C. R. Palevol 15 (2016) 621–634

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Palaeontology, Systematics and Evolution (Biostratigraphy)

Updated Atapuerca biostratigraphy: Small-mammal distribution and its implications for the biochronology of the Quaternary in Spain

Mise à jour de la biostratigraphie d'Atapuerca : distribution des petits mammifères et ses implications sur la biochronologie du Quaternaire en Espagne

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ARTICLE INFO

Article history:
Received 4 April 2015
Accepted after revision 10 September 2015
Available online 4 February 2016

Handled by H.A. Blain

Keywords:
Quaternary
Biostratigraphy
Statistic Analysis
Small Mammals
Ages of *Homo*
Atapuerca

ABSTRACT

The Sierra de Atapuerca (Burgos, Spain) contains the most comprehensive archaeological and paleontological evidence of human evolution in Europe during the Quaternary. The time scale based on the microfossil content of the sedimentary infillings of the caves of Atapuerca has been used to attribute relative ages to the various paleontological and archaeological levels and correlate amongst the different sites. Microfossils are particularly significant as they are the dominant constituents of the caves from the Pleistocene to the Holocene of the Sierra de Atapuerca. The microfossils of the Atapuerca sites are mainly composed of isolated bones and teeth from small vertebrates, and the hard tissue of the vertebrate skeleton can be taxonomically classified. In revisiting the distribution and the classification of the small-mammal taxa along five of the main stratigraphic sequences from Atapuerca (Sima del Elefante, Gran Dolina, Galería-Zarpazos, Sima de los Huesos, and Portalón), we apply a new method, the "Unitary Associations" method, in order to refine the existing biozones, adding five new Faunal Units, and interpret their relative age. Finally, we correlate Atapuerca with other Pleistocene sites of Europe.

Mots clés :
Quaternaire
Biostratigraphie

RÉSUMÉ

La Sierra de Atapuerca (Burgos, Espagne) contient la preuve archéologique et paléontologique la plus complète sur l'évolution humaine en Europe au cours du Quaternaire. L'échelle de temps basée sur le contenu de microfossiles des remplissages sédimentaires

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http://dx.doi.org/10.1016/j.crpv.2015.09.006
1631-0683/

Analyse statistique
Petits mammifères
Âge de *l'Homo*
Atapuerca

des grottes d'Atapuerca a été utilisée pour attribuer les âges par rapport aux niveaux paléontologiques et archéologiques et pour établir des corrélations entre les différents sites. Les microfossiles sont importants et sont les principaux constituants des grottes du Pléistocène à l'Holocène de la Sierra de Atapuerca, près de la ville de Burgos, en Espagne. Les microfossiles habituels des sites d'Atapuerca sont composés d'os et de dents isolés du squelette de petits vertébrés et les tissus durs du squelette de vertébré peuvent être classés d'un point de vue taxonomique. En revisitant la distribution et la classification des taxons des petits mammifères le long de cinq des principales séquences stratigraphiques d'Atapuerca (Sima del Elefante, Gran Dolina, Galería-Zarpazos, Sima de los Huesos et Portalón), nous appliquons une nouvelle méthode, la méthode des « associations unitaires », afin d'affiner les biozones existantes, ajoutant ainsi cinq nouvelles unités fauniques et d'interpréter leur âge relatif. Enfin, nous mettons Atapuerca en corrélation avec d'autres sites du Pléistocène d'Europe.

1. Introduction

The paleoanthropological sites of Atapuerca (Burgos, Spain) contain the most extraordinary accumulation of evidence of human occupation in Europe, ranging nearly continuously from the Early Pleistocene to the Late Pleistocene and Holocene (Arsuaga et al., 2014; Bermúdez de Castro et al., 1997; García-Medrano et al., 2014; Huguet et al., in press; Ollé et al., 2013; Ortega et al., 2013; Rodríguez et al., 2011). This evidence is based upon the study of the paleontological and archaeological content of the five-key Atapuerca caves with long stratigraphic sequences: Sima del Elefante, Gran Dolina, Galería-Zarpazos, Sima de los Huesos, and Portalón. Studies of the faunal remains have made it possible to establish the relative ages of the sites and to reconstruct the landscape, increasing our understanding of human evolution and the activities of the first inhabitants of western Europe during the transition from the Early to the Middle Pleistocene, at the Matuyama-Brunhes Boundary (MBB) (0.78 Ma).

At the same time, the biostratigraphy of the Pleistocene in continental Europe has made substantial progress in recent decades, though there are only a few cases where several stratigraphic sequences are located within the same geographic area, as with the sites of Atapuerca Hill. Furthermore, few of these are close to being complete or calibrated with chronological data, and therefore, most biostratigraphic proposals are based on isolated sites, representing short time intervals. The biostratigraphy based on the stratigraphic distribution of the fossil vertebrates found in the cave-infilling sequences of the sites of Atapuerca Hill is thus of the utmost importance because these fossils provide a comprehensive local biostratigraphy. Moreover, for the first time, several paleontological studies have shed light on the regional and trans-regional evolution of several small-mammal species (Cuenca-Bescós et al., 1995, 2010, 2014a, 2014b; Firmat et al., 2014; Lozano-Fernández et al., 2013a, 2013b; Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013, 2014), as well as on the succession of faunal events (First and Last Appearance Data, FAD, LAD) pertaining to important fossil markers, which can be calibrated with magnetostratigraphic and radiometric data (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2013, 2015).

Biostratigraphic events permit the definition of biozones (Faunal Units, Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010). Using statistical methods such as the "Unitary Associations" (UA) method (Guex, 1991; Hammer et al., 2001), in this paper, we aim to refine the Faunal Units of Atapuerca.

The vertebrate fauna from the Pleistocene sites of the Atapuerca caves is dominated by microvertebrates. As fossils, small vertebrates are particularly important in that they constitute a major fraction of the biota and provide significant data for biochronologic control and for paleoenvironmental-paleoclimatic reconstruction (Blain et al., 2009, 2010; Desclaux, 2013; Kotsakis et al., 2003; López-García et al., 2008, 2010a; Markova, 2005; Maul and Markova, 2007; Parfitt et al., 2005, 2010; Rabinovich and Biton, 2011). The microvertebrates of the Pleistocene sites of Atapuerca have provided a strong tool for the biostratigraphic dating of the paleoanthropological sites. The small vertebrates considered in the present work have been recovered from these localities since 1990. These faunas are rich and diverse, with more than 100 species from all major groups of small vertebrates present: osteichthyans, lissamphibians, squamates, chelonians, birds, and small mammals. Since the 1990s, new paleontological and archaeological discoveries with significant paleoanthropological and biostratigraphic implications have been made. Taphonomic studies have also recently been updated (Bennàsar et al., in press; Sala et al., 2014, 2015).

Further, our studies are an important contribution to what is known of human evolution in Europe because we provide the relative age of the *Homo* species and contribute to their paleoecology.

The age of the localities of Atapuerca

Several radiometric and paleomagnetic dating techniques indicate that the Atapuerca sites embody a time span running from the Early Pleistocene to the Holocene (Arnold et al., 2014; Demuro et al., 2014; Falguères et al., 2014). A recent revision of the Early Pleistocene levels of the Atapuerca sites TE and TD has allowed a continuous biostratigraphic succession of faunas from the interval around the Jaramillo subchron to be studied in terrestrial sequences (Cuenca-Bescos et al., 2015). However, there remains the question of correlating the absolute dating with the major events in the evolution of the faunal assemblages of the Early-Middle Pleistocene of Europe.

This is of special interest because in the last few decades, a number of issues relating to the earliest arrival of hominins in Europe have been subject to intense debate, including the chronology of the first human settlements, their dispersal routes, the techno-cultural developments of the population that dispersed out of Africa, and the ecological context and climatic conditions of the dispersal event (for reviews and references, see Agustí et al., 2009, 2015; Bermúdez de Castro et al., 1997; Cuenca-Bescós et al., 2013; Duval et al., 2012; García et al., 2014; Kahlke et al., 2011; Parfitt et al., 2005, 2010; Toro-Moyano et al., 2013).

