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## The geographical and chronological pattern of herpetofaunal Pleistocene extinctions on the Iberian Peninsula

*Patron géographique et chronologique des extinctions herpétofauniques durant le Pléistocène dans la péninsule Ibérique*Hugues-Alexandre Blain<sup>a,\*,b</sup>, Salvador Bailon<sup>c,d</sup>, Jordi Agustí<sup>e,a,b</sup><sup>a</sup> IPHES, Institut català de Paleocologia Humana i Evolució Social, c/Marcel·lí Domingo s/n (Edifici W3), Campus Sescelades, 43007 Tarragona, Spain<sup>b</sup> Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain<sup>c</sup> MNHN, CNRS, « Histoire naturelle de l'Homme préhistorique », UMR 7194, Sorbonne universités, 1, rue René-Panhard, 75013 Paris, France<sup>d</sup> UMR 7209, « Archéozoologie, archéobotanique : sociétés, pratiques, environnements », Sorbonne universités, MNHN, CNRS, 55, rue Buffon, CP 55, 75005 Paris, France<sup>e</sup> Institut Català de Recerca i Estudi Avançat (ICREA), Barcelona, Spain

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## ABSTRACT

Despite the postulation of the “herpetofaunal stability hypothesis”, which suggests that the herpetofauna underwent relatively few changes during the Pleistocene, the amphibian and squamate faunas of western Europe are known to have progressively diminished during the Pliocene and the beginning of the Pleistocene. Iberian Early Pleistocene sites continue to document the presence of “exotic” herpetofaunal elements that are supposed to have disappeared from the mainland, such as Oriental vipers, agamid lizards, the anguids *Pseudopus* and *Dopasia*, and a representative of the green toad group (*Bufo viridis* sensu lato), as well as possibly gekkonids, a scincid lizard (Lygosominae), the anguid *Ragesaurus* and blind snake (Scoleophidia). The geographical and temporal pattern of these progressive southward withdrawals and extirpations on the Iberian Peninsula shows that extirpation events occurred in northern Spain at roughly the Olduvai paleomagnetic event and in southern Spain just before the Jaramillo paleomagnetic reversal, thus permitting us to establish a framework that can be used to complement the biochronological zonation of the Iberian Early Pleistocene.

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## R É S U M É

Malgré le postulat de l'*herpetofaunal stability hypothesis*, qui suggère que l'herpétofaune fossile n'a subi que relativement peu de changements durant le Pléistocène, les faunes d'amphibiens et de squamates d'Europe occidentale sont connues pour s'appauvrir progressivement durant le Pliocène et le début du Pléistocène. Les sites du Pléistocène inférieur de la péninsule Ibérique documentent encore la présence de taxons « exotiques » supposés avoir disparu d'Europe occidentale, comme les vipères orientales, les agamidés, les anguidés

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*Pseudopus* et *Dopasia*, ainsi qu'un représentant du groupe des crapauds verts (*Bufo viridis* sensu lato), auxquels se rajoutent probablement des gekkonidés, un scincidé de type lygosominé, l'anguidé *Ragesaurus* et un serpent scolécophidien. Le patron géographique et temporel de ces régressions progressives vers le sud et extinctions locales dans la péninsule Ibérique montre que ces événements prennent place approximativement durant le chron paléomagnétique d'Olduvai pour le Nord de l'Espagne et juste avant l'inversion paléomagnétique de Jaramillo, permettant ainsi d'établir un cadre pouvant être utilisé comme complément pour la zonation biochronologique du Pléistocène inférieur ibérique.

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## 1. Introduction

In ecology, *extirpation* denotes local disappearance of a taxon, in which it ceases to exist in the chosen area of study, but may still exist elsewhere. This phenomenon is incorrectly called “local extinction”, because “extinction” can only be used when the last known individual of a lineage disappears. Since the 1960s, declines in amphibian and reptile populations, including population crashes and mass extirpations, have been noted in locations all over the world (e.g. Houlahan et al., 2000; Pounds et al., 2006; Stuart et al., 2004). These declines are perceived as one of the most critical threats to global biodiversity, and several causes are believed to be involved, including disease, habitat destruction or modification, exploitation, pollution, pesticide use, introduced and invasive species, and ultraviolet-B radiation (UV-B). In the Pleistocene, when the influence of humans on the environment is assumed to be much less extensive than it is today, the extinction of small vertebrates is usually linked to climate changes (and their associated habitat destruction and fragmentation) and/or competition with (and consequent exclusion from) new emigrants.

Global climate change affects organisms in all biomes and ecosystems. Two natural compensatory responses are possible. Given enough time and dispersal opportunities, species may shift to more favorable thermal environments, or they may adjust to new environments by behavioral plasticity, physiological plasticity, or adaptation. Alternatively, failure to adjust or adapt culminates in demographic collapse and extinction (Sinervo et al., 2010).

As small amphibians and reptiles usually have poor dispersal abilities or strong attachments to a limited territory, major changes in population structure may therefore be more confidently attributed to the effects of environmental change. Moreover, the metabolic processes of most amphibians and squamates are linked to environmental temperature (e.g. Zug et al., 2001) and consequently, climate shifts to colder conditions may reduce their dispersal abilities even further.

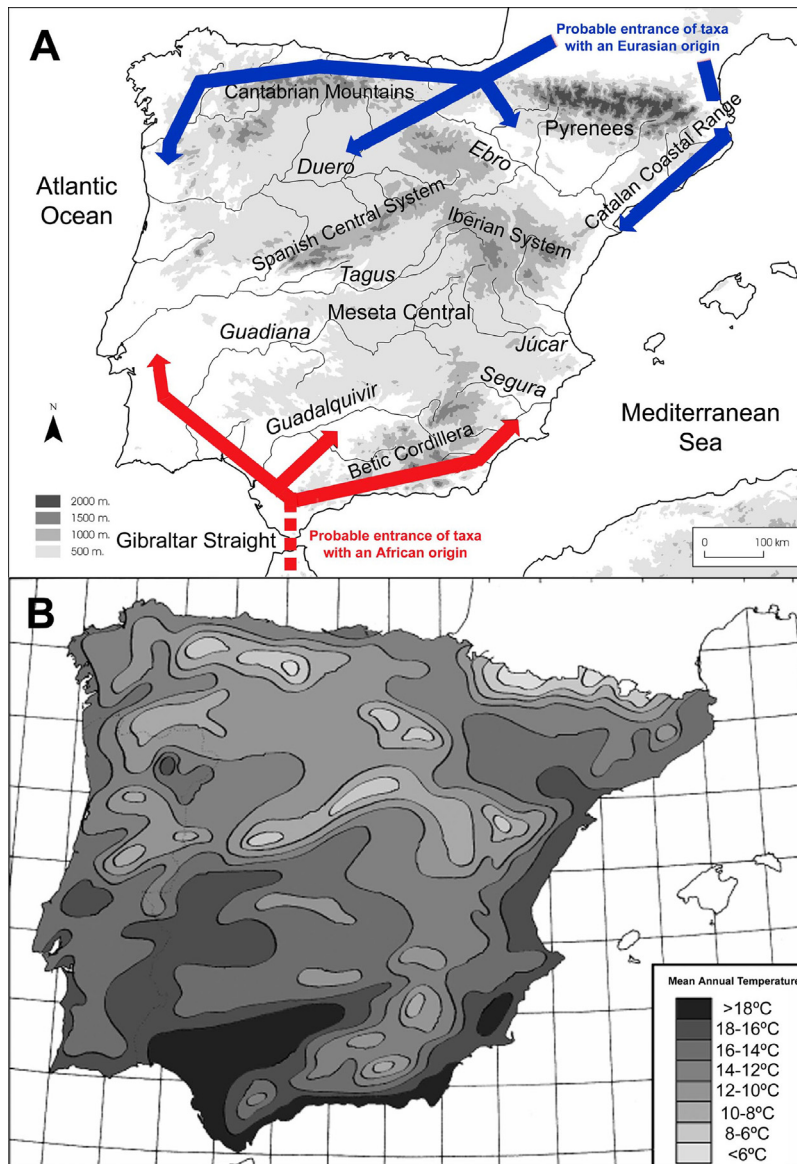
Despite profound ecological and climatic changes during the Quaternary period, several authors have shown that relatively few extinctions (and extirpations?), no appearances of new species, and few range adjustments occurred among the fossil herpetofauna in North America (Auffenberg and Milstead, 1965; Brewer, 1985; Holman, 1991, 1995) and by extension in Europe (Holman, 1989, 1998, 1999) during the last 1.8 or 1.6 Ma (depending on the definition of the beginning of the Early Pleistocene

