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Introduction

Quaternary small vertebrates: State of the art and new insights

1. Introduction to this special issue

During the last three decades, studies of small vertebrates (rodents, insectivores, bats, birds, reptiles, amphibians and fishes) have increased notably, and have progressively overflowed from specialized journals to find their place in general and multidisciplinary scientific journals.

For the first time, a volume dedicated to Quaternary small vertebrates is presented in *Quaternary Science Reviews*. This volume is the result of the symposium on Quaternary small vertebrates ("*Quaterposium*") held at the last EAVP (European Association of Vertebrate Palaeontologists) Congress, celebrated in Lisbon from 26th June to July 1, 2018, in which some thirty specialists from Africa, Asia and Europe participated with oral communications and/or posters.

Our goal was to make the point about studies of Pleistocene and Holocene microvertebrates in order to deepen what is known of each of the studied taxonomical groups but also to face the new challenges posed by multidisciplinary studies of archaeological sites, and their contributions to the debate about climate change and biodiversity. As a result of their reduced size, small habitat ranges and in most cases low mobility, small vertebrates are known to be more susceptible to regional changes than large mammals and plants, especially in Europe where mountain ranges and sea barriers block their retreat to the south. Among the microvertebrates, rodents are known to be the best tools for biochronological, biostratigraphic and palaeoecological reconstructions. Amphibians and reptiles also have an increasing reputation in the context of palaeoclimatic and palaeoenvironmental analyses, especially for periods such as the Early and early Middle Pleistocene, where almost all of the herpetofaunal species have current analogues but the small mammals (especially rodents) progressively include more extinct species, with uncertain ecology. In addition, an increasing number of researchers have become increasingly more interested in other groups of small vertebrates, such as shrews, bats, birds or fishes, and in the palaeoecological data they can furnish for Pleistocene sites.

Little by little, new studies are enlarging the field of work to include peripheral areas of the European continent such as the Near East, the Middle East and North Africa. In such cases, the main task is the description of the species represented in these fossil assemblages, and there remain many species still undescribed osteologically. A comparison of modern atlases and osteological knowledge reveals that only 10–20% of the species living in satellite areas of Europe have been described from an osteological point of view and in most cases, only on the basis of a few specimens, i.e. without taking into account intraspecific variability.

In the field of human palaeoecology, small vertebrates provide important information for studies of the archaeological sites that document early hominin dispersals out of Africa, hominin activities in response to Middle Pleistocene glacial/interglacial dynamics, and the climatic dynamics that influenced the last Neanderthals and the first anatomically modern humans (AMH) during the Middle to Upper Palaeolithic transition.

Another rising issue is how far small vertebrate palaeontology can help with modern conservation biology or predict future based on long-term biodiversity archives. In general, knowledge of the small vertebrate Quaternary record can help better understanding of current extinction dynamics, response to climatic changes or ecological turning points. Key parameters, such as size, growth or diet, can also be investigated in the past and may bring further arguments to ecological theories such as the temperature–size rule (Bergmann's Rule), the heat-balance or the starvation resistance hypotheses and ecosystem resilience. Zooarchaeological data has sometimes also been applied in the categorization, as native, of certain endangered or extirpated taxa, leading to their subsequent reintroduction. In contrast, apparent absence of a species in the fossil record has led to their categorization as invasive, leading to a policy of extermination. In more recent times, human disturbance of biodiversity or of particular groups of vertebrates, which may cause extinction or extirpation and be a factor in the introduction of new species, is documented during the Holocene, for example the occurrence of commensal and anthropophilic species from the Neolithic to the Bronze and Copper Ages.

Finally, taking advantage of synergies with other disciplines, small vertebrate studies are progressively incorporating new methodologies such as ancient DNA extraction, oxygen isotope studies or geometric morphometrics, and introducing computer science and more complex modelling into their analyses. These types of studies very much complement, but do not replace, fundamental methods in osteological and morphometric description.

We felt the time had come to present in a single volume the multiplicity of approaches that have been pursued in the last 30 years, and to summarize and propose new solutions to old problems using new methodologies and tools (such as geometric morphometrics, GIS, microwear or skeletochronology).

1.1. New insights from ancient DNA, isotopes and modelling

The four papers in this thematic block present new approaches and methodologies applied to small vertebrate studies.