Our goal in this article is to provide an updated analysis of the small-mammal assemblages from the localities of Atapuerca. Then, we will reconstruct a synthetic, diachronic sequence, and correlate the different faunal events with the known geological events of Atapuerca over time on the basis of cave studies, stratigraphy, paleomagnetism, and radiometric ages.

2. Material and methods

2.1. Recovery of the small mammals

Microvertebrates are not encountered through standard excavating methods, and specialized recovery techniques are generally required to obtain such taxa (Cifelli et al., 1996; Daams and Freudenthal, 1988). Once the sediments have been washed off, we pick out the small fossils in laboratories by the River Arlanzón during field campaigns, and subsequently in the Aspanias Foundation Centre of Burgos and in the laboratory of the University of Zaragoza. Except for the coarsest concentrate, which is separated with the naked eye, fossil extraction is done with the aid of a binocular microscope at a magnification of 10× to 20×. In both cases, fine and coarse concentrates are spread thinly and evenly in a sorting tray that is marked with a grid system, from which fossils are removed with fine forceps. Larger fossils and lithic artefacts are usually found during the excavation of the site, but some fragments are so small that they are only brought to light in the sieves, during the washing-screening of the sediments. The fossil specimens of small vertebrates are deposited in the collections of the Museum of Natural Sciences of the University of Zaragoza.

2.2. Taphonomy

All the localities belong to the taphonomically influenced type of cave sites; hence, it is better to compare them with sites of the same nature. Taphonomy is important in the analysis of the fossil assemblages of small vertebrates because it may make it possible to distinguish:

- natural from cultural depositional agents;
- the identity of the depositional agents;
- fossorial disturbance of the sediments;
- disturbances of the sediments caused by colluviation (Krajcarz et al., 2012; Weisbrod and Zaidner, 2013; Weisbrod et al., 2005). In the case of the micromammals recovered from the caves of Atapuerca, the agent of accumulation is frequently associated with predation by owls (Bennàsar et al., 2016).

2.3. Taxonomy

The taxonomic classification follows previous studies of small mammals in Spain (Anchelerges Tarraco et al., 2015; Cuenca-Bescós et al., 1995, 2010, 2014a, 2014b; Furió, 2007; Furió et al., 2015; Laplana and Cuenca-Bescós, 2000; Lozano-Fernández et al., 2013a, 2013b, 2015; Minwer-Barakat et al., 2011, 2012; Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013, 2014) and the bibliographical references therein.

2.4. Biostratigraphy

Once the fossils are taxonomically classified, we proceed to analyse the distribution of each species of small mammal throughout the stratigraphic sequences of the main sections of Atapuerca: Gran Dolina (TD), Galería-Zarpazos (G-Z), Sima del Elefante (TE), Sima de los Huesos (SH), and Portalón. We consider:

- the species of small mammals that occur in the succession of site sections;
- the diversity, i.e. the number of species through the section;
- the first and last occurrence of each species in the section, i.e. the stratigraphic range of the species;
- the recognition of marker species and biostratigraphic datum levels;
- the application of quantitative biostratigraphic methods that involve using the stratigraphic range and the datum levels to ascertain correlations among the sites (Guex, 1991; Hammer et al., 2001).

The small-mammal succession obtained from the composite diachronic sequence of Atapuerca is analysed by means of the "Unitary Associations" (UA) method of Guex (1991). The data input is a Presence-Absence Data Matrix (PAM) that uses the 64 taxa distributed in the five sections; the stratigraphic layers are in rows and the small-mammal species in columns (Fig. 1). Then, a composite section is built up, as explained in Guex (1991) and Hammer et al. (2001). The diachronic development of the data is ensured by the stratigraphic order and the radiometric ages of the different localities of Atapuerca studied by the authors (see below).

2.5. Geology and Age

Studies of the geology and caves of the Sierra de Atapuerca karst system have been extensively presented in Ortega et al. (2013) and Benito-Calvo and Pérez-González (2015). Independent geochronological data from the different stratigraphic layers and from the five localities of Atapuerca are used. The geological age of the layers of these localities was determined by geological methods – mainly by the superposition of the layers in the section. The ages of the different strata were determined by multiple methods including paleomagnetism and radiometric dating (see Arnold et al., 2014; Demuro et al., 2014, Falguères et al., 2014 and references therein).

Atapuerca Sequences	TELRU								TDLOW						TDUP		SH	TG-TZ		TEURU	PORTALON			Species Abbreviations→ Atapuerca Sequences/FU
Atapuerca UA	1								2					3	4 & 5			5		6	7	8	9	
Atapuerca Faunal Units	1								2		3	4	5a	5b	6a			6b		6c	7	8	9	
Atapuerca Levels	TE7	TE8	TE9	TE10	TE11	TE12	TE13	TE14	TD 3-4	TD 5	TD 6-2-3	TD 6-1	TD 7	TD 8a	TD 8b	TD 10-11	SH	TG II	TG III TZ	TEURU	ATPPle	ATPCalc	PortAct	
Beremendia fissidens	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Bf*
Asoriculus gibberodon	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Ag*
Crocidura kornfeldi	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Ck*
Galemys cf. kormosi	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Gk*
Erinaceus praeglacialis	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Ep*
Talpa cf. *europaea*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	0	*Te*
Sorex D. margaritodon	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*SDm*
Sorex sp.	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	*Ssp*
Crocidura spp.	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	0	0	0	1	*Csp*
Erinaceus europaeus	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	0	0	0	*Ee*
Dolinasorex gliphodon	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	*Dg*
Sorex minutus	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	1	1	0	*Sm*
Galemys pyrenaicus	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	1	0	0	*Gp*
Neomys sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	*Nsp*
Neomys fodiens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	*Nf*
Neomys anomalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	*Na*
Sorex araneus-coronatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	*Sa-c*
Myotis sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	*Mysp*
Rhinolophus sp.	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	1	1	1	0	1	0	0	0	*Rhsp*
Miniopterus schreibersii	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	1	1	1	0	*Msch*
Oryctolagus cf. *lacosti*	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Ol*
Lepus sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	*Lsp.*
Oryctolagus spp.	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	*Osp*
Allophaiomys lavocati	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Al*
Allophaiomys nutiensis	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*An*
Allophaiomys burgondiae	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Ab*
Ungaromys cf. Nanus	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Usp*
Arvicola jacobaea	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Aj
Castillomys rivas	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Cr*
Pliomys simplicior	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Pls*
Sciurus sp.	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	*Scsp*
Eliomys quercinus	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	*Eq*
Castor sp.	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	*Ctor*
Apodemus spp.	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	*Aspp*
Victoriamys chalinei	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	*Vch*
Stenocranius gregaloides	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	*Stgr*
Hystrix sp.	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	*Hy*
Terricola arvalidens	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	*Tarv*
Microtus seseae	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	*Mses*
Pliomys episcopalis	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	*Ple*
Mimomys savini	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	*Mimsav*
Iberomys huescarensis	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	*IberH*
Marmota spp.	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	0	0	0	0	*Marm*
Allocricetus bursae	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	*Allb*
Micromys minutus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	*Micrm*
Microtus ratticepoides	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	*Mrat*
Terricola atapuerquensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	*Tata*
Iberomys mediterraneus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	*Iberm*
Allocricetus correzensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	*Allc*
Microtus arvalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	*Marv*
Microtus jansoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	*Mja*
Microtus agrestis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	*Magr*
Pliomys lenki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	*Pllk*
Hystrix vinogradovi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	*Hyv*
Arvicola sapidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	*Asap*
Arvicola terrestris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	*Aterr*
Clethrionomys acrorhyza	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	*Cleta*
Clethrionomys glareolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	*Cletg*
Microtus oeconomus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	*Moec*
Terricola duodecimcostatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	*Terd*
Terricola pyrenaicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	*Terpy*
Terricola lusitanicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	*Terlus*
Chionomys nivalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	*Chio*
Iberomys cabrerae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	*Iberc*
Atapuerca Sequences	TELRU								TDLOW						TDUP		SH	TG-TZ		TEURU	PORTALON			Atapuerca Sequences/FU
Atapuerca UA	1								2					3	4 & 5			5		6	7	8	9	
Atapuerca Faunal Units	1								2		3	4	5a	5b	6a			6b		6	7	8	9	
Atapuerca Levels	TE7	TE8	TE9	TE10	TE11	TE12	TE13	TE14	TD 3-4	TD 5	TD 6-2-3	TD 6-1	TD 7	TD 8a	TD 8b	TD 10-11	SH	TG II	TG III TZ	TEURU	ATPPle	ATPCalc	PortAct	