used). This has been called the “herpetofaunal stability hypothesis” (Bell et al., 2010). Nevertheless, as emphasized by Holman (1998, 1999), geographical/orographical differences between North America and Europe may explain greater rates of extinction and extirpation for the European herpetofauna, like the presence of a marine barrier (the Mediterranean Sea) in Europe as opposed to the terrestrial continuity of North America (like the Mexican Altiplano as a possible refuge area), as well as the different orientation of the main mountain ranges (north-south in North America, like the Rockies and Appalachians, as opposed to west-east in Europe, like the Alps, the Pyrenees, and the Balkans).

In western Europe, amphibian and squamate populations are known to have progressively declined during the Pliocene and the beginning of the Pleistocene (here considered to begin at 2.6 Ma), probably associated with the intensification of glaciation pulses in the northern hemisphere (e.g. Bailon, 1991; Bailon and Blain, 2007; Blain, 2005, 2009; Rage, 2013). At the end of the Ruscinian stage (ca. 3.2 Ma), the tropical families Varanidae, Aniliidae s.l. and Elapidae disappeared. At the end of the Early Villanyian (the current boundary between Pliocene and Pleistocene, at ca. 2.6 Ma), Erycinae (Boidae) disappeared from this area, whereas during the same period, other thermophilous groups (Agamidae, Blanidae, some Anguidae, some Colubridae and oriental vipers) underwent a southward withdrawal. The last “exotic squamates” assumed to have disappeared from western Europe were the Agamidae and the anguid *Dopasia* (at the end of the Early Pleistocene, ca. 1.1 Ma). As far as amphibians are concerned, a representative of the green toad group (*Bufo viridis* s.l.), possibly linked to the Pliocene record, has been documented at the end of the Early Pleistocene (ca. 1.3 to 1.1 Ma). This work analyzes the geographical and temporal pattern of these progressive southward withdrawals and local extinctions on the continental mainland (i.e. islands have been excluded from this study) in order to establish a framework that can be used to complement the biochronological zonation of the Iberian Early Pleistocene.

## 2. Geographical and climatic setting

The Iberian Peninsula (Fig. 1), located in the extreme Southwest of the European continent, covers an area of approximately 582,000 km<sup>2</sup> and has an average elevation of some 660 m above sea level (Gil Olcina and Gómez Mendoza, 2001). It is bordered by the Mediterranean Sea to the east and by the Atlantic Ocean to the west, which come together in the Strait of Gibraltar in the south, separating



**Fig. 1.** (Color online). Geographical (A) and climatic (B: mean annual temperature according to Font Tullot, 2000) setting of the Iberian Peninsula, with indication of probable fauna arrival routes.

**Fig. 1.** (Couleur en ligne). Cadre géographique (A) et climatique (B : température moyenne annuelle selon Font Tullot, 2000) de la péninsule Ibérique, avec indication des probables chemins d'entrée de la faune.

the landmass from Africa. In the north, it is completely closed off from the European continent by the Pyrenees and their foothills, the Pre-Pyrenees. About three-quarters of the peninsula is covered by the Meseta Central, a vast plateau ranging from 610 to 760 m in elevation, ringed by mountains and containing the sources of most rivers, which find their way through gaps in the mountain barriers on all sides. The major rivers flow through the wide valleys between the mountain systems. In addition, there are three mountain ranges outside of this Meseta Central: the Pyrenees in the north, the Catalan Coastal Range along the north-east coast and the Betic Cordillera in the south. Two large basins are located between these external mountain ranges and the cordilleras that surround the Meseta:

the Ebro Basin in the north-east and the Guadalquivir Basin in the south.

Climatically, the Iberian Peninsula can be considered a mini-continent due to its large latitudinal range (between the parallels 36° and 44° N), its geographical position between Atlantic (temperate-cold) and African-Mediterranean (temperate-warm or subtropical) influences, and its complex orography (Font Tullot, 2000). There are several reasons for the climatic particularities of the Iberian Peninsula:

- it is located in the South of the temperate zone, so temperatures are warmer and days longer during the winter months;

- it is surrounded by seas, which means that large coastal areas enjoy mild temperatures with a less intense contrast between winter and summer and a mean annual temperature of over 14 °C;
- the peripheral distribution of its mountain ranges, most of them located near the coast and isolating the interior of the Peninsula, blocks the marine influence and causes colder winters and less rainfall;
- the mountain ranges in the West of the Iberian Peninsula create the areas with the highest mean annual precipitation (up to 2000 mm);
- the relatively high mean elevation of the Peninsula causes colder temperatures in the highest mountain ranges (Font Tullot, 2000).

This climatic and geographic background has a great influence on the modern distribution of flora and fauna on the Iberian Peninsula, with the presence of species adapted to aridity most common in the south and the presence of species adapted to humidity in the north. Moreover, from a biogeographical point of view, there are only two potential means of access to the Iberian Peninsula (Fig. 1): in the north, through the Pyrenees or along the coastal areas (as evidenced by the presence of Eurosiberian taxa in the northernmost part of the Iberian Peninsula), or in the south through the Strait of Gibraltar, a marine barrier with a width of 13 km at its narrowest point (as evidenced by the presence of taxa of African origin in the South and the South-east of the Peninsula, and vice versa). Finally to this modern complexity of the Iberian territory, the climatic oscillations characteristic of the Pleistocene (the last 2.6 my) and their correlative sea-level fluctuations may also have had a marked influence on the history of the fauna in this area, even if the Iberian Peninsula is often described as a refuge area for northern species during the glaciations.

### 3. The Pleistocene “exotic” herpetofaunal record in south-western Europe

Although Holman (1998, 1999) suggested that the “herpetofaunal stability hypothesis” can also be applied to the European Pleistocene (considered to begin at 1.64 Ma in these publications), some “exotic” taxa have been found at sites on the Iberian Peninsula (Fig. 2). These are mainly reptiles, such as anguid (*Pseudopus* and *Dopasia*) and agamid lizards. More recently, the presence of green toads (*Bufo viridis* s.l.) from the Iberian late Early Pleistocene (Blain et al., 2010a) has also been reported. Here, we will review the “exotic” taxa from the last 2.6 Ma recovered on the Iberian Peninsula.

#### 3.1. Oriental vipers

The genus *Vipera* sensu lato comprises about 30 species inhabiting northern Africa, Europe and Asia (Ananjeva et al., 2006). Traditionally, paleontologists draw distinctions between a number of groups within the genus *Vipera* s.l. on the basis of morphological differences in trunk vertebrae (Bailon et al., 2010; Szyndlar and Rage, 1999):

- the “European vipers” including the *V. berus* and *V. aspis* complexes;
- the “Oriental viper” complex (except *Daboia*);
- *Daboia* consisting of the extant *D. russelii* and the fossil *D. maxima* from the Pliocene of Spain (Szyndlar, 1988).

The “Oriental vipers” are mainly large snakes (with a body length close to or greater than two meters) which are found today in diverse desert and mountain-steppe biotopes.