The first paper (Markova et al., 2020) studies the consequences of population bottlenecks for dental phenotypes in the Arvicolinae subfamily (genus *Dicrostonyx*, *Lemmus*, *Myopus* and *Microtus*). The comparative morphological analysis of the extant representatives of these genera reveals similar phenotypic shifts, surviving

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bottlenecks in captivity or in the areas favouring genetic drift (coastal zones and islands, patchy landscapes in mountainous areas, declining peripheral populations). The application of the results to the fossil record of *Dicrostonyx* (collared lemmings) from northwestern Siberia show periods of genetic drift in the ancestral forms of these lemmings in the late Middle and early Late Pleistocene.

The second paper (Baca et al., 2020) uses ancient DNA to investigate the impact of the abrupt climate changes that occurred during the Late Glacial and the Pleistocene/Holocene transition on common vole (*Microtus arvalis*) populations in Europe. The mtDNA cytochrome *b* gene is analysed from more than one hundred common vole specimens from 36 archaeological and/or palaeontological sites across Europe, showing that at mid and high latitudes, these vole populations underwent local extinctions and that at low latitudes, there was continuity in the common vole populations. These data show variations in the response of *Microtus arvalis* populations to climatic and environmental changes across Europe and corroborate the hypothesis of significant impact on populations of abrupt climate changes.

The third manuscript (Fernández-García et al., 2020) presents a palaeoenvironmental and palaeoecological reconstruction with complete taphonomic analyses based on the small mammal assemblage of the Abric Romaní (Capellades, Barcelona, Spain) rock shelter sequence. Oxygen isotope analyses were performed on rodent incisors from the site, showing that climatic conditions were globally cooler and slightly wetter than at present in northeastern Iberia, but fairly stable across the Late Pleistocene sequence.

The last article in this block (Fagoaga et al., 2020) seeks to improve the accuracy of small vertebrate palaeoclimatic reconstructions derived from the mutual ecogeographic range (MER) method, using the uncertain distribution area (UDA) − occupied distribution area (ODA) discrimination methodology as applied to stratigraphic Unit Xb and Upper Unit V from el Salt (Alcoi, Valencia, Spain). This methodology proves to be more accurate for palaeoclimatic reconstructions, showing significant differences between the climatic values provided by MER and the UDA-ODA discrimination methodology. The paper also shows that the discrimination analysis makes it possible to work with species whose distribution is currently disturbed, which was not possible using the MER method.

1.2. Investigating biotic responses to climate changes

The four papers in this section examine the response of particular small vertebrate taxa or groups of taxa to the climate changes that occurred during the Quaternary.

The first paper (Montuire et al., 2020) assesses the climate-driven changes through time undergone by the genus *Dicrostonyx* (collared lemming), which is a species adapted to the extreme conditions of the Arctic environment. Using geometric morphometrics to analyse shape changes in the lemming molars over the last 100,000 years, the associations with dispersal events in Western Europe are evaluated. The resulting temporal and geographical trends might relate to the different migratory pulses also documented from ancient DNA haplotypes.

The second paper (Luzi and López-García, 2020) analyses the variations in relative size of the first lower molar (m1) of the common vole *Microtus arvalis* and the field vole *Microtus agrestis* from three long sequences of Late Pleistocene age: Fumane cave (in Italy) and El Portalón and l'Arbreda caves (in Spain). Relative size is quantified using the Lagr/Larv index, in an attempt to link the changes in index values to the climatic fluctuations of Marine Isotope Stages 3 and 2 and comparing these values with the previous palaeoenvironmental and palaeoclimatic reconstructions carried out at the studied sites. The study thus shows the Lagr/Larv index to be a potentially useful tool for identifying climatic oscillations and changes between humid/dry conditions in southwestern Europe.

The third manuscript (Lozano-Fernandez et al., 2020) highlights the relevance of the fossil arvicoline *Mimomys savini* as a tool for reconstructing the chronology of the first arrival of hominin populations and their expansion across the European continent. This study seeks to shed further light on the evolution of this small mammal species by examining morphological changes in the first lower molars (m1), using 2-D geometric morphometric analysis based on landmark configurations applied to specimens from three Early Pleistocene Iberian sites: Gran Dolina (Atapuerca, Burgos), Barranco León (Orce, Granada) and Barranc de la Boella (la Canonja, Tarragona). The results show a set of differences in the shape of the occlusal surface between the more recent and the older populations, with the m1 length and width also increasing during the evolution of the species, and the size of the occlusal surface decreasing. This comparison of the shape and size of the studied populations reinforces previous proposals for the age of Barranc de la Boella, suggesting a similar age to that of Gran Dolina (section TD6-TD5), between 1 Ma and 0.77 Ma.