Fig. 1. Presence-Absence Matrix for the small-mammal faunas from the localities of the Pleistocene to the Holocene of Atapuerca (Burgos, Spain). The species are listed in the first column. Abbreviations of the taxa used in the biostratigraphic analysis are in the last column. Our previous works (see text) are the main input of the data base, except for the barn owl (*Tyto alba*) nest of Portalón, which is presented here for the first time. TE7-TE14: Lower Red Levels from Sima del Elefante (TELRU); TD3-TD7: Lower levels from Gran Dolina (TDLOW); TD8-TD10-11: Upper levels from Gran Dolina (TDUP); SH: Sima de los Huesos; TG-TZ: Trinchera Galeria-Zarpazos; ATPPle, ATPCalc, ATPAct, Portalón: Pleistocene levels, Chalcolithic level and present-day remains respectively.

Fig. 1. Matrice présence-absence des petits mammifères des localités du Pléistocène à l'Holocène d'Atapuerca (Burgos, Espagne). Les espèces sont classées dans la première colonne. Les abréviations des taxons utilisés dans l'analyse biostratigraphique sont dans la dernière colonne. Nos travaux antérieurs (voir texte) sont l'entrée principale de la base de données, sauf pour le nid de l'effraie des clochers (*Tyto alba*) du Portalón, qui est présenté ici pour la première fois. TE7-TE14 : Niveaux inférieurs rouges de Sima del Elefante (TELRU) ; TD3-TD7 : niveaux inférieurs de la Gran Dolina (TDLOW) ; TD8-TD10-11 : niveaux supérieurs de la Gran Dolina (TDUP) ; SH : Sima de los Huesos ; TG-TZ : Trinchera Galeria-Zarpazos ; ATPPle, ATPCalc, ATPAct, Portalón : niveaux du Pléistocène, niveau chalcolithique et restes actuels, respectivement.

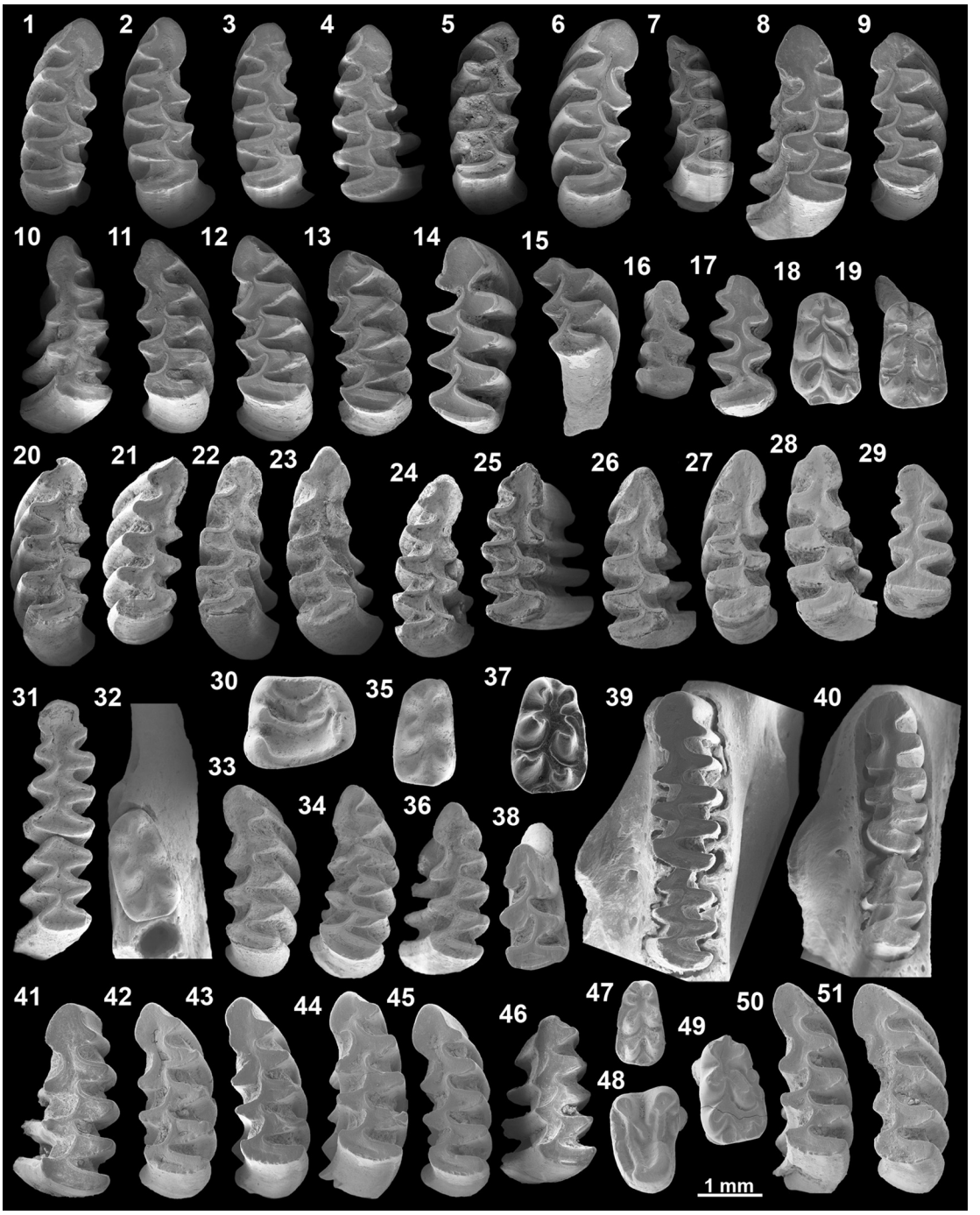

Fig. 2. Selected specimens of rodent taxa from the Early Pleistocene of Atapuerca, Sima del Elefante, Lower Red Levels (TELRU: TE7 to TE9+). The specimens consist of isolated lower first molars (m1), except 32, 39, and 40, which are mandibles with m1, and with m2 in the case of 31, 32, 39, and 40, attached to the mandible, and 15, 16, and 38, which are upper molars (M) represented upside-down. 1–19: Level TE 9a+. 1–13. *Allophaiomys* spp.; 14–15: *Pliomys simplicior*; 16, M3 of *Allophaiomys* spp.; 17, *Ungaromys* cf. *nanus*; 18, *Apodemus* sp.; 19, *Castillomys rivas*; 20–30: Level TE 9b. 20–28, *Allophaiomys* spp.; 29, *Ungaromys* cf. *nanus*; 30, *Eliomys* spp.; 31–36: Level TE 9c. 31, *Ungaromys* cf. *nanus*; 32, *Castillomys rivas*; 33–36, *Allophaiomys* spp. 37–40: Level TE 8. 37, *Castillomys rivas*; 38–40, *Allophaiomys* spp. 41–51: Level TE 7. 41–46, 50–51, *Allophaiomys* spp.; 47, 49, *Apodemus* sp.; 48, *Eliomys* spp.

