



Systematic palaeontology (Vertebrate palaeontology)

## First report of a green toad (*Bufo viridis* sensu lato) in the Early Pleistocene of Spain: Palaeobiogeographical and palaeoecological implications

*Première mention d'un crapaud vert (Bufo viridis sensu lato) dans le Pléistocène inférieur d'Espagne : implications paléobiogéographiques et paléoécologiques*

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### ABSTRACT

For the first time unequivocal fossil remains of a green toad (*Bufo viridis* s.l.) are described in the Iberian Peninsula. The fossils come from the Cueva Victoria site, a late Early Pleistocene (ca. 1.1–1.2 Ma) karstic filling in semi-arid southeastern Spain (Murcia region). By extension, other remains from two other Early Pleistocene Spanish localities, Barranco León D (ca. 1.3 Ma) and Almenara-Casablanca 3 (ca. 1.1 Ma), are cautiously attributed to the group *B. viridis*. The *B. viridis* group was previously reported with some uncertainty to the west of its current distribution area in Western Europe (Spain and France) in the Pliocene (*Bufo* cf. *viridis*) and less probably in the Early Miocene (*Bufo* aff. *viridis*). Since no osteological differences have been established between the recently described extant species of *B. viridis* s.l. (e.g. *Bufo balearicus*, *Bufo siculus*, *Bufo boulengeri*, *B. viridis* sensu stricto and *Bufo variabilis*) no precise palaeobiogeographical relationships can be drawn for the Spanish fossils. However, the occurrence of a third species of bufonid toad during the Pleistocene in the South of the Iberian Peninsula raises some interesting ecological questions in relation to the local disappearance of the green toad, which can be hypothetically linked to the intensification of the Pleistocene glacial/interglacial climate dynamic or to probable competition with another toad, *Bufo calamita*.

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### RÉSUMÉ

Pour la première fois sans équivoque, les restes fossiles d'un crapaud vert (*Bufo viridis* s.l.) sont décrits dans la Péninsule ibérique. Ces fossiles proviennent du gisement de Cueva Victoria, un remplissage karstique daté du Pléistocène inférieur (environ 1,1–1,2 Ma) et situé dans le Sud-Est de l'Espagne semi-aride (région de Murcie). Par extension, quelques restes provenant de deux autres gisements espagnols du Pléistocène inférieur : Barranco León D (environ 1,3 Ma) et Almenara-Casablanca 3 (environ 1,1 Ma) sont rapportés avec prudence

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au groupe *B. viridis*. Le groupe *B. viridis* a été précédemment rapporté à l'Ouest de sa distribution actuelle en Europe de l'Ouest (France et Espagne), avec quelques incertitudes dans le Pliocène (*Bufo* cf. *viridis*) et aussi, bien que moins probable, dans le Miocène inférieur (*Bufo* aff. *viridis*). Comme aucune différence ostéologique n'a été établie à ce jour pour permettre de différencier les diverses espèces nouvellement créées de *B. viridis* s.l. (ex. *Bufo balearicus*, *Bufo siculus*, *Bufo boulengeri*, *B. viridis* sensu stricto et *Bufo variabilis*), aucune relation paléobiogéographique précise ne peut être suggérée pour ces fossiles espagnols. Toutefois, la présence d'une troisième forme de bufonidé durant le Pléistocène dans le Sud de la Péninsule ibérique soulève d'intéressantes questions écologiques sur l'extinction locale du crapaud vert, qui peut être mise en relation avec l'accentuation de la dynamique climatique glaciaire/interglaciaire, ou bien alors avec une compétition avec un autre crapaud *Bufo calamita*.

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## 1. Introduction

In a recent paper Carrión et al. (2010) discuss the extension and history of the semi-arid landscape of southeastern Iberia. Aridity has been a feature of southeastern Spain ever since the Middle Miocene, 16 million years ago, which is characterized by complex palynological assemblages including a subdesert component. For the Pliocene (5.3–2.6 Ma), pollen records also reflect the occurrence of episodes with abundant herbs, and subdesert elements, suggesting that an arid thermo-Mediterranean belt with Saharo-Irano-Turanian elements continued to occur during the Pliocene along the Mediterranean coast of Iberia from Andalusia to southern Catalonia. Although Early to Mid-Pleistocene palaeobotanical records of the region are rather scarce, Early Pleistocene landscapes are characterized by the presence of shallow lakes with swampy marginal zones and extensive areas of savanna with tall grass and shrubs. However, humid woodland areas are not absent from such landscapes, as evidenced by palynological and palaeontological studies (e.g. Blain et al., in press; Jiménez Moreno, 2003).