In the Miocene, “Oriental vipers” were widely distributed throughout the southern half of Europe (Delfino, 2002; Szyndlar, 1991; Szyndlar and Rage, 1999, 2002). In the Pliocene of western Europe, “Oriental vipers” have been mentioned in southern France (Bailon, 1989, 1991) and in the Iberian Peninsula (Bailon, 1991; Blain, 2005). The dates of their last appearance are recorded from the Earliest Pleistocene (*Kislangia gusii* zone) of Cova Bonica in the South of the Province of Barcelona (Bailon, 1991; Blain, 2005, 2009; Blain and Bailon, 2006) and in the Earliest Pleistocene of Islas Medas in the Province of Girona (Bailon, 1991).

The Iberian Pleistocene “Oriental viper” record is essentially based on the presence of a few large and robust trunk vertebrae, typically wider and shorter in dorsal view and with a generally less convex centrum and better defined lateral margins than in the “European viper complex” (Bailon, 1991; Szyndlar and Rage, 1999). The trunk vertebrae of this group differ from the genus *Daboia* in their lesser development of the neural spine, which is longer than it is high (Szyndlar, 1988).

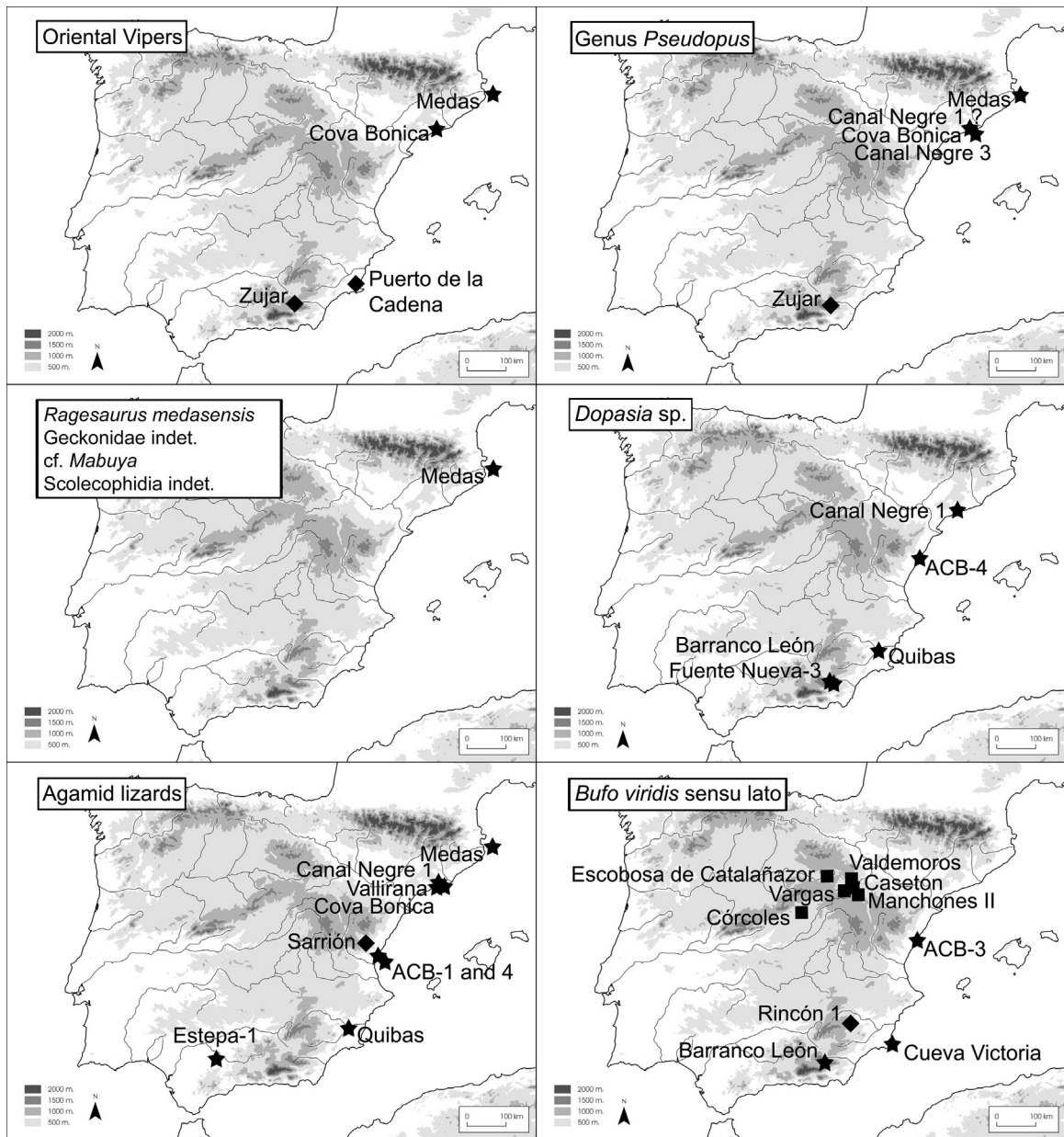
Among the “Oriental viper complex”, some distinctions have been tentatively made based on the morphology of the prezygapophyseal surface of articulation (oval in *V. platyspondyla*, *V. xanthina*, *Macrovipera mauritanica* or subrectangular in *V. lebetina*) and the occurrence of the epizygapophyseal spine (Bailon, 1991; Szyndlar, 1987a,b; Szyndlar and Schleich, 1993). Fossil vertebrae from Cova Bonica, possibly pathologic or teratologic due to their widened neural spine, have oval prezygapophyseal surfaces of articulation and lack epizygapophyseal spines (Bailon, 1991; Blain, 2005, 2009), whereas vertebrae from Islas Medas have subrectangular prezygapophyseal surfaces of articulation (Bailon, 1991). However, these characters have to be taken very cautiously (Szyndlar and Rage, 1999).

#### 3.2. Anguid lizards

Although mention has only been made of a few anguid lizard fossils on the Iberian Peninsula, they are quite diverse, and consist of four genera: *Anguis*, *Dopasia* (or *Ophisaurus* s.l.), *Pseudopus* and *Ragesaurus*.

*Anguis fragilis* is the only anguid lizard present today in the northern half of the studied area, in particular in the Cantabrian region, Iberian System and Pyrenees. The southernmost Iberian population is located in Portugal (south of the Tagus river), while the southernmost Spanish populations are found along the Central System mountain range, and in the Mediterranean coastal area, north of the Ebro Delta. Slow worms (*Anguis*) are semifossorial (burrowing) lizards, reaching about 50 cm long, and live





**Fig. 2.** Geographical distribution of Pleistocene “exotic” amphibians and squamate reptiles on the Iberian Peninsula. Symbols: square, Miocene; diamond, Pliocene; star, Pleistocene.

**Fig. 2.** Distribution géographique des amphibiens et squamates « exotiques » dans la péninsule Ibérique. Symboles : carré, Miocène ; losange, Pliocène ; étoile, Pléistocène.

in dense meadows and other humid environments of the Eurosiberian region, from the coast to 2,400 meters above sea level. In the Mediterranean region, they are generally restricted to wooded areas, at elevations ranging from 600–900 and 1200–1800 meters (Galán and Salvador, 2006). The earliest representative of this species is reported from the Pliocene (MN 14) of Hungary (Venczel, 2001).

### 3.2.1. Genus *Pseudopus*

Five species of *Pseudopus* can be discerned in the Cenozoic record of Eurasia (Klembara, 2012, 2014; Klembara

et al., 2010): *Pseudopus rugosus* and *Pseudopus ahnikoviensis* (Early Miocene), *Pseudopus laurillardi* (Early-Middle Miocene), *Pseudopus pannonicus* (Late Miocene-Middle Pleistocene) and *Pseudopus apodus* (Early Pleistocene-Recent). The extant *P. apodus* is a large glass lizard found from southern central Europe to central Asia which can reach a length of 135 cm. It inhabits open formations such as short grassland or sparsely wooded hills. In contrast to their extant representatives and to the fossils *P. rugosus*, *P. ahnikoviensis*, *P. laurillardi* and *P. pannonicus*, extinct representatives of *P. apodus* seem to have had greater ecological

plasticity and to have lived in various types of environments. The fossil remains of these taxa are most frequently found in localities characterized by sub-humid to humid climates, which may indicate that their preferential habitats include forested environments (Klembara, 2012, 2014; Klembara et al., 2010).