Fig. 2. Spécimens sélectionnés de rongeurs du Pléistocène inférieur d'Atapuerca, Sima del Elefante, niveaux inférieurs rouges (TELRU : TE7 à TE9+). Les spécimens sont constitués de premières molaires inférieures isolées (m1), sauf 32, 39 et 40, qui sont des mandibules avec la m1, et avec m2 dans le cas de 31, 39, 40, et sauf 15, 16, 38, qui sont des molaires supérieures (M) représentées à l'envers. 1–19 : Niveau TE 9a+ 1–13. *Allophaiomys* spp. ; 14–15 : *Pliomys simplicior* ; 16, M3 de *Allophaiomys* spp. ; 17, *Ungaromys* cf. *nanus*; 18, *Apodemus* sp. ; 19, *Castillomys rivas* ; 20–30 : Niveau TE 9b. 20–28, *Allophaiomys* spp. ; 29, *Ungaromys* cf. *nanus* ; 30, *Eliomys* spp. ; 31–36 : Niveau TE 9c. 31, *Ungaromys* cf. *nanus* ; 32, *Castillomys rivas* ; 33–36, *Allophaiomys* spp. 37–40 : Niveau TE 8. 37, *Castillomys rivas* ; 38–40, *Allophaiomys* spp. 41–51 : Niveau TE 7. 41–46, 50–51, *Allophaiomys* spp. ; 47, 49, *Apodemus* sp. ; 48, *Eliomys* spp.

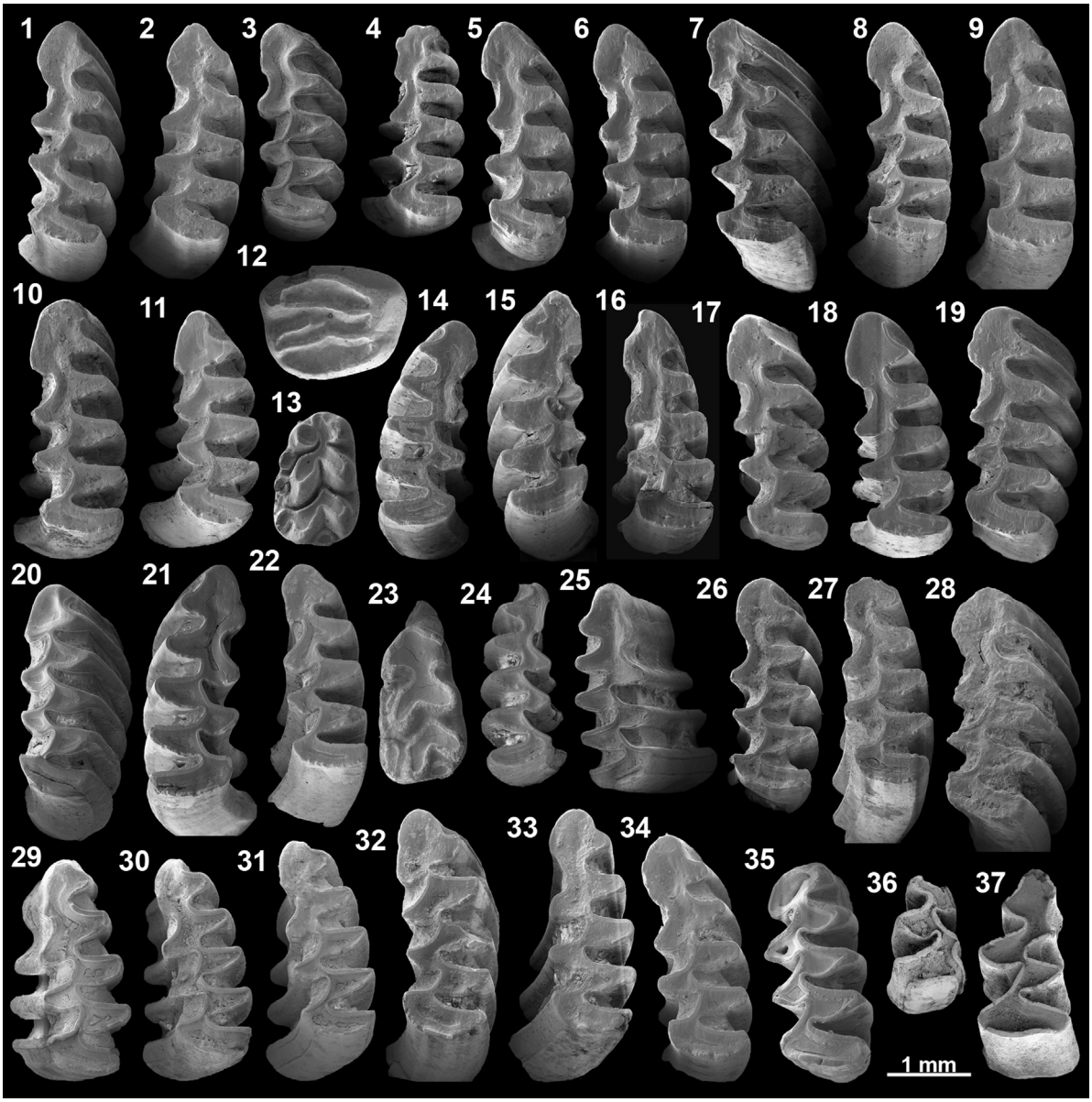

Fig. 3. Selected specimens of rodent taxa from the Early Pleistocene of Atapuerca, Sima del Elefante, Lower Red Levels (TELRU: TE10 to TE12). The specimens consist of isolated lower first molars (m1), except 12 and 36–37, which are upper molars (M). 1–13: Level TE12. 1–11, *Allophaiomys* spp.; 12, *Eliomys* spp.; 13, *Apodemus* sp.; 14–24: Level TE11. 14–22, 24, *Allophaiomys* spp.; 23, *Apodemus* sp. 25–37: Level TE10. 25–37, *Allophaiomys* spp.
Fig. 3. Spécimens sélectionnés de rongeurs du Pléistocène inférieur d'Atapuerca, Sima del Elefante, niveaux inférieurs rouges (TELRU : TE10 à TE12). Les spécimens sont constitués de premières molaires inférieures isolées (m1), à l'exception de 36 à 37 et 12, qui sont des molaires supérieures (M). 1–13 : Niveau TE12. 1–11, *Allophaiomys* spp. ; 12, *Eliomys* spp. ; 13, *Apodemus* sp. ; 14–24 : Niveau TE11. 14–22, 24, *Allophaiomys* spp. ; 23, *Apodemus* sp. ; 25–37 : Niveau TE10, 25–37, *Allophaiomys* spp.

3. Results

The taxonomic list of the small vertebrates recovered from the localities of Atapuerca since 1990 has increased with the years, and various new taxa have been discovered. Some of the insectivore species of the order Eulipotyphla have been cited for the first time in the Pleistocene of Spain (Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013, 2014), while others are still in revision. The rodents of the subfamily Arvicolinae are studied elsewhere (Arsuaga et al., 2014; Cuenca-Bescós et al., 1995, 1999a, 1999b, 2009, 2014; Firmat et al., 2014; Lozano-Fernández et al., 2013a, 2013b, 2015), whereas the murines, the dormice and the sciurid group (marmots and squirrels) are in preparation. For this reason, and to facilitate an overview of the species present in Atapuerca, we present some of the variability of the relevant species in the biostratigraphy of Atapuerca by including several specimens per species (Figs. 2–6). Extended papers on the large rodents such as the beaver, the birds and the bats were presented at the UISPP 2014