Today anuran diversity in the semi-arid landscape of southeastern Spain is rather low (Pleguezuelos et al., 2002). This is probably due to the fact that because they are ectotherms and have a permeable body covering, they are more susceptible to the vicissitudes of the environment than any other tetrapod (Duellman and Trueb, 1994). Typical of such Iberian biotopes today are a few anurans such as the Iberian painted frog (*Discoglossus jeanneae*), the Parsley frog (*Pelodytes punctatus*), the common toad (*Bufo bufo*), the Natterjack toad (*Bufo calamita*), the stripeless tree frog (*Hyla meridionalis*) and Perez's frog (*Pelophylax perezii*), *B. bufo*, *B. calamita* and *P. perezii* being the most widely distributed anurans in the provinces of Almería and Murcia (Pleguezuelos et al., 2002). Up to now, all the anurans recovered as fossils in the Pleistocene localities of the Iberian Peninsula only document extant species living today in the Iberian Peninsula, suggesting that no change may have occurred in the composition of anuran communities since the end of the Pliocene (Bailon, 1991; Blain, 2005; Rage and Roček, 2003; Sanchíz, 1998). Here we report for the first time in the late Early Pleistocene of Spain the unequivocal presence of a green toad (*Bufo viridis* s.l.). This is today essentially a lowland group of species that often live in dry, sandy areas (although not restricted to

such situations). Its occurrence in the Early Pleistocene of southeastern Spain is discussed in relation to palaeobiogeography and palaeoecology.

## 2. Cueva Victoria site

Cueva Victoria is a karstic cavity located on the eastern slopes of the Cerro de San Ginés (massif of San Ginés de la Jara), near the city of Cartagena (Murcia) and a small lagoon adjacent to the Mediterranean Sea, called Mar Menor (Fig. 1). During the Early Pleistocene, the cavity opened out and filled up with detrital material dominated by heterometric breccias, coarse sands and clays, constituting the so-called fossiliferous breccia. The cavity at that time was used as a hyena's den, as evidenced by the large amount of coprolites and gnawed and broken bones (Gibert et al., 1992).

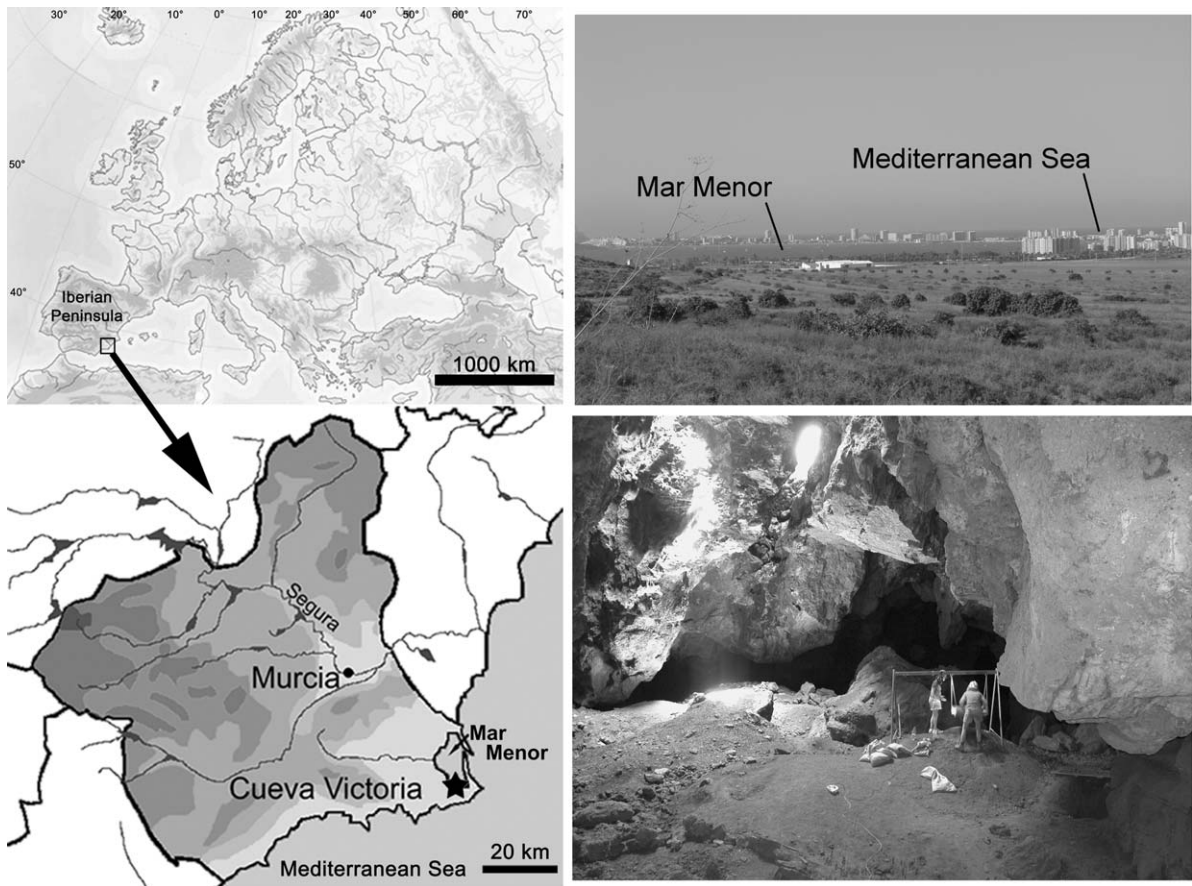
The age of the fossiliferous layers has been established from the biochronology (see Blain et al. (2008a) for a discussion) and palaeomagnetism (the top of the breccia (8 m) is slightly older than the base of the Jaramillo normal event estimated at  $1072 \pm 2$  ka (Blain et al., 2008a; Gibert et al., 2006).