The extinct species *P. pannonicus* has been described as the largest and most robust species of the genus *Pseudopus*, with significant morphological differences in the parietal (Klembara et al., 2010), although most attributions are based on the larger size of the fossils (Estes, 1983; Fejérváry-Langh, 1923; Klembara, 1981; Młynarski, 1960, 1962; Młynarski et al., 1984), and the Iberian Pleistocene record is not an exception to this rule (Bailon, 1991; Blain, 2005, 2009).

On the Iberian Peninsula, *Pseudopus pannonicus* has been documented at the site of Canal Negro 1 (Latest Miocene to the Middle Pleistocene) by means of two dentaries, one parietal, six vertebrae and various osteoderms (Guillén Castejón, 2010). From these materials, only a fragment of dentary with seven preserved very large, pleurodont teeth without cuspids has been illustrated (Plate 2–9 in Guillén Castejón, 2010). Unfortunately, the age of these remains, recovered from a chronological sequence going probably from the Latest Miocene to the Middle Pleistocene, has not been definitively identified by the author. Its last date of appearance may correspond to the Earliest Pleistocene record (*Kislangia gusii* zone) from Cova Bonica (attributed to *P. cf. pannonicus*), where material is quite abundant: four maxilla, three dentaries, one fragmentary parietal, four trunk vertebrae, 11 caudal vertebrae and some 160 osteoderms (Blain, 2005, 2009; Blain and Bailon, 2006). The morphology and size of these fossils are similar to other elements attributed to *P. pannonicus*, such as the maxilla and vertebrae.

At the Early/Middle Pleistocene (from 1.5 to 0.5 Ma) site of Canal Negro 3, Guillén Castejón (2012) described one maxilla, four trunk vertebrae, five caudal vertebrae and numerous osteoderms attributed to the extant species *Pseudopus apodus*. The vertebra represented (p. 15 in Guillén Castejón, 2012) is rather short and robust with a centrum length (around 6–7 mm) slightly larger than mean values for *Anguis fragilis* (deduced from the illustration). The fragment of maxilla (depicted on p. 15 in Guillén Castejón, 2012) with the typical robust teeth with blunt apex and the osteoderms described as bearing a longitudinal carina may correspond to the first mention of the genus *Pseudopus* in the Early/Middle Pleistocene of Spain but, in our opinion, attribution at the species level is not fully supported. Such a late occurrence on the Iberian Peninsula is in agreement with the French fossil record where *Pseudopus* is also largely present in the Early Pleistocene at the sites of Montoussé 5 (Early Pleistocene) and Montoussé 3 (Middle Pleistocene) both in southeastern France, where a few vertebrae and osteoderms have been described (Bailon, 1991). Finally, careful mention at the genus level has been made in the Pliocene record of Zujar (MN15/16, Granada) and in the Earliest Pleistocene record of Islas Medas (Girona), where at both sites a single trunk vertebra has been described as *cf. Pseudopus* sp. (Bailon, 1991).

### 3.2.2. Genus *Dopasia*

According to Nguyen et al. (2011), the non-*Pseudopus* anguines comprise 13 species grouped into three clades. The New World clade contains five species from North and Central America: *Ophisaurus attenuatus*, *O. ceroni*, *O. compressus*, *O. mimicus*, and *O. ventralis*. The East and Southeast Asian clade comprises seven species, for which the generic name *Dopasia* must be used (Conrad and Norell, 2008; Conrad et al., 2010), distributed from northern India through the Indochinese peninsula southwards to Indonesia: *Dopasia buettikoferi*, *D. gracilis*, *D. hainanensis*, *D. harti*, *D. sokolovi*, *D. wegneri*, and *D. ludovici*. And the North African clade contains only one species, *Dopasia koellikeri*.

The history of the systematics of Anguinae has recently been summarized in Delfino et al. (2011) and in Klembara et al. (2010). Here, we follow these views, according to which Neogene and Quaternary European and African anguines may be referred to the genera *Anguis*, *Dopasia*, and *Pseudopus*, mostly on the basis of the morphology and number of teeth as well as the morphology of the vertebrae and osteoderms. *Dopasia* corresponds to Old World species, excluding American representatives of *Ophisaurus* sensu stricto, which bear more numerous cylindrical teeth with apices that are finely striated and slightly pointed. Although Macey et al. (1999), on the basis of genetic differences (mtDNA), have proposed the revalidation of the genus *Hyalosaurus* for the African species *koellikeri*, here we refer to it as *Dopasia koellikeri*, in keeping with Augé (2005) and Delfino et al. (2011). In the paleontological literature, the genus *Dopasia* (sensu Augé, 2005) is sometimes referred to as *Ophisaurus* (sensu Klembara, 2014).

In the Iberian Pleistocene record, attribution to the genus *Dopasia* was mainly based on maxillae, trunk and caudal vertebrae and associated osteoderms. The genus has been mentioned in the Earliest Pleistocene record of Almenara-Casablanca-4 (*Kislangia gusii* zone; Blain, 2005, 2009) and more recently at Canal Negro 1, where three dentaries have been described but not illustrated (Guillén Castejón, 2010). After these, all other instances come from the late Early Pleistocene (*Allophaiomys* aff. *lavocati* zone) at the sites of Barranco León and Fuente Nueva-3, both in the Province of Granada (Blain, 2005, 2009) (= *Ophisaurus* in Blain and Bailon, 2010), where the general morphology of the fossil maxilla (above all the relative spacing of the teeth, which are subpleurodont, monocuspid, and have a more or less enlarged base and a caniniform morphology with a pointed apex recurved postero-medially) is characteristic of the northern African and Eurasian representatives of the subfamily Anguinae (tribe Anguini sensu Augé, 2005). No comparison can be made with other species of the genus *Dopasia* on the basis of the fossils recovered at those sites, as most diagnoses are based on the parietal (Klembara, 1979, 1981, 2014; Klembara et al., 2010), frontal (Klembara, 2014) and dentary Augé, 1992; Roček, 1984). We hope, therefore, that the ongoing archaeological excavations at these two sites might in the future yield new anguine fossils. Finally, quite diverse, yet unpublished fossil material (comprising maxilla, dentaries, parietals, vertebrae and osteoderms) from the late Early Pleistocene record (*Allophaiomys* aff. *lavocati* zone)

of Quibas in the Region of Murcia will certainly give rise to new knowledge on these last populations in western Europe.

As mentioned earlier, the genus *Dopasia* is no longer represented in Europe today. Its geographically closest representative, *D. koellikeri*, lives in northern Morocco and northeastern Algeria (Bons and Geniez, 1996). The genus has been documented in the fossil record of Morocco, in particular from the Late Miocene (Vallesian) at Guefaït 1 (Blain et al., 2013a), and the Latest Pliocene or Earliest Pleistocene at Ahl al Oughlam (Bailon, 2000). Koelliker's Glass Lizard (*D. koellikeri*) is present today in the deciduous and coniferous forests of the sub-humid bioclimatic level (Bons and Geniez, 1996), with very warm and dry summers and relatively wet and mild winters (Benabid, 1985; Ragala and Refass, 2002). Paleoclimatic reconstructions of the late Early Pleistocene of southern Spain show similar climatic conditions at the sites where fossils of the genus *Dopasia* have been documented (Blain et al., 2011a).