The last paper in this block (Berto et al., 2020) helps clarify numerous aspects of small mammal communities from 51 Late Pleistocene sites in the Italian Peninsula, using a georeferenced database to investigate the species range distribution and evolution of these small mammal communities. Since the early Late Pleistocene, the Italian Peninsula has been divided into two biotic macroregions: the northern Italian Peninsula and the southern Italian Peninsula; major oscillations corresponding to Dansgaard-Oeschger (DO) cycles and Heinrich Events (HE or H) are identified in both macroregions. The Lateglacial (Bølling-Allerød) Interstadial can also be considered a period of major faunal renewal in the Italian Peninsula. Finally, the Italian small mammal communities follow the same general path recognized in Mediterranean Europe as a whole during the Late Pleistocene. Mainly characterized by differences in the expansion of taxa from eastern Europe related to mountain barriers and by the lack of this kind of species in south areas of southern Mediterranean peninsulas, which it is offset by the presence of endemic species.

1.3. Understanding the long-term human influence/disturbance

The two papers in this thematic block explore the interaction between human populations and small vertebrate communities during different time periods in the Quaternary.

The first paper (Galán-García et al., 2020) discusses the variations observed in fossil bat communities through the Early and Middle Pleistocene sequences of the Sierra de Atapuerca (Burgos, Spain) with relation to palaeoclimatic and palaeoenvironmental fluctuations and the intensity of hominin activities inside the cave. The results show a marked deterioration in the Sierra de Atapuerca chiropteran faunas that occurred from 500 ka onwards, coinciding with a succession of extreme cold events during glacial periods, but also with the intensification of human occupation. Also, some features of the bat assemblages in these levels, such as the differences in species composition between synchronous levels, suggest that anthropic disturbance could have played a significant part in the decline of the Middle Pleistocene bat palaeocommunities of the Sierra de Atapuerca.

The second manuscript (Domínguez García et al., 2020) provides new evidence from the Castillejo del Bonete (southeastern Spain) site sequence for a reconstruction of the biogeographical history of certain small mammals recently introduced to western Europe. The results show the relative abundance of the western

Mediterranean mouse (*Mus spretus*), present at a few sites in these early Holocene localities. Its occurrence suggests that this species did not colonize southwestern Europe until the Late Neolithic. Also, the absence of both the black rat (*Rattus rattus*) and the Etruscan shrew (*Suncus etruscus*) is in agreement with previous hypotheses that support the idea that the Iberian Peninsula was colonized by these two species at a more recent date.

1.4. New perspectives in regional synthesis

In this last thematic block, regional syntheses on Quaternary small vertebrate assemblages from North Africa and Central Europe are presented in two manuscripts.

The first paper (Stoetzel et al., 2020) provides a synthesis of the recent advances in Quaternary microvertebrate studies from North Africa, which is recognized as a hotspot of biodiversity and a major area for both human and faunal evolution. The results show that small vertebrate studies are increasingly adopting an integrated approach combining archaeology, palaeontology, (palaeo)genetics, taphonomy, palaeoecology and systematics, and using new methods such as geometric morphometrics and isotopic analyses on both fossil and modern specimens. The paper also shows how recent multidisciplinary studies have provided new perspectives on, and evidence for, the respective influences on evolution of climate change and increasing human pressure.

Finally, the last paper in this special issue (Jovanovic et al., 2020) reviews herpetofaunal studies in Serbia, producing new palaeoenvironmental and palaeoclimatic data and examining how climate change affected the amphibians and reptiles during the last part of the Late Pleistocene. This geographical territory is of particular interest thanks to its location within the Balkan Peninsula, which represents a crossroads for many dispersing species. Most of the studied sites can be related to the final part of the Late Pleistocene, and even though there still remain many chronological uncertainties regarding the precise attribution of the different layers from the three main Serbian caves that have delivered rich assemblages of small vertebrates, the authors integrate their palaeoenvironmental data within the Mousterian-Aurignacian-Gravettian chrono-cultural succession, i.e. from Marine Isotope Stages 5 to 2. The overall analysis reveals that the herpetofaunal composition underwent substantial changes between MIS 3 and MIS 2, which saw both a loss of diversity and the coexistence of species adapted to cold climates and environments.

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