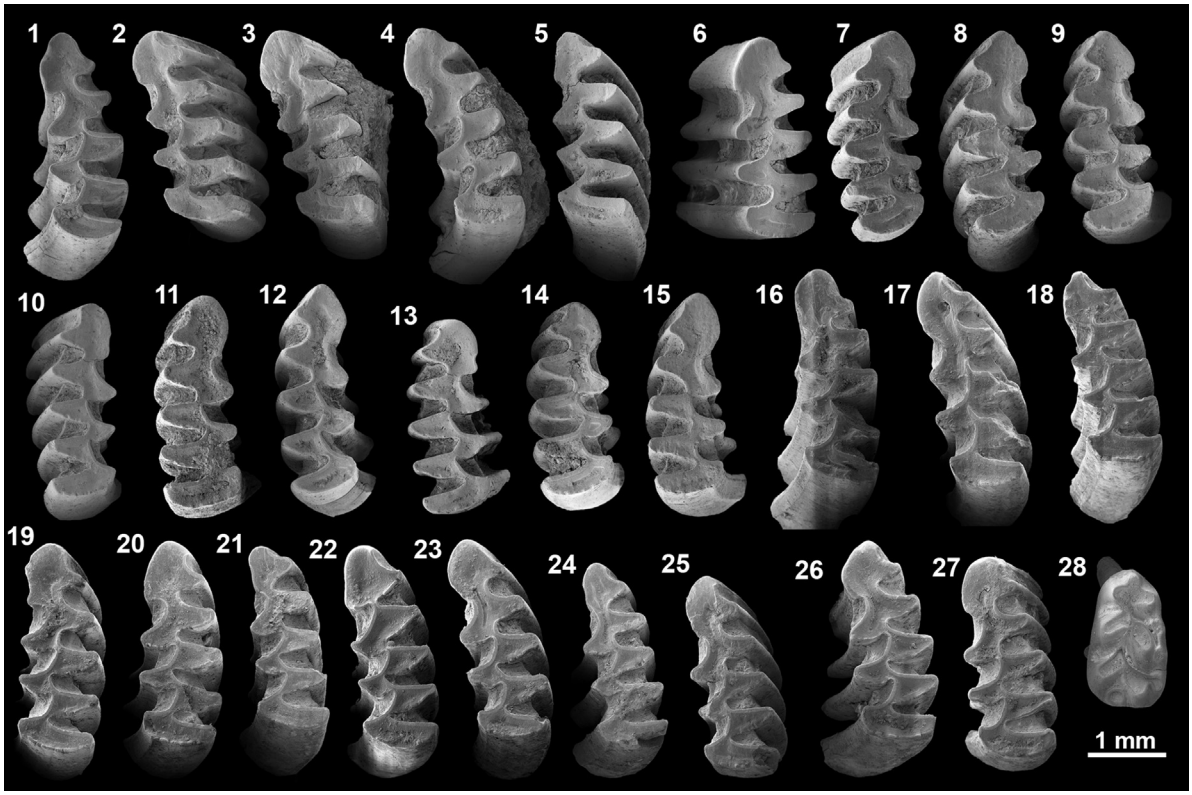

Fig. 4. Selected specimens of rodent taxa from the Early Pleistocene of Atapuerca, Sima del Elefante, Lower Red Levels (TELRU: TE13 to TE14). The specimens consist of isolated lower first molars (m1). 1–15: Level TE14; 16–28: Level TE13. 1–27, *Allophaiomys* spp.; 28, *Apodemus* sp.
Fig. 4. Spécimens sélectionnés de rongeurs du Pléistocène inférieur d'Atapuerca, Sima del Elefante, niveaux inférieurs rouges (TELRU : TE13 à TE14). Les spécimens sont constitués de premières molaires inférieures isolées (m1). 1–15 : Niveau TE14 ; 16–28 : niveau TE13. 1–27, *Allophaiomys* spp. ; 28, *Apodemus* sp.

Congress and will be published elsewhere (Cuenca-Bescós et al., 2014a; Galán-García et al., 2016; Núñez-Lahuerta and Cuenca-Bescós, 2015).

3.1. Stratigraphic distribution of the main taxa

The current number of recorded small-mammal taxa present in the Atapuerca localities is 64. These are stratigraphically distributed from bottom to top in the Atapuerca composite sequence, grouped according to the five main sections (TD, G-Z, TE, SH, Portalón) (see Fig. 1).

3.2. Biochronological analysis of the small-mammal fauna

Statistical analysis of the Atapuerca small mammals sheds new light on the established local biochronological sequence and the Atapuerca Faunal Units defined in previous papers. Five new Faunal Units, (FU), are added. A comparison of the FU that emerge from this analysis and the stratigraphy of Atapuerca is shown in Fig. 7.

4. Discussion

The nine sets of UA generated in the present work serve to refine our previous attempts at biozonation in Atapuerca, which resulted in the proposal of the "Atapuerca Faunal Units" by Cuenca-Bescós and García (2007) as well as a new FU by López-García et al. (2011). The new methodology, as well as the addition of new data and new FU (López-García et al., 2010b; Ordiales et al., 2014; this work), enhances the biozonation based on the Atapuerca Faunal Units (Fig. 7).

We also perform a cluster analysis to ascertain the robustness of the UAs obtained using the Guex (1991) method. This results in a cladogram of five groups, which may be further divided into nine groups, which correlate with the UAs and FU as shown in Fig. 8. Principal component analysis also shows five groups (Fig. 9), though it is less clear whether they may further be divided.

Interestingly, our biostratigraphic ages results, which are obtained independently of the work of Demuro et al. (2014), situate the stratigraphic sequence of TG-TZ (GIIa, GIIb, GIIIa, GIIIb in Demuro et al., 2014: Fig. 9) by biostratigrahy, above the levels of TD10 (in the upper levels of the Gran Dolina section, TDUP in tables and figures) and the levels with human fossil remains of Sima de los Huesos, recently dated in 434Ka (Stratigraphic Unit LU-6 of Aramburu et al., 2015; Arsuaga et al., 2014), TDUP and SH in Fig. 1. The difference with respect to our previous studies was that TG-TZ had been situated below TDUP (Cuenca-Bescós et al., 1999a, 2001; Galindo-Pellicena et al., 2011). This difference results from the fact that we now use new quantitative biostratigraphic methods (the UAs),