### 3.2.3. Genus *Ragesaurus*

The small anguine lizard *Ragesaurus medasensis*, the only representative of the genus, was described by Bailon and Augé (2012) based on a dentary dating to the Earliest Pleistocene recovered from the Islas Medas (NE Spain). *Ragesaurus* differs from other extant and fossil Anguinae in the special morphology of its antero-inferior alveolar foramen, closed by a septum and, to a lesser extent, its tooth morphology.

### 3.3. Agamid lizards

Agamids today inhabit Africa, Asia, Australia, and Europe (Pough et al., 2001; Zug et al., 2001). The only genera currently in Europe are *Stellagama* (according to Baig et al., 2012) or *Laudakia* (according to Gasc et al., 1997 and Sillero et al., 2014), *Trapelus*, and *Phrynocephalus*. These are only found on the southeastern periphery of the continent, in a small area of continental Greece (Thessaloniki area) in addition to a few islands (Corfu, Cyclades archipelago and few Greek islands near Asian Turkey) (Gasc et al., 1997; Sillero et al., 2014). The genera *Agama* and *Trapelus* (Bons and Geniez, 1996; Trape et al., 2012) are present in northwestern Africa. European and African agamid lizards usually live in savannahs, steppes and deserts, and have a way of life that is constantly linked to warm arid areas in rocky or sandy environments. Mediterranean representatives live mainly at the thermo- and meso-Mediterranean bioclimatic levels, with mean annual temperatures ranging from 15 to 18 °C and low mean annual precipitation (less than 300 mm) (Önol and Semazzi, 2009). The mean temperature of the warmest month is at least 24 to 26 °C and the mean temperature of the coldest month ranges from 5 to 11 °C. Paleoclimatic reconstructions, using the mutual climatic range method, of the Earliest Pleistocene at Iberian sites with agamid remains reveal similar climatic conditions, even when agamids are excluded from the analysis (Agustí et al., 2009).

The Earliest European agamid fossils are from the Early Eocene of western and northern Europe and, after an

apparent hiatus, the family reappears later in the Oligocene of France (Augé, 2005; Augé and Smith, 1997). During the Miocene, they were rather widespread across the continent, from France to Ukraine (Delfino et al., 2008; Rage, 2013). Later, in the Pliocene, finds are restricted to localities in the Mediterranean area (Bailon, 1987, 1991; Bailon and Blain, 2007; Delfino et al., 2008). In the Iberian Peninsula, fossil agamid lizards have rarely been documented and, except for an instance in the Pliocene record of Sarrión 1 (Delfino et al., 2008), they are now considered as part of the Early Pleistocene record. Agamids have been described in the Earliest Pleistocene record of Islas Medas (Girona; Bailon, 1991), in the Earliest Pleistocene of Almenara-Casablanca-4 (*Kislangia gusii* zone) in the Province of Castellón, and in the Early Pleistocene (Miomys cf. *reidi* zone) of Vallirana (Barcelona) and Almenara-Casablanca-1 (Castellón) (Blain, 2005, 2009; Blain and Bailon, 2006; Rage, 2013). More recently, some 50 dentaries of agamid lizards were documented at the site of Canal Negre 1 (Latest Miocene to Middle Pleistocene) in the Province of Barcelona (Guillén Castejón, 2010). Although as yet unpublished, one anterior fragment of a dentary with two caniniform teeth and two preserved acrodont teeth has been documented at the Villafranchian (Earliest Pleistocene?) (Castillo et al., 1990) site of Estepa-1 (Sevilla; Bailon, personal observation). The date of their last appearance corresponds to the Early Pleistocene (*Allophaiomys* aff. *lavocati* zone), documented at Quibas (Blain et al., 2014).

Heterodont dentition, characterized by pleurodont and acrodont teeth, unambiguously identifies the family Agamidae (Ananjeva, 1981; Baig et al., 2012; Bailon, 1987, 1991; Delfino et al., 2008; Moody, 1980; Moody and Roček, 1980). The fossil material from the Iberian Pleistocene therefore seems to resemble the African-West Asian agamid clade Agaminae (sensu Macey et al., 2000; Group VI of Moody, 1980) by possessing “only” two anterior pleurodont teeth on the dentary, whereas in most other agamids, there are at least three such teeth on the dentary (Maul et al., 2011). Other features, such as simple tooth morphology, unicuspid crowns with triangular labial and lingual profiles and without significant longitudinal grooves or irregularities, are present in the same manner as in Agaminae (Maul et al., 2011).

### 3.4. *Bufo viridis sensu lato*

Green toads (*Bufo viridis sensu lato*), as used in this work, correspond today to a widespread group of closely related species with a range that extends from eastern France and Italy to central Asia, including northern Africa and numerous Mediterranean islands. Because of the high morphological variability of the green toads, several forms, as species and subspecies, have been described within its extensive range: *Bufo balearicus* (Apennine Peninsula, Corsica, Sardinia, Balearic Islands), *Bufo siculus* (Sicily), *Bufo boulengeri* (northern Africa), *Bufo viridis sensu stricto* (central and eastern Europe) and *Bufo variabilis* (the Balkans, Anatolia) (Stöck et al., 2001, 2006, 2008). Although Frost et al. (2006) discerned different species within the *Bufo*



groups, we have not adopted their nomenclature here (i.e. the new genera) and *B. viridis* s.l. is used in this paper as it was previously accepted before molecular biology separated it into the various species cited above in the western zone of its distribution area. We did this because these newly created species and subspecies have not yet been diagnosed separately from an osteological point of view. These taxa today inhabit a wide variety of habitats, from mesic to arid, from subtropical to cold temperate, and from below sea level in Israel to more than 4000 m a.s.l. in the Himalayas (Dessauer et al., 1975). They are common along coasts, due to their ability to survive and breed in brackish waters. Their typical reproductive sites are temporary shallow bodies of water (El Hamouni et al., 2007; Sicilia et al., 2006).

*B. viridis* s.l. is reported in the fossil record at numerous localities dating from the Early and Middle Miocene in Spain, France, Italy, Germany, Austria, Slovakia, Hungary, Greece, Rumania and Turkey (Bailon and Hossini, 1990; Martín and Sanchiz, 2014; Rage and Roček, 2003; Sanchiz, 1998). Its Pliocene and Pleistocene European record is also very abundant, and to the west of its current range, the earliest extant green toads (*B. cf. viridis*) are mentioned in the Pliocene record of Rincon 1 (MN16, Spain; Alberdi et al., 1982) and Mas Genegals (MN16/17, France; Bailon, 1991) and in the Middle Pleistocene of Terra Amata, Nice (Bailon et al., 2011). In northern Africa, *B. viridis* dated to the Early Pleistocene has been documented at Ahl al Oughlam (Casablanca, Morocco; Bailon, 2000).

On the Iberian Peninsula, besides the Early and Middle Miocene localities of Escobosa de Catalañazor, Córcoles, Manchones II and Rincón 1, which correspond to its earliest record (Martín and Sanchiz, 2014; Sanchiz, 1998), *B. viridis* s.l. has been described in the late Early Pleistocene (*Allophaiomys* aff. *lavocati* zone) record of Cueva Victoria (Blain, 2015; Blain et al., 2010a). In addition, the fossils from the late Early Pleistocene (*Allophaiomys* aff. *lavocati* zone) record of Almenara-Casablanca-3 (Blain et al., 2007) and Barranco León (Blain, 2005, 2009; Blain and Bailon, 2010; Blain et al., 2011a) previously attributed to *Bufo* sp. have been attributed to *Bufo viridis* s.l. (Blain et al., 2010a). The green toad remains recovered at Cueva Victoria are by far the most numerous and diverse fossils attributed to *B. viridis* in Spain and comprise some 498 elements representing almost every part of the skeleton, whereas only a single ilium has been recovered in Almenara-Casablanca-3 (Blain et al., 2007; Blain et al., 2010a), and five ilia in Barranco León (Blain et al., 2010a). New materials currently under study from the Quibas site in the region of Murcia also seem to belong to this species (Blain, personal observation).