Until now Cueva Victoria has yielded a large amount of vertebrate fossils that document the richness of the Early Pleistocene biomes of southeastern Spain: more than 80 species have been described (Blain et al., 2008a; Gibert et al., 2006), with at least 39 bird species (Sánchez Marco, 2004). Of great relevance is the occurrence of the primate *Theropithecus* (Gibert et al., 1995), which suggests a possible dispersal route through the Strait of Gibraltar from North Africa to Europe.

According to the geological work of Montenat (1977) on the palaeogeography of the area, the seashore was closer to the cavity at the end of the Early Pleistocene than today, as shown by the presence of marine mammal fossil remains such as *Phoca* (Gibert et al., 1992, 2006) and four unpublished cetaceous vertebrae.

## 3. Material and methods

The amphibian fossil remains used for this study consist of disarticulated elements collected by water-screening the sediments obtained during the palaeontological excavation of the Cueva Victoria cave during the field campaigns of the years 1984–2009. The fossils are



**Fig. 1.** Geographical location of the Cueva Victoria site and pictures of the landscape in front of the site (above) and in part of the cavity during the excavation (below).

**Fig. 1.** Localisation géographique du site de Cueva Victoria et photographies du paysage devant le gisement (en haut) et dans une partie de la cavité pendant les fouilles (en bas).

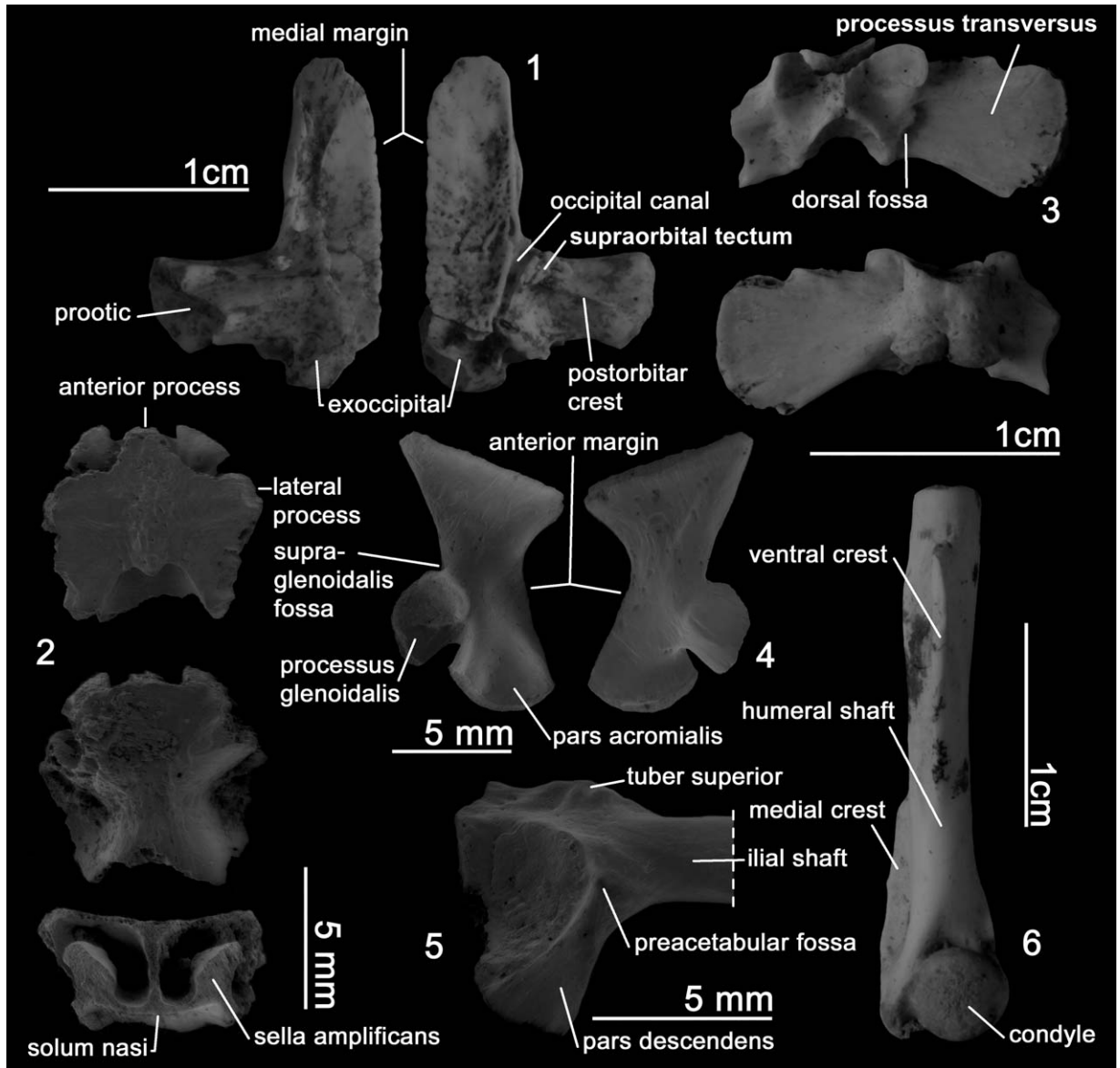
provisionally housed in the collections of the Museo Arqueológico Municipal de Cartagena (Spain). The green toad remains recovered from Cueva Victoria correspond for the moment to 498 elements that represent almost all the parts of the skeleton: 1 maxilla, 2 sphenethmoids, 1 parasphenoid, 2 pterygoids, 3 frontoparietal–prootic–exoccipital complexes, 4 mandibles, 56 vertebrae, 5 sacral vertebrae, 19 urostyles, 6 clavicles, 14 scapulae, 4 coracoids, 111 humeri, 59 radioulnae, 78 ilia, 25 femurs, 67 tibiofibulae, 19 tarsals and 20 phalanges. A complete osteological description of all the taxa present in Cueva Victoria is given in another publication (Blain, in press). Note that previous publications on Cueva Victoria amphibians and squamate reptiles were based on the material housed in the collections of the Museu de Geologia de Barcelona, and that no evidence of green toads was found (Blain, 2005, 2009; Blain and Bailon, 2006; Blain et al., 2008a).