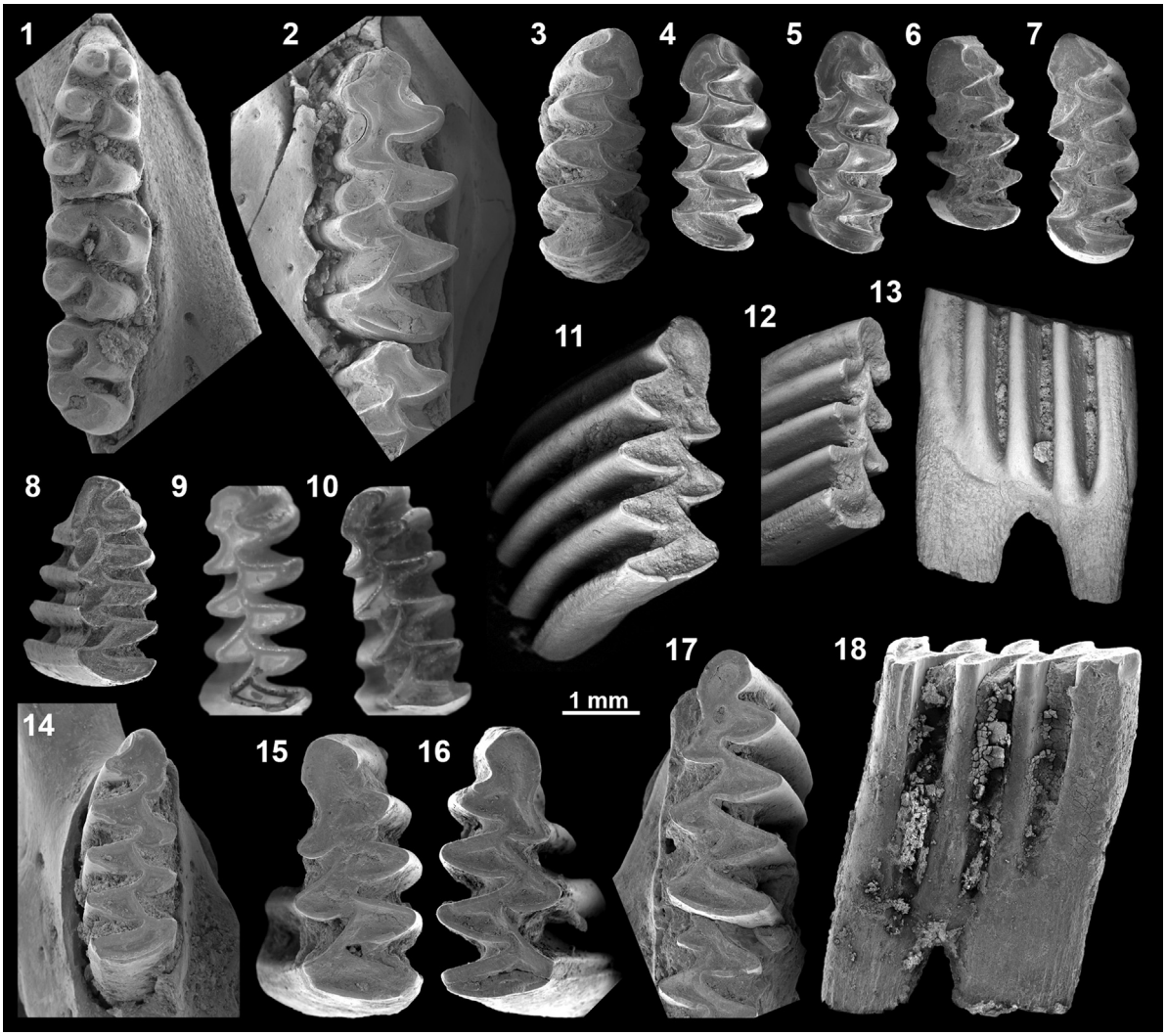

Fig. 5. Selected specimens of rodent taxa from the Pleistocene of Atapuerca, Gran Dolina, lower and upper levels (TDLOW and TDUP). The specimens consist of isolated lower first molars (m1), except 1, 2, and 14, which are mandibles with m1, and with m2, m3 in the case of 1, and m2 in the case of 2. 1–5: Level TD10. 1, *Allocricetus correzensis*; 2, *Arvicola* sp.; 3–5, *Iberomys mediterraneus*; 6–8: Level TD6. 6–8, *Iberomys huescarensis*; 9–10: *Pliomys lenki* from Level TD10; 11–14: Level TD5. 11, *Mimomys savini*; 12–13, *Pliomys episcopalis* in occlusal and lingual views; 14, *Iberomys huescarensis*; 15–18: Level TD4, *Mimomys savini* in occlusal (15–17) and lingual views (18).

Fig. 5. Spécimens sélectionnés de rongeurs du Pléistocène d'Atapuerca, Gran Dolina, niveaux inférieurs et supérieurs (TDLOW et TDUP). Les spécimens sont constitués de premières molaires inférieures isolées (m1), sauf 1, 2, et 14, qui sont des mandibules avec m1, m2, m3 dans le cas 1, et m2 dans le cas 2. 1–5 : Niveau TD10. 1, *Allocricetus correzensis* ; 2, *Arvicola* sp. ; 3–5, *Iberomys mediterraneus* ; 6–8 : Niveau TD6. 6–8, *Iberomys huescarensis* ; 9–10 : *Pliomys lenki* du Niveau TD10 ; 11–14 : Niveau TD5. 11, *Mimomys savini* ; 12–13, *Pliomys episcopalis* en vues occlusale et linguale ; 14, *Iberomys huescarensis* ; 15–18 : niveau TD4, *Mimomys savini* en vues occlusale (15–17) et linguale (18).

while in the former works, we used the evolutionary stages of selected arvicoline rodents from TG-TZ (Cuenca-Bescós et al., 1999a, 2014a, 2014b) (Fig. 7).

In the light of the refinement made possible by the Unitary Associations method, we here discuss the Faunal Units (FU) of Atapuerca and the biozones of the continental biostratigraphy of the Iberian Peninsula, and compare with the European biochronology (Fig. 7).

4.1. Faunal Unit 1 = Allophaiomys lavocati Biozone

Atapuerca Faunal Unit 1 (FU1), the *Allophaiomys lavocati* Biozone, does not change from our earlier proposal. This unit is characterized by the first presence of *Homo* in western Europe, in Spanish localities such as Barranco Leon D and Sima del Elefante TE9 (Agustí et al., 2015; Carbonell et al., 2008; Toro-Moyano et al., 2013).

4.2. Faunal Unit 2+ Faunal Unit 3 = Victoriamys chalinei Biozone

The species *V. chalinei* was formerly classified as *Allophaiomys chalinei* (see Cuenca-Bescos et al., 2015). In Atapuerca, this biozone is characterized by the association of the species *Homo antecessor* from the Early Pleistocene of Europe (Bermúdez de Castro et al., 1997), as well as large

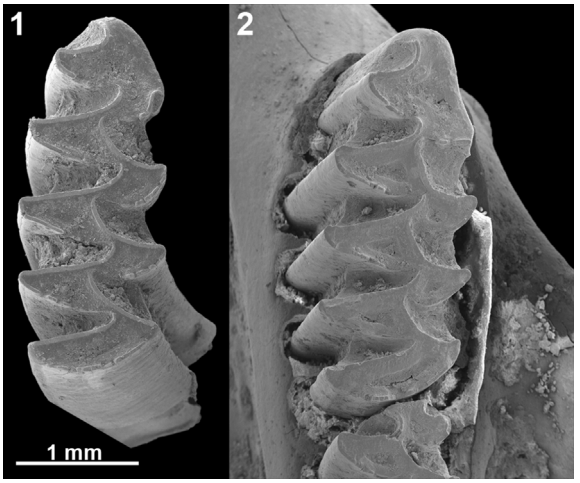

Fig. 6. Selected specimens of rodent taxa from the Pleistocene of Atapuerca, Sima del Elefante, upper levels (TEURU). 1, 2, *Iberomys mediterraneus*: 1, right isolated m1 from level TE18; 2, right mandible with m1, m2 from level TE19 (only the anterior part of m2 is seen in the picture).
Fig. 6. Spécimens sélectionnés de rongeurs des niveaux supérieurs du Pléistocène d'Atapuerca, Sima del Elefante (TEURU). 1, 2, *Iberomys mediterraneus* : 1, m1 droite isolée du niveau TE18 ; 2, mandibule droite avec m1, m2 du niveau TE19 (seulement la partie antérieure de m2 est visible sur l'image).

mammals that characterize the late Early Pleistocene in Spain and other parts of western Europe in general, designated the Villafranchian and/or Epivillafranchian by the authors (Kahlke et al., 2011; Rook and Martínez-Navarro, 2010).

4.3. Faunal Unit 4+ Faunal Unit 5a = unnamed Biozone

The statistical analysis splits what was formerly FU5 into two: FU5a and FU5b. FU4 and FU5a are in the same, yet unnamed Biozone, with its upper limit demarcated by the LAD of *Dolinasorex glyphodon, Terricola arvalidens* and *Microtus seseae* and the FAD of *Microtus ratticepoides* (Figs. 1 and 7). No characteristic taxa in this biozone for the moment.