All of the osteological characteristics seen in Iberian Early Pleistocene fossils fit well with the morphology of extant representatives of *B. viridis* s.l.; however, a supraorbital tectum (although poorly developed) on the frontoparietals from Cueva Victoria seems to be reminiscent of the Miocene and Pliocene fossils from France, Slovakia and Hungary (Bailon and Hossini, 1990; Špinar et al., 1993; Venczel, 1997, 2001), although it is possible that variability for this characteristic may be greater than previously thought in *B. viridis* s.l.

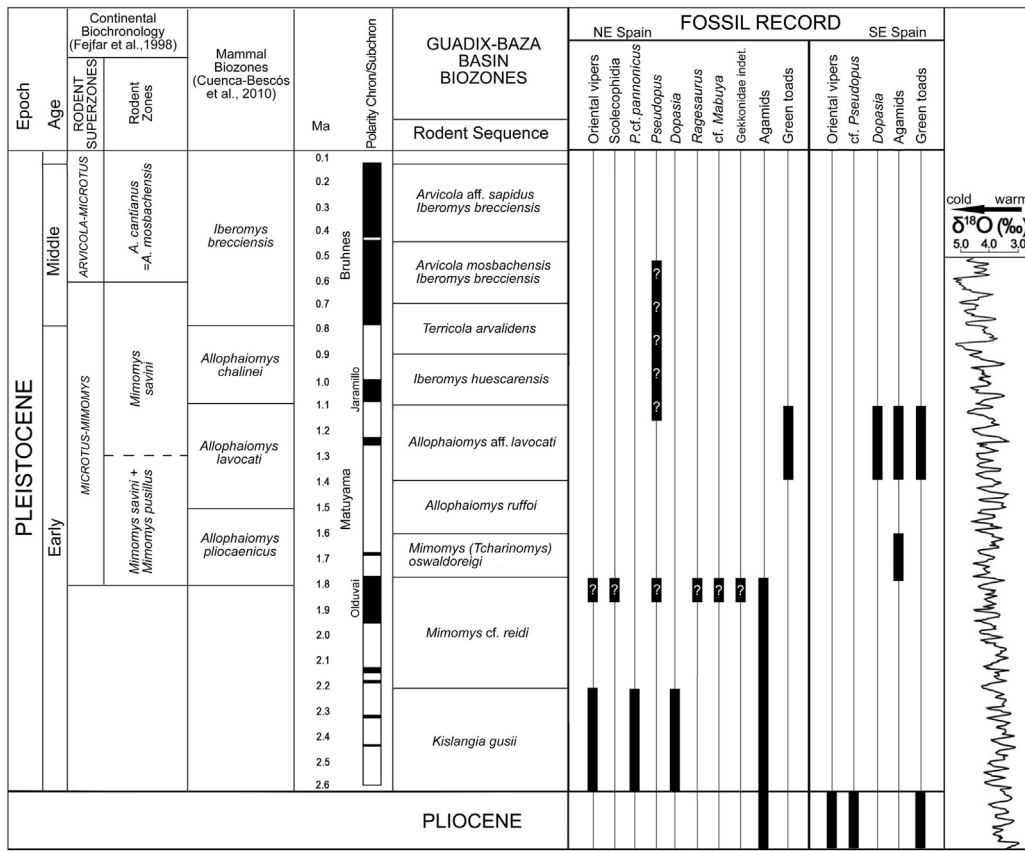
### 3.5. Questionable “exotic” taxa

In addition to this short review of the “exotic” herpetofaunal elements found at the Pleistocene archaeological and paleontological sites of the Iberian Peninsula, some localities have yielded several taxa that represent the only mention of such taxa in the entire Iberian or western European fossil record to date, or their only mention in the Pleistocene. At some of these sites, the taxonomic attribution can be considered doubtful due to a lack of precise osteological description, uncertainty concerning the chronology of the site itself or because of the probable mixing of various levels or intrusion from other nearby sites, especially in the case of karstic fissures and old excavations. Although it is always delicate to cast doubt on older studies or fieldwork, and because simply disregarding such sites is not a solution, we wanted to discuss some of the sites that have yielded “too many” exotic amphibians and reptiles in comparison with other Pleistocene sites on the Iberian Peninsula. For the moment, we can only characterize these isolated fossil mentions as outliers, and await new fossils and new sites to provide more information that would confirm this “exotic” presence in the Iberian Pleistocene.

#### 3.5.1. Canal Negre 1

The impressive but very general paper by Guillén Castejón (2010), in which a single author described all of the taxonomic groups recovered as fossils dating to the Late Miocene to Middle Pleistocene at the site of Canal Negre 1 (Barcelona), from mollusks to monkeys (comprising gastropods, sea urchins, fish, birds, amphibians, reptiles, rodents, insectivores, bats, lagomorphs, carnivores, artiodactyls, perissodactyls and primates), includes information on amphibians and reptiles that represent the first and only mention of these species in the Pleistocene record of the Iberian Peninsula and/or western Europe, such as *Triturus* cf. *cristatus*, *Pliobatrachus* cf. *langhae*, *Pelobates* cf. *fuscus*, *Chamaeleo* sp., *Podarcis* cf. *taurica*, *Amphisbaena* sp., *Vipera berus* and *Vipera ammodytes*. Despite the admirable effort made by this author, we can only regret the lack of chronological precision (due to, as the author says, the lack of clear stratification of the karstic site) and the very incomplete descriptions. Moreover, we think that before fossil documentation such as this can be added to the current body of knowledge on past herpetofauna, the collection must be revised, fully described and illustrated. For now, we can only infer opinions based on the illustrations of some of the taxa. The attribution of six vertebrae to *Triturus* cf. *cristatus* is wrong as the author said that they have a “high and robust neural spine” (Plate 2-2 in Guillén Castejón, 2010), whereas in *Triturus cristatus*, the neural spine is very low. The attribution of ten vertebrae, one humerus and one tibiofibula to *Pliobatrachus* cf. *langhae* in Canal Negre 1 seems to be based on the large size of the material and the morphology of the “dorso-ventrally compressed” vertebrae. Only the humerus is depicted (Plate 2-4 in Guillén Castejón, 2010) and may correspond to *Bufo bufo* sensu lato, as it does not bear any cubital crest. Seven dentaries have been attributed to *Chamaeleo* sp. (Plate 2-6a and 6b in Guillén Castejón, 2010) representing the first fossil mention for this group on the Iberian Peninsula, except for their inclusion in the





**Fig. 3.** Biochronological synthesis of the “exotic” amphibian and squamate reptile Iberian fossil record, divided into north-eastern Spain (regions of Catalonia and Valencia) and south-eastern Spain (regions of Andalusia and Murcia). Pleistocene small-mammal biozonation according to Agustí et al. (in press). **Fig. 3.** Synthèse biochronologique des mentions fossiles, dans la péninsule Ibérique, des amphibiens et squamates « exotiques », séparée entre l’Espagne du Nord-Est (régions de Catalogne et de la communauté de Valence) et l’Espagne du Sud-Est (Andalousie et région de Murcie). Biozonation du Pléistocène à partir des micromammifères selon Agustí et al. (in press). (Cuenca-Bescós et al., 2010 and Fejfar et al., 1998).