Comparisons have been drawn mainly using publications (Bailon, 1991, 1999; Bailon and Hossini, 1990; Blain, 2005; Böhme, 1977; Delfino et al., 2009; Hodrova, 1986; Hossini, 2001, 2002; Ratnikov, 2001; Sanchíz, 1977, 1998) and using the dry skeleton collections of the Museo Nacional de Ciencias Naturales (Madrid, Spain),

of the Muséum national d'Histoire naturelle (Collections d'Anatomie Comparée, Paris, France) as well as Blain's and Bailon's personal collections.

In this work the fossils from Cueva Victoria have been compared with fossil and extant Eurasian and North-African species from the *B. bufo* group (i.e. genus *Bufo* sensu stricto (Frost et al., 2006): *B. bufo*, *Bufo gargarizans* and *Bufo verrucosissimus*), *B. viridis* group (i.e. genus *Pseudepidalea* sensu (Frost et al., 2006): *B. viridis* s.l., *Bufo raddei*, *Bufo brongersmai* and possibly the Early Miocene fossil *Bufo* aff. *viridis* and *Bufo priscus*), *Bufo mauritanicus* (“*Bufo*” *mauritanicus* according to Frost et al. (2006)), *B. calamita* (i.e. genus *Epidalea* sensu Frost et al. (2006)) and *Bufo regularis* (i.e. genus *Amietophrynus* sensu Frost et al. (2006)). Although the separation of the different species within *Bufo* groups is made according to Frost et al. (2006), we have not retained here their nomenclature (i.e. the new genera). *B. viridis* sensu lato is here used as its former acceptance before that molecular biology separates it in the western part of its distribution area into *Bufo balearicus*, *Bufo siculus*, *Bufo boulengeri*, *B. viridis* sensu stricto and *Bufo variabilis*.

The osteological nomenclature follows Bailon (1999); Blain (2005, 2009); Sanchíz (1998). The fossil bones have



**Fig. 2.** Fossil remains of *Bufo viridis* s.l., late Early Pleistocene, Cueva Victoria, Murcia, Spain. 1. right frontoparietal-prototic-exoccipital complex, ventral and dorsal views; 2. sphenethmoid, dorsal, ventral and anterior views; 3. sacrum, dorsal and ventral views; 4. right scapula, dorsal and ventral views; 5. right ilium, lateral view; 6. left humerus, ventral view.

**Fig. 2.** Fossiles de *Bufo viridis* s.l., Pléistocène inférieur final, Cueva Victoria, Murcie, Espagne. 1. complexe frontopariétal-prototique-exoccipital droit, vues ventrale et dorsale; 2. sphénethmoïde, vues dorsale, ventrale et antérieure; 3. vertèbre sacrée, vues dorsale et ventrale; 4. scapula droite, vues dorsale et ventrale; 5. ilion droit, vue latérale; 6. humérus gauche, vue ventrale.

been illustrated (Fig. 2) using the Environmental Scanning Electron Microscope from the Universitat Rovira i Virgili (Tarragona, Spain) and photographic pictures for larger bones (G. Campeny, IPHES, Tarragona).

