02 TE 9b L31 550-560	M2 sup	isolated tooth	MPZ 2008/449
ATA02 TE 9b K30 640-650	M2 sup	isolated tooth	MPZ 2008/450
ATA02 TE 9b K29 620-630	M2 sup	isolated tooth	MPZ 2008/451
ATA03 TE 9c L30 L31 1290-1300	M2 sup	isolated tooth	MPZ 2008/452
ATA03 TE 9c L30 L31 1290-1300	M2 sup	isolated tooth	MPZ 2008/453
ATA03 TE 9c L30 L31 1290-1300	M2 sup	isolated tooth	MPZ 2008/454
ATA03 TE 9c L30/31 1350-1360	M2 sup	isolated tooth	MPZ 2008/455
ATA03 TE 9c L30/31 1350-1360	M2 sup	isolated tooth	MPZ 2008/456
ATA02 TE 9b J30 630-640	M3 sup	isolated tooth	MPZ 2008/457
ATA02 TE 9b J30 630-640	M3 sup	isolated tooth	MPZ 2008/458
ATA02 TE 9b I30 680-690	M3 sup	isolated tooth	MPZ 2008/459
ATA02 TE 9b k31 630-640	M3 sup	isolated tooth	MPZ 2008/460
ATA02 TE 9b J30 640-650	M3 sup	isolated tooth	MPZ 2008/461
ATA02 TE 9c M31 1270-1280	M3 sup	isolated tooth	MPZ 2008/462

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