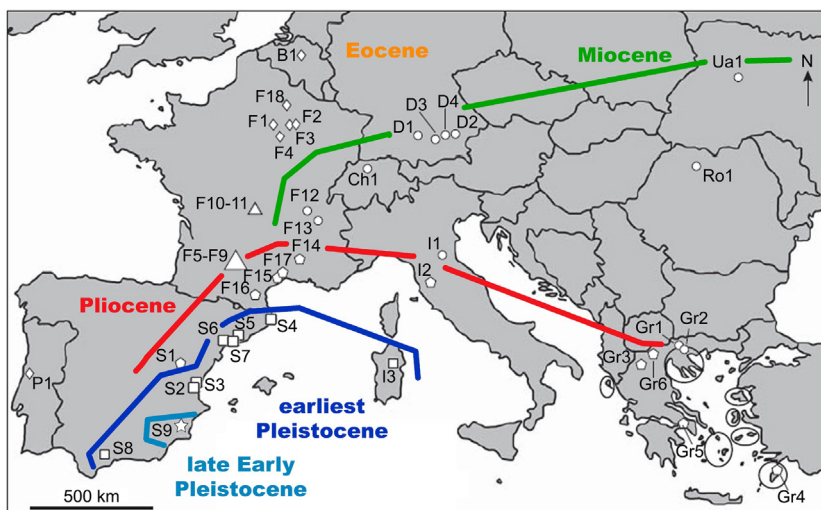
Holocene record of Málaga (southernmost Spain; Talavera and Sanchiz, 1985). According to the photographs of one of these dentaries, we think that it may also be an intensely worn Agamid dentary. In chameleons, teeth are usually not so close one from each others. Most lacertid attributions (*Lacerta* sp., *Podarcis* cf. *taurica*, *Timon* cf. *lepidus*, *Acanthodactylus* cf. *erythrurus* and *Psammmodromus* cf. *algerus*) are based on fragments of dentaries, which are not good skeletal indicators for diagnoses. *Amphisbaena* is a genus from South America and Antillean Islands: the maxilla has not been described. No illustrations of the snakes have been published. Finally, attribution of two fragments of a maxilla to *Pelobates* cf. *fuscus* is very tentative and more likely corresponds to *Pelobates cultripes*.

### 3.5.2. Islas Medas

As far as amphibians and reptiles are concerned, Bailon (1991) and Bailon and Augé (2012) mentioned the following taxa at the Islas Medas site: *Triturus marmoratus*, *Discoglossus* sp., *Pelobates* cf. *cultripes*, *Bufo bufo*, *Bufo* cf. *calamita*, *Rana* sp., *Blanus cinereus*, *Agama* s.l., *Gekkonidae* indet. (different from extant geckos of the Iberian Peninsula), Scincidae of Lygosominae type (cf. *Mabuya*), *Timon*

*lepidus*, *Lacerta* sensu stricto, cf. *Podarcis*, *Anguis fragilis*, cf. *Pseudopus*, *Ragesaurus medasensis* (= aff. *Ophisaurus* in Bailon, 1991), *Scolecophidia* indet., *Coluber* sp., *Coronella* cf. *gironnica*, *Natrix* cf. *natrix*, *Vipera* sp. (*V. aspis* group) and *Vipera* sp. (*V. lebetina* group).

Among this extensive list, the questionable exotic taxa are indeterminate *Gekkonidae* (different from genera *Tarentola* and *Hemidactylus*), the scincid lizard cf. *Mabuya* and the blind snake *Scolecophidia* indet. In the preliminary study of the vertebrates from Islas Medas, de Villalta (1965) suggested an attribution to the Villafranchian. Later, based on the rodent assemblage, Barrière and Michaux (1970) proposed that the site was Early Pleistocene, whereas for Michaux (1980), it was Pliocene (between 3 and 2.5 Ma). Even later, Alberdi et al. (1982), Renaud et al. (1996) and Minwer-Barakat et al. (2008) propose an age now considered Early Pleistocene (MN17) for the site. Finally, Renaud et al. (2005 and 2006) suggested an age of around 1.85 Ma for Islas Medas. In any case, the chronological attribution of this site is mainly based on the presence of an extinct rodent, *Mimomys medasensis*, which lived between 2.6 and 1.8 Ma. Consequently, this may suggest that “exotic” geckos, scincids and blind snakes may have



**Fig. 4.** (Color online). Example of a climate-related regression: the European fossil record of Agamidae (modified from the compilation by Delfino et al., 2008). Symbols: diamond, Eocene; triangle, Oligocene; circle, Miocene; pentagone, Pliocene; square, Earliest Pleistocene (formerly Late Pliocene, MN17); star, late Early Pleistocene. The approximate European modern range of *Laudakia stellio* is represented by the empty ellipses. **Belgium:** B1, Dormaal (*Tinosaurus europeocaenus*; Early Eocene, MP 7). **France:** F1, Condé-en-Brie (*T. europeocaenus*; Early Eocene, MP 8+9); F2, Avenay (*T. europeocaenus*; Early Eocene, MP 8+9); F3, Mutigny (*T. europeocaenus*; early Eocene, MP 8+9); F4, Sézanne (*T. europeocaenus*; Early Eocene, MP 8+9); F5, La Plante 2, Phosphorites du Quercy (*Uromastix europaeus*, Early Oligocene, MP 22); F6, Mas de Got B, Phosphorites du Quercy (*U. europaeus*, Early Oligocene, MP 22); F7, Roqueprune, Phosphorites du Quercy (?*Quercygama galliae*; Early Oligocene, MP 23); F8, Rigal-Jouet, Phosphorites du Quercy (Agamidae indet., Late Oligocene, MP 25); F9, Garouillas, Phosphorites du Quercy (*Quercygama galliae*; Late Oligocene, MP 25); F10, Coderet (Agamidae indet., Late Oligocene, MP 30); F11, “Allier” (Agamidae indet.; Late Oligocene); F12, “Lyonnais” (Agamidae indet.; Miocene); F13, La Grive (Acrodonta; Miocene); F14, Seynes (*Agama* sp.; Pliocene, MN 16); F15, Sète (*Agama* sp.; Pliocene, MN 15); F16, Mas Genegas II and IX (*Agama* sp.; Pliocene, MN 15/16). **Germany:** D1, Burtenbach 1b (Agamidae indet.; Middle Miocene, MN 5); D2, Furth 460 m (Agamidae indet.; Middle Miocene); D3, Laimering 3 (aff. *Stellio* sp.–Agamidae indet.; Middle Miocene, MN 6); D4, Unterempfenbach 1b (Agamidae indet.; Early Miocene, MN 5). **Greece:** Gr1, Maramena (*Agama* sp.; Late Miocene–Earliest Pliocene? MN 13–14?); Gr2, Ano Metochi 3 (*Agama* s.l.; Late Miocene, MN 13); Gr3, Kastoria (*Agama* s.l.; Middle–Late Pliocene?); Gr4, Maritsa A, Rhodes (*Agama* s.l.; Early Pliocene, MN 14); Gr5, Tourkoubounia 1 (*Agama* s.l.; Pliocene, MN 16); Gr6, Vevi (*Agama* s.l.; early Pliocene, MN 15); Gr7, Rema Aslan 1 – not located – (*Agama* s.l.; Mio–Pliocene). **Italy:** I1, Cava Monticino (*Agama* s.l.; Late Miocene, MN 13); I2, Montagnola Senese (*Agama* s.l.; Earliest Pleistocene, MN 17); I3, Monte Tuttavista (*Agama* s.l.; Plio–Pleistocene). **Portugal:** P1, Silveirinha (cf. *Tinosaurus* sp.; Early Eocene, MP 7). **Romania:** Ro1, Tasad (Agamidae indet.; Middle Miocene, MN 8). **Spain:** S1, Sarrion 1 (Cerro de los Espejos) (*Agama* sp.; Pliocene, MN 16); S2, Casablanca-Almenara 4 (Agamidae indet.; from Earliest Pleistocene, MN 17); S3, Casablanca-Almenara 1 (Agamidae indet.; from Earliest Pleistocene, MN 17); S4, Medas Islands (*Agama* sp.; Early Pleistocene, MN 17); S5, Cova Bonica (Agamidae indet.; Earliest Pleistocene, MN 17); S6, Vallirana (Agamidae indet.; Earliest Pleistocene, MN 17); S7, Canal Negre 1 (*Agama* sp.; Earliest Pleistocene?; Guillén Castejón, 2010); S8, Estepa-1 (Agamidae indet., Earliest Pleistocene; unpublished data); S9, Quibas (Agamidae indet., late Early Pleistocene; Blain et al., 2014). **Switzerland:** Ch1, Rumikon (*Agama* sp.; Middle Miocene, MN 6). **Ukraine:** Ua1, Gritsev (Agamidae indet.; Late Miocene, MN 9).