#### 4. Systematic study

##### 4.1. Cueva Victoria

All the fossil bones have the osteological characteristics of the genus *Bufo*. We do not detail here these general characteristics, which the reader may find in other

works. Detailed descriptions of the species discussed below are from Bailon (1991, 1999); Bailon and Hossini (1990); Blain (2005); Böhme (1977); Delfino et al. (2009); Hodrova (1986); Hossini (2001, 2002); Ratnikov (2001); Sanchíz (1977, 1998). Note that in the following systematic discussion, *B. viridis* s.l. is employed as a synonym for the species *B. balearicus*, *B. siculus*, *B. boulengeri*, *B. viridis* sensu stricto and *B. variabilis*, because these newly created species and subspecies have not yet been diagnosed separately from an osteological point of view. The attribution of the fossil material from Cueva Victoria to green toads is based mainly on the morphology of the frontoparietal-prototic-

exoccipital complex, sphenethmoid, ilium, scapula, sacrum and humerus.

The frontoparietal (Fig. 2.1) is not fused with its homolog. In dorsal view, its dorsal surface is concave, and an occipital canal (fossula limitans) is present and relatively well developed. A small supraorbital tectum seems to be present however it is more developed than the variability seen in all the consulted modern specimens of *B. viridis* s.l., where generally there is no supraorbital tectum. In the *B. viridis* group the frontoparietal is usually fused to the prootic and to the exoccipital at an early stage, whereas it is usually still isolated in adults of *B. bufo*, *B. mauritanicus*, *B. gargarizans* and *B. verrucosissimus*. The frontoparietal is moderately wider anteriorly, with a medial margin (margo medialis) that is more or less regular, an occipital canal generally shorter and narrower than in *B. calamita*, and with a postorbital crest on the medial or posterior part of the prootic. In *B. calamita* the frontoparietal is narrower anteriorly, with an irregular medial margin, an occipital canal antero-laterally steeped and a postorbital crest located anteriorly on the prootic. In *B. bufo* it has a sub-rectangular shape, and the dorsal surface is flat and the occipital canal long and moderately wide. In *B. raddei*, it is rather similar to *B. calamita* but with a sinuous medial margin, and in *B. brongersmai* the anterior part of the frontoparietal is always reduced to a narrow process.

The fossils from Cueva Victoria differ from *Bufo priscus* Špinar, Klembara and Meszároš, 1993 from the Middle Miocene of Bonanza Quarry (MN6, Slovakia in Sanchíz (1998); Špinar et al. (1993)) because they do not have any dorsal rugosities on the frontoparietal (even if some shallow grooves are present), the supraorbital tectum is strongly less developed and finally differ by the presence of a well developed postorbital crest well visible in dorsal view.

In *Bufo* aff. *viridis* Bailon and Hossini, 1990 from the Early Miocene of Vieux-Collonges (MN4, France (Bailon and Hossini, 1990) and from the Middle Miocene of La Grive-Saint-Alban (MN7 and 8, France (Bailon and Hossini, 1990)), the occipital canal is more parallel to the major axis of the frontoparietal than in our fossil and in the extant *B. viridis* s.l. and a developed supraorbital tectum is present. The postorbital crest is somewhat similarly developed and located than on our fossils.

In *B. viridis* from the Late Miocene (MN13) and Early Pliocene (MN14) of Hungary described in Venczel (1997, 2001), a well developed supraorbital tectum is present and the postorbital crest is lacking (or at least invisible in dorsal view) unlike in our fossil but similar to *Bufo priscus*. The occipital canal is similarly opened and oriented that on our fossils. According to Venczel (1997) a secondary ossification is present on the surface of the frontoparietal and the tectum supraorbital in the Polgárdi 5 fossil (Late Miocene, Hungary).

The sphenethmoid (Fig. 2.2) is just as wide as long, with short anterior and lateral processes. It shows a typical thickening (sella amplificans) on the floor (solum nasi) of each anterior alveolus (antrum olfactorium). In *B. viridis* s.l. this thickening is particularly well developed, whereas it is less high in *B. calamita*, *B. raddei* and in particular in *B. brongersmai*, thinner in *B. mauritanicus*, and absent in

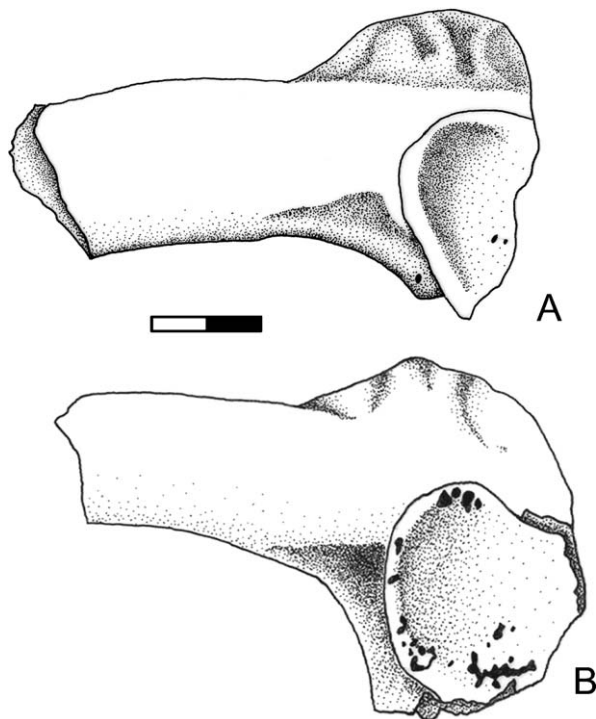
*B. bufo*, *B. gargarizans* and *B. verrucosissimus*. Moreover, in *B. brongersmai*, the lateral walls and lateral process of the sphenethmoid usually show a fenestration. Our fossils are rather similar in shape to *B. aff. viridis* from the Miocene of La Grive-Saint-Alban figured in Bailon and Hossini (1990).