4.4. Faunal Unit 5b = Microtus ratticepoides Biozone

FU5b, the *Microtus ratticepoides* Biozone, represents the upper part of what was formerly FU5 in Cuenca-Bescós et al. (2010). It is defined here for the first time. This biozone is represented by the lower part of layer TD8 of Gran Dolina, which is TD8a or the TD8 lithostratigraphic unit in Rodríguez et al. (2011). It includes the FAD and LAD of the species *Microtus ratticepoides*, and the LAD of *Terricola arvalidens* and *Microtus seseae*. We are aware of the poor resolution of these taxa, making further systematic paleontological studies necessary. It is interesting to note that the limit between FU5a and FU5b coincides with the Matuyama-Brunhes magnetostratigraphic reversal (see Rodríguez et al., 2011: Fig. 4). Therefore, FU5b represents the first biozone of the Middle Pleistocene in Atapuerca. The large-mammal association of FU5b is also unique; it presents a high ungulate carrying capacity and has the largest number of ungulate species among the Atapuerca sites (Rodríguez et al., 2014).

4.5. Faunal Unit 6a = Iberomys mediterraneus Biozone

The species *Iberomys mediterraneus* was formerly classified as *Iberomys brecciensis* (see Cuenca-Bescós et al., 2014a, 2014b) for a recent taxonomic revision of the *Iberomys* species). This biozone clusters the sites with the largest and longest human presence in Atapuerca, such as the hominid accumulation site of SH (Arsuaga et al., 2014) and the hominid occupation site of TD10 (Ollé et al., 2013). We classify the fossil human remains from SH as *Homo* sp. (Arsuaga et al., 2014, 2015; Sala et al., 2015).

4.6. Faunal Unit 6b = Unnamed Biozone

This corresponds to stratigraphic units GII and GIII of the site TG-TZ (Demuro et al., 2014 and literature therein). Further studies will probably allow a better definition of this biozone.

4.7. Faunal Unit 6c = Clethrionomys glareolus Biozone

We give a redefinition of the upper part of the former *Iberomys mediterraneus* Biozone. Its lower limit is the FAD of the species *Clethrionomys glareolus*. The extant bank vole is slightly different from the extinct *C. acrorhiza* present in the FU6a, in SH (see supplementary info in Arsuaga et al., 2014). This biozone is represented in Atapuerca by the upper levels of the TE section, TEURU (TE18 and TE19), which also have the lowest ungulate carrying capacity of the Atapuerca sequence (López-García et al., 2011; Rodríguez et al., 2014).

4.8. Faunal Unit 7 = Iberomys cabrerae Biozone

As in the work of Cuenca-Bescós et al. (2014a, 2014b), FU7 represents the Late Pleistocene of the Atapuerca sequence. To date, we have studied only the Late Pleistocene layers of Portalón, though the site of Galeria de las Estatuas also contains Late Pleistocene faunas which may fit well into this biozone (work in preparation).

4.9. Faunal Unit 8 = Terricola lusitanicus? Biozone

FU8 is a new addition to the biostratigraphy of Atapuerca. Still in progress, it is the result of preliminary studies of the Chalcolithic (Holocene) layers of the Portalón sequence (Ordiales et al., 2014). The most characteristic event of this FU is the appearance for the first time of the species *Terricola lusitanicus*, though we need more paleontological studies to be able to provide a definition of this unit. The estimated age of the Chalcolithic layers of Portalón follows Alday et al. (2011) (Fig. 7).

Atapuerca Sequences	Atapuerca Levels	Former Atapuerca FU	Biozones & significative species, this work	Atapuerca FU this work	Radiometric ages Ma	Europe	FAD/LAD
PORTALON	PortAct		Present day fauna	9	0.00	Present	
	ATPCalc		*Terricola lusitanicus*	8	0.003-0.0026	Holocene	
	ATPPle	7	*Iberomys cabrerae*	7		Late Early Pleistocene	F *I. cabrerae*
TEURU	TEURU		*Clethrionomys glareolus*	6c		*Clethrionomys glareolus*	F *C. glareolus*
TG-TZ	TG III TZ		Unnamed	6b	0.240	Middle Pleistocene fauna	
	TG II				0.313		
TDUP	TD 10-11	6			0.337-0.418		
SH	SH		Iberomys mediterraneus -middle Ple Homo	6a	0.434	Cromerian Complex	F *I. mediterraneus, Arvicola* cf. *sapidus*
TDUP	TD9(=TD 8b)						
TDLOW	TD 8a	5	*Microtus ratticepoides*	5b	0.611	Bavelian / Early Cromerian	L *Mimomys savini*
	TD 7		Unnamed	5a	0.780		
	TD 6-1	4		4			L *D. glyphodon, S. gregaloides*
	TD 6-2-3	3		3	0.851-0.833	Villafranchian/ Epivillafranchian transition	
	TD 5	2	*Victoriamys chalinei* FAD and LAD of *Homo antecessor*	2			F, L *V. chalinei, F. Mimomys*
	TD 3-4						
TELRU	TE14						
	TE13						
	TE12						
	TE11	1	*Allophaiomys lavocati* (First Appearance *Homo* sp. Ple Eu)	1		Villafranchian Pirro Nord Colle Curti	L *Allophaiomys* species, *Castillomys* species,
	TE10						
	TE9				1.2		
	TE8						
	TE7						

Fig. 7. Correlation chart for the sequences, levels (or stratigraphic units), and Faunal Units (FU) of Atapuerca. The European biochronology from Rook and Martínez-Navarro (2010), Kahlke et al. (2011).
Fig. 7. Tableau de corrélation pour les séquences d'Atapuerca, les niveaux (ou unités stratigraphiques) et les Unités fauniques de Atapuerca (FU). Biochronologie européenne de Rook et Martínez-Navarro (2010), Kahlke et al. (2011).

4.10. Faunal Unit 9 = ? Present-day fauna Biozone

FU9 is a new addition to the biostratigraphy of Atapuerca. It comprises the present-day fauna of the Sierra de Atapuerca represented in the assemblage of the owl pellet remains from a *Tyto alba* lair in the entrance to the cave of Portalón. We need a broader sample of the small mammals living today in the Sierra de Atapuerca and the surrounding area in order to decide the best rodent taxon for naming FU9. We are aware that the definition of biozones with present-day fauna is not usual, though it serves for comparison and statistical analysis.

4.11. Correlation with the European chronology

Quantitative or semi-quantitative methods for studying the biostratigraphy of the terrestrial assemblages of the Pleistocene of Europe are not yet in common use. Graphical correlation has been applied to the biostratigraphy of Spain and other regions in northern, central, and southern Europe (Agustí et al., 2015; Nadachowski et al., 2011; among others), though there is a need for a full statistical work of correlation and study. Therefore, we do not here seek to emend the existing biostratigraphy of Europe; the following paragraphs are merely a guide for correlating the Atapuerca biozones with the European biochronology. See Table and Fig. 7.

FU1: on the basis of the PAMs for the small mammals of Atapuerca FU1 and including other Spanish localities of late Early Pleistocene age (Agustí et al., 2009, 2015; Cuenca-Bescos et al., 2015; García et al., 2014; Madurell-Malapeira et al., 2010; Minwer-Barakat et al., 2011), there can be seen to be a correlation between FU1 (TELRU levels) and levels D3 of Vallparadis, Barranco Leon D, and Fuente Nueva 3. In Italy, this FU1 may be similar to the Pirro and Colle Curti FU of Kotsakis et al. (2003).

FU2, *FU3*, *FU4* and *FU5a* are typical of the late Early Pleistocene in Spain, and also in western Europe in general, where they are known as the Villafranchian and/or Epivillafranchian (Cuenca-Bescós et al., 2013, 2015; Kahlke et al., 2011; Rook and Martínez-Navarro, 2010).