**Fig. 4.** (Couleur en ligne). Exemple d’une régression climatique : les mentions fossiles européennes des Agamidae (modifié de la compilation de Delfino et al., 2008). Symboles : losange, Éocène ; triangle, Oligocène ; cercle, Miocène ; pentagone, Pliocène ; carré, Pléistocène basal (anciennement Pliocène supérieur, MN17) ; étoile, Pléistocène inférieur final. La distribution européenne moderne de *Laudakia stellio* est représentée par des ellipses.

survived during the Early Pleistocene at the Islas Medas site. However, because no additional instance of such taxa has been documented in the Iberian Pleistocene record, we prefer to await confirmation of the age of these specimens and to consider their presence in the Iberian Pleistocene as probable but uncertain.

#### 4. Herpetofauna as a complement to the biochronological zonation of the Iberian Early Pleistocene

The distribution of documented fossils of “exotic” herpetofauna on the Iberian Peninsula (Fig. 2) shows that they all occur on the Mediterranean side of the landmass or in southern Spain. As these mainly consist of “exotic” reptiles with thermophilous affinities, this observation is not surprising. “Exotic” taxa seem to be absent from the entire western side of the Iberian Peninsula (under the influence of the Atlantic) and the Meseta (continental influence); however, this absence may be due to the low number of

sites (for example in Galicia), a lack of studies or poorly prospected regions (Portugal and Extremadura). The central area of the Iberian Peninsula has traditionally been well prospected for paleontological and archaeological purposes and has yielded a long list of Neogene and Quaternary fossiliferous localities. Thus, the absence of “exotic” taxa dating to the Pleistocene from central and northern Spain must be significant, for example at the Early and Middle Pleistocene sites of the Sierra de Atapuerca (Burgos), which is very rich in small vertebrate remains (Blain, 2005, 2009; Blain et al., 2008, 2009, 2010b, 2011b). The Middle and Late Pleistocene have also been well studied on the Iberian Peninsula and have not yielded any “exotic” herpetofaunal taxa to date.

From a biochronological point of view (Fig. 3), the Iberian fossil record has been split into two regions: northeastern Spain (Catalonia and the region of Valencia) and southeastern Spain (Andalusia and Murcia) in order to distinguish differences in last appearance data (LAD) between the north and south. In northeastern Spain, the

LADs of oriental vipers, *Pseudopus pannonicus*, *Dopasia* and agamids may (although there is uncertainty concerning the age of Islas Medas and Canal Negro 1) occur just before or during the Olduvai paleomagnetic event (around 2.0 Ma for the lower limit). Meanwhile, green toads, although absent from the Pliocene record in northeastern Spain, are present in Almenara-Casablanca-3 (Castellón) at the same time that they are present in southeastern Spain. The only record of *Pseudopus apodus* (or *Pseudopus* sp.) in Canal Negro 3 (Early-Middle Pleistocene) must be further studied, particularly the chronological range of the site, and likely corresponds to the last “exotic” taxon of north-eastern Spain. For southeastern Spain, the fossil record is truncated, despite the continuous sedimentary sequence of the Guadix-Baza Basin (Granada) (Agustí et al., in press). The few paleontological studies from the Earliest Pleistocene have not yielded “exotic” herpetofaunal elements (i.e. Agustí et al., 2013). However, late Early Pleistocene sites (*Allophaiomys* aff. *lavocati* zone) extensively excavated for archaeological purposes (the earliest hominin sites in western Europe) have contained some “exotic” elements, like the anguid *Dopasia*, agamid lizards and green toads. No “exotic” amphibians or reptiles have been documented at the numerous Middle and Late Pleistocene sites in south-eastern Spain (i.e. Bailon, 1991; Barroso Ruiz and Bailon, 2003; Barroso Ruiz et al., 2011; Blain et al., 2013b), thus suggesting that the LAD of such taxa may roughly coincide with the Jaramillo event (1.07 to 0.99 Ma). These data may suggest that the local extinction (or disappearance) of these “exotic” herpetofauna may have been relatively contemporaneous for each region, but with different timings between them: earlier in the north (Olduvai) and later in the south (Jaramillo).

In accordance with the thermophilous affinities of such “exotic” taxa (in particular squamate reptiles), hypotheses have been put forth attributing their local disappearance to the progressive cooling during the Quaternary, which led to the southern withdrawal of thermophilous taxa followed by their extinction when temperatures became too cold for their survival (Bailon and Blain, 2007). LADs are crucial for evaluating hypotheses regarding the timing and causes of species disappearance in the fossil record but also for understanding broad-scale geographic patterns. This is well illustrated by the whole European fossil record of agamid lizards, suggesting a probable climate-driven disappearance (Fig. 4) in accordance to what has been described in the North American herpetofauna (Smith, 2009). According to the overall record of Agamidae (updated from Delfino et al., 2008), agamid lizards have been documented dating to the Eocene as far north as Belgium. During the Miocene, their northernmost distribution goes from central France to southern Germany (Bavaria) and northern Ukraine. Then, in the Pliocene, their distribution became restricted to the modern Mediterranean area, from Spain to Greece. Finally, from the Earliest Pleistocene until today, they have only been reported in Spain and possibly Sardinia. Their LAD as fossils in western Europe corresponds to two sites on the southernmost Iberian Peninsula, showing a clear southward withdrawal in Europe from the Eocene to the late Early Pleistocene. As pointed out by Delfino et al. (2008), the biogeographical

status of current Balkan populations is not supported by any Pleistocene occurrence in Greece. However, even if progressive cooling during the whole Neogene and particularly during the Pleistocene was the main factor affecting the distribution (and subsequent local disappearances) of amphibian and reptile fauna in Europe, other hypotheses such as competition or exclusion due to the arrival of new competitors in western Europe cannot be ruled out.

## 5. Conclusions

This work compiles the geographical and temporal pattern of the progressive southward withdrawal and local extinctions of “exotic” amphibians and squamate reptiles (i.e. that do not currently live in western Europe) and analyzes them from a chronological and geographical perspective in order to complement the biochronological zonation of the Iberian Pleistocene. The fossil record of such “exotic” taxa occurs in eastern Spain, mainly in the vicinity of the Mediterranean coast, an area propitious for warm and dry climatic conditions. Sites in western and central Spain are devoid of “exotic” taxa. The chronological range of this fossil record only reaches the Early Pleistocene (pending the determination of a precise age of Canal Negro 3). No “exotic” taxa have been recovered with certainty from the Iberian Middle and Late Pleistocene. This review of the “exotic” herpetofauna suggests that their biochronological distribution must be pondered by the geographic location of the recovery sites. In northern Spain, the Earliest Pleistocene (*Kislangia gusii* and *Mimomys* cf. *reidi* zones) is characterized by the presence of oriental vipers, agamid lizards, *Dopasia*, *Pseudopus pannonicus* (and also probably *Ragesaurus*, extinct geckos, cf. *Mabuya* and *Scolocophidia* indet.) until the Olduvai paleomagnetic event. Slightly after, in southern Spain, the disappearance of *Dopasia*, agamid lizards and green toads occurs just before the Jaramillo paleomagnetic reversal, thus creating characteristic post- and pre-Jaramillo fauna. Further prospecting and herpetofaunal studies on the Iberian Peninsula will certainly lead to the completion and/or confirmation of such conclusions.

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