The sacrum (Fig. 2.3) has an anterior cotyle and two posterior condyles. The processus transversus are moderately antero-posteriorly spread, and a laterally opened dorsal fossa is present at the base of the processus as in *B. viridis* s.l., *B. raddei*, *B. mauritanicus*, *B. brongersmai* and *B. calamita*, whereas in *B. bufo*, *B. gargarizans* and *B. verrucosissimus* there is no (or a lesser developed) fossa. According to Bailon (1999); Bailon and Hossini (1990), this fossa opens more laterally in *B. viridis* s.l. than in *B. calamita*. This characteristic seems to be quite variable in *B. brongersmai*. Our fossils are rather similar in shape to *B. aff. viridis* from the Miocene of La Grive-Saint-Alban figured in Bailon and Hossini (1990).

The scapula (Fig. 2.4) is longer than wide, with a processus glenoidalis separated from the bone and well visible in dorsal view. The pars acromialis and the processus glenoidalis are robust. A shallow supraglenoidalis fossa is present, as usually in *B. viridis* s.l., *B. calamita* and *B. mauritanicus*, whereas it is absent in the *B. bufo* group, *B. regularis*, *B. brongersmai* and generally absent in *B. aff. viridis* from the Miocene of La Grive-Saint-Alban (Bailon and Hossini, 1990). In *B. priscus* and *B. raddei* no mention has been made of the presence of a supraglenoidalis fossa and the shape of the bone is quite different from our fossils in particular for the processus glenoidalis in *B. priscus* and the slenderness of the collum scapulae in *B. raddei*.

The ilium (Fig. 2.5) lacks a dorsal crest, and the tuber superior is low and has a round and uni- or bilobated dorsal edge as in *B. viridis* s.l., *B. raddei*, *B. regularis*, *B. brongersmai* and *B. mauritanicus*, whereas in *B. calamita* and *B. bufo* it is always unilobated. A well-developed preacetabular fossa is present, as in *B. viridis* s.l., *B. mauritanicus*, *B. regularis*, *B. brongersmai* and *B. raddei*. The fossil ilia do not show any latero-ventral outgrowth (“calamita ridge”) on the ilial shaft (pars cylindriciformis), unlike *B. calamita* and *B. raddei*. The pars descendens is poorly developed and does not have the markedly convex outline seen in *B. brongersmai* and *B. regularis*, where the angle between the pars cylindriciformis and the pars descendens is close to 90°. *B. mauritanicus* generally reaches a larger size than our fossil material.

The humerus (Fig. 2.6) has a slightly curved and relatively thick shaft, the distal condyle is slightly displaced laterally, and the condyle and epicondyles are relatively little developed. In male specimens, the humerus bears a long and well-developed transversal medial crest (crista medialis). The diaphysis is less curved, less robust and more elongated than in *B. calamita*, whereas in *B. bufo*, *B. gargarizans* and *B. verrucosissimus* it is generally thicker. The ventral crest, according to Hossini (2002), is slightly shorter in *B. viridis* s.l. than in juveniles of *B. mauritanicus*. In *B. raddei* the diaphysis is generally shorter and thicker than in *B. viridis* s.l. and strongly curved. In *B. regularis* the diaphysis is similar in shortness and thickness but slightly more curved than in our fossils. Our fossils are rather similar in shape and robustness to *B. aff. viridis* from the Miocene of La Grive-Saint-Alban, nevertheless the medial crest is more



**Fig. 3.** Left ilia of the *Bufo viridis* group previously published as *Bufo* sp. **A.** Barranco León D, Early Pleistocene, Granada, Spain (Blain, 2005); **B.** Almenara-Casablanca 3, late Early Pleistocene, Castellón, Spain (Blain, 2005, 2009; Blain et al., 2007). Scale bar = 2 mm.

**Fig. 3.** Iliions gauches du groupe *Bufo viridis*, antérieurement publiés comme *Bufo* sp. **A.** Barranco León D, Pléistocène inférieur, Grenade, Espagne (Blain, 2005); **B.** Almenara-Casablanca 3, Pléistocène inférieur final, Castellón, Espagne (Blain, 2005, 2009; Blain et al., 2007). Barre d'échelle = 2 mm.

developed in the figured fossil humerus of male (Bailon and Hossini, 1990).