The limit between FU5a and FU5b represents the Early-Middle Pleistocene transition. The faunal record shows a significant response to climatic and environmental change representing a major faunal turnover, namely the

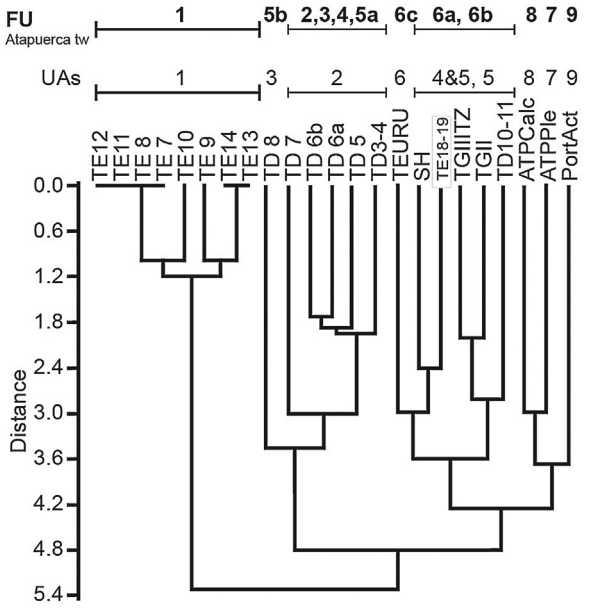

Fig. 8. Phenogram from the cluster analysis (UPGMA algorithm) of the stratigraphic layers of Atapuerca on the basis of their pairwise similarity in composition of small-mammal species.
Fig. 8. Phénogramme résultant du « cluster analysis » ou analyse par regroupements (algorithme UPGMA) des couches stratigraphiques d'Atapuerca, sur la base de leur similitude dans la composition d'espèces de petits mammifères.

transition from Villafranchian to Galerian mammal ages (Blain et al., 2012; Head and Gibbard, 2005).

FU5b: this is still too poorly known to be correlated accurately with a European assemblage. It represents the LAD of *Mimomys savini*, and the FAD of advanced *Microtus*, which may relate this FU with the faunas of Pakefield and Happisburgh in the United Kingdom (Parfitt et al., 2005, 2010) or the faunas of the Bavelian and Early Cromerian in central Europe (Maul and Markova, 2007).

FU6a: this is equivalent to the faunas with the earliest *Arvicola* species in Europe, such as Isernia in Italy (Kotsakis et al., 2003), and Cullar de Baza 1 in Spain (Ruiz Bustos, 1988). The transition between the LAD of *Mimomys* and the FAD of *Arvicola* is well represented in the faunas of the "Cromerian Complex" and in the succession of Kärlich in central Europe (Kolfschoten and Turner, 1996; Nadachowski et al., 2011).

FU6b: FU6b has primitive *Arvicola* sp. and the species *Iberomys mediterraneus*. It may be correlated with Middle Pleistocene faunas such as Orgnac 3 (Cuenca-Bescós et al., 2014b).

FU6c: it represents the end of the Middle Pleistocene in Atapuerca. It may be equivalent to the faunas with *Clethrionomys glareolus* in central and eastern Europe (Maul and Markova, 2007).

FU7: this has faunas typical of the Late Pleistocene of the Iberian Peninsula, which is different from that of central and eastern Europe. This is because the Iberian Peninsula was a place of refuge for European faunas during the Late Pleistocene (López-García et al., 2010a).

FU8: this represents the Holocene in the Sierra de Atapuerca as well as in the rest of the Iberian Peninsula and part of the Southwest of Europe (Cuenca-Bescós et al., 2009; Ordiales et al., 2014; Rofes et al., 2013; Villa et al., 2010).

FU9: present. This represents the fauna living today in the Sierra de Atapuerca and in the greater part of northern Spain (Palomo and Gisbert, 2005).

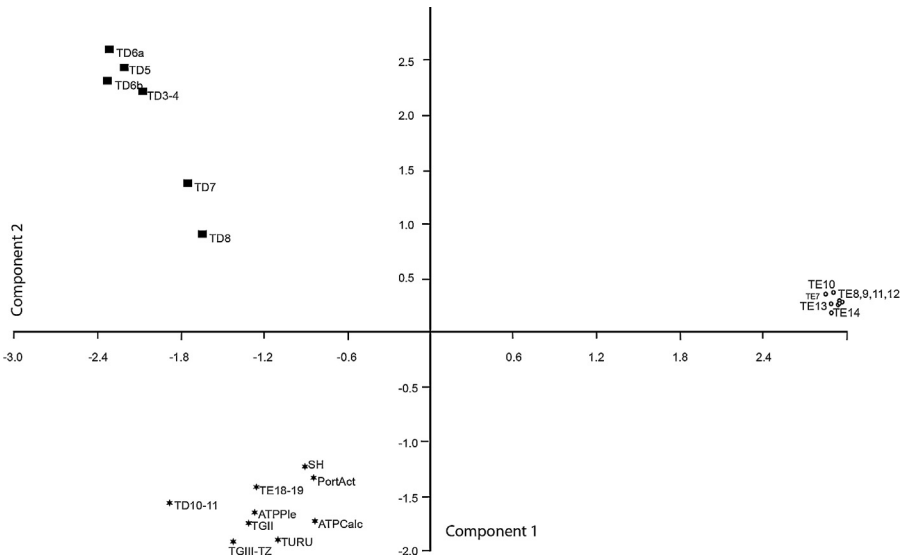

Fig. 9. Principal component analysis (PCA) showing plots of components 1 against 2. See Fig. 7 and text for abbreviations of each stratigraphic unit.
Fig. 9. Analyse en composantes principales (ACP) montrant les points représentatifs des composantes principales 1 en regard de ceux des composantes principales 2. Voir la Fig. 7 et texte pour les abréviations de chaque unité stratigraphique.

5. Conclusions

Five caves from the Sierra de Atapuerca contain stratigraphic sequences with rich, diverse, and well-preserved vertebrate fossils. The stratigraphic sections of these sites represent major parts of the continental Pleistocene and Holocene of north-central Spain.

We have revisited the taxonomic list of small vertebrates recovered since 1990 from these five localities. New taxa have also been discovered in this time. Small vertebrates from the sites have been added and revised continuously; some are still in revision. The vertebrate fauna of the Pleistocene sites from the Atapuerca caves is dominated by microvertebrates.

On the basis of our paleontological and biostratigraphic studies, we have established a 23×64 Presence-Absence Data Matrix (PAM), where the 64 small-mammal taxa are distributed along the diachronic, stratigraphic sequence of the 23 levels of the Atapuerca composite section.

The PAM of the small-mammal succession obtained from the composite diachronic sequence of Atapuerca is analysed using the UA quantitative method, a first among biostratigraphic studies of Atapuerca. Statistical analysis of the small mammals from Atapuerca has made it possible to refine what is known of the local biochronological sequence of FUs defined to date.

Nine FUs have been defined; five of these are new, and the former FU5 and FU6 are further divided in two and three subunits respectively. With the upgrading performed here, the FUs from Atapuerca provide a robust biostratigraphic foundation for correlations both among the stratigraphic sequences of the five localities from Atapuerca and with other localities in the Iberian Peninsula and Europe.

Acknowledgements

We gratefully acknowledge the exchange of opinions with Oyvind Hammer (Paleontological Museum, University of Oslo) and Jean Guex (University of Lausanne). The excavation campaigns and the sorting of material were supported by the Junta de Castilla y León, the Fundación Atapuerca, the MINECO project CGL2012-38434-C03-01, the Fundación de Atapuerca, and the H54_Grupos consolidados del Gobierno de Aragon and the Fondo Social Europeo (European Social Fund). We gratefully acknowledge the work of the Atapuerca team in extracting the sediments with the microfossils, especially the leaders J.M. Bermúdez de Castro, E. Carbonell and J.L. Arsuaga, and the main persons responsible for excavation at each site, Andreu Ollé, Jesús Rodríguez, Jordi Rosell, Rosa Huguet, Isabel Cáceres, and José Miguel Carretero, especially for their fruitful comments in the field. J. Galán and C. Núñez-Lahuerta are the recipients of a Ph.D. fellowship from the Gobierno de Aragon (DGA). Thanks to the referees for their useful and interesting comments, which have improved this article. Finally, to Rupert Glasgow who revised the English texts.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2015.09.006.

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