In conclusion, all the osteological characteristics shown by the fossil material from Cueva Victoria permit a clear attribution to *B. viridis* s.l. and to exclude attribution to the extant *B. bufo* group, *B. calamita*, *B. mauritanicus*, *B. raddei*, *B. brongersmai* and *B. regularis* and to fossil *B. priscus*. Nevertheless our fossils differ to what as been observed in extant *B. viridis* s.l. by the presence (although poorly developed) of a supraorbital tectum on the frontoparietal. Such a characteristic seems to be reminiscent from the Miocene and Pliocene fossils from France, Slovakia and Hungary (Bailon and Hossini 1990; Špinar et al., 1993; Venczel, 1997, 2001). However it is possible that variability for this characteristic is greater than though in *B. viridis* s.l.

#### 4.2. Barranco León D and Almenara-Casablanca 3

As an extension of the study of the abundant material from Cueva Victoria, some previously published material from two other Early Pleistocene localities in southeastern Spain can be newly interpreted (Fig. 3): Barranco León D (ca. 1.3 Ma, Guadix-Baza, Granada, see Fig. 4) and Almenara-Casablanca 3 (ca. 1.1 Ma, Castellón, see Fig. 4). Previously a few bones have been published as *Bufo* sp. (Agustí et al.,

2009, 2010, in press; Blain, 2005, 2009; Blain et al., in press) because they do not match the two modern Iberian bufonid species: *B. bufo* and *B. calamita*. The presence of a low tuber superior with a round, bilobated dorsal edge as well as a developed preacetabular fossa led one to suppose that these bones might belong to the *B. viridis* group, but in the absence of more material this assignation was uncertain, because no other Iberian locality yielded unequivocal fossil remains of this group at that time.

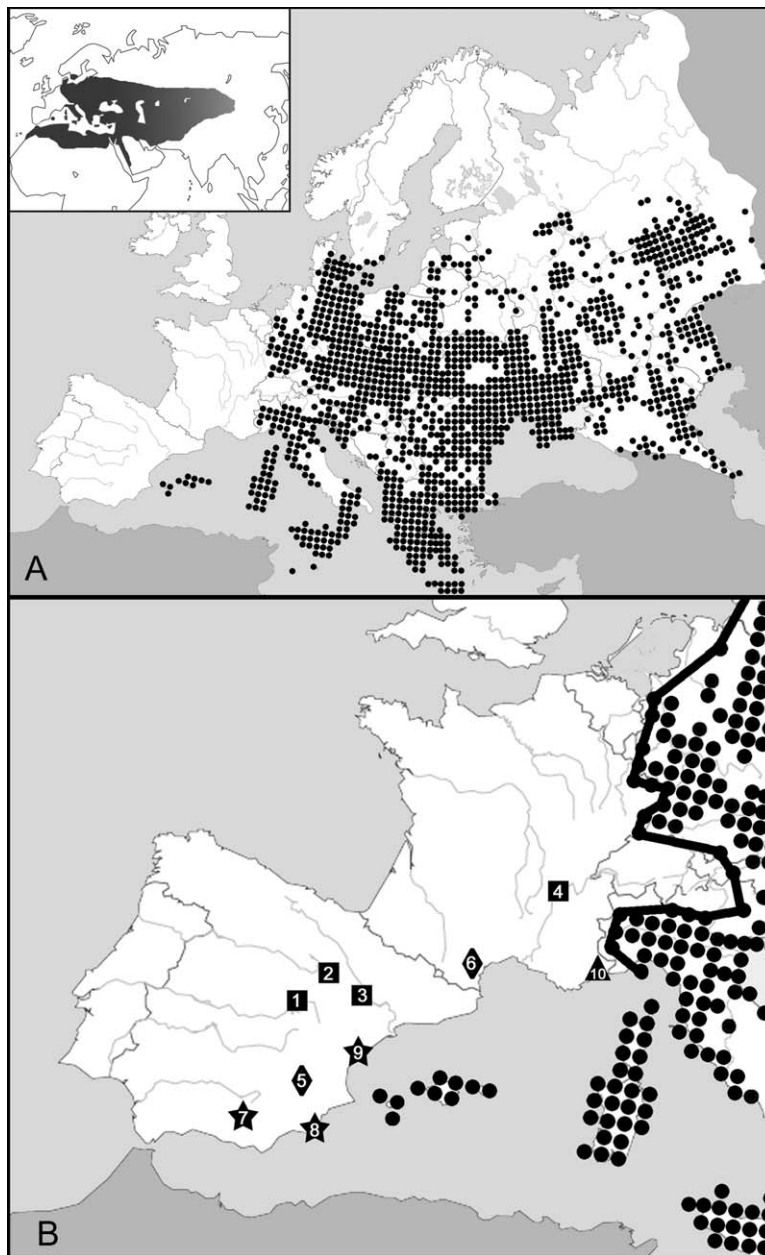
Consequently, in the light of the numerous remains of the *B. viridis* s.l. from the Early Pleistocene of Cueva Victoria, the fossil material from Barranco León D (now comprising five ilia (Blain, 2005; Blain et al., in press)) and Almenara-Casablanca 3 (only one left ilium (Blain, 2005, 2009; Blain et al., 2007)) can be now determined as pertaining to the *B. viridis* group.

#### 5. Palaeobiogeographical implications

*B. viridis* s.l. as used in this work corresponds 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 (Fig. 4A). Because of the high morphological variability of the green toad, several forms, as species and subspecies, have been described within its extensive range: *Bufo balearicus* (Apennine Peninsula, Corsica, Sardinia, Balearic Islands), *B. siculus* (Sicily), *Bufo boulengeri* (North Africa), *B. viridis* sensu stricto (central and eastern Europe) and *B. variabilis* (the Balkans, Anatolia) (Stöck et al., 2001, 2006, 2008). These species 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 and shallow water bodies (El Hamouni et al., 2007; Sicilia et al., 2006).

In the fossil record of western Europe (west of its current continental distribution area, Fig. 4B (Bailon and Hossini, 1990; Rage and Roček, 2003; Sanchíz, 1998)) the *B. viridis* group is reported in the Early to Middle Miocene of Spain in Córcoles (MN4), Escobosa de Catalañazor (MN7–8) and Manchones II (MN6) and from France in Vieux-Collonges (MN4) and La Grive-Saint-Alban (MN7 and 8). The earliest extant green toads (*B. cf. viridis*) are mentioned in the Pliocene of Rincón 1 (MN16, Spain (Alberdi et al., 1982; Sanchíz, 1998)) and Mas Genegals (MN16/17, France (Bailon, 1991)). As an extension of this work, we consider that two other Spanish Early Pleistocene sites (Barranco León D (Granada) and Almenara-Casablanca 3 (Castellón)) have delivered some remains (mainly ilia) that document the presence of a green toad but whose attribution has until now remained cautiously as *Bufo* sp. (Agustí et al., 2009, 2010, in press; Blain, 2005, 2009; Blain et al., in press). The youngest recorded occurrence of the *B. viridis* group outside but very near to the current westernmost limit of its distribution area was in the Middle Pleistocene of Terra Amata, southeastern France (Bailon, 1991).

A few elements have been attributed to *B. aff. viridis* in the Late Pleistocene of Cueva Horá (Granada, Spain (Bailon,



**Fig. 4. A.** Current distribution area of *Bufo viridis* s.l. (modified from Gasc et al. (1997); Stöck et al. (2006)). **B.** fossil localities with the *Bufo viridis* group to the west of its present-day distribution. **Miocene** (square), 1. Córcoles (Guadalaraja, MN4), 2. Escobosa de Catalañazor (Soria, MN7-8), 3. Manchones II, (Zaragoza, MN6), 4. Vieux-Collonges (Rhône, MN4) and La Grive-Saint-Alban (Isère, MN7 and 8); **Pliocene** (diamond), 5. Rincón 1 (Albacete, MN16), 6. Mas Genegals (Hérault, MN16/17); **Early Pleistocene** (star), 7. Barranco León D (Granada, ca. 1.3 Ma), 8. Cueva Victoria (Murcia, ca. 1.1–1.2 Ma), 9. Almenara-Casablanca 3 (Castellón, ca. 1.1 Ma); **Middle Pleistocene** (triangle), 10. Terra Amata (Alpes-Maritimes, ca. 0.4 Ma).

**Fig. 4. A.** Aire de distribution actuelle de *Bufo viridis* s.l. (modifiée de Gasc et al. (1997); Stöck et al. (2006)). **B.** sites ayant livré des fossiles du groupe *Bufo viridis*, à l'ouest de son aire de distribution moderne. **Miocène** (carré), 1. Córcoles (Guadalaraja, MN4), 2. Escobosa de Catalañazor (Soria, MN7-8), 3. Manchones II, (Saragosse, MN6), 4. Vieux-Collonges (Rhône, MN4) et La Grive-Saint-Alban (Isère, MN7 et 8); **Pliocène** (losange), 5. Rincón 1 (Albacète, MN16), 6. Mas Genegals (Hérault, MN16/17); **Pleistocène inférieur** (étoile), 7. Barranco León D (Grenade, environ 1,3 Ma), 8. Cueva Victoria (Murcie, environ 1,1–1,2 Ma), 9. Almenara-Casablanca 3 (Castellón, environ 1,1 Ma); **Pleistocène moyen** (triangle), 10. Terra Amata (Alpes-Maritimes, environ 0,4 Ma).

1986)), but these probably correspond more exactly to *B. calamita* (S. Bailon, personal communication). In addition, *B. viridis* has been mentioned by Holmann (1998) in the Middle Pleistocene of East Farm (Suffolk, England), although Sanchíz (1998) does not mention it.

On the other side of the Mediterranean Sea, in North Africa, *B. viridis* is known since the Late Pliocene of Ahl Oughlam (Casablanca, Morocco (Bailon, 2000)).

Various authors have suggested that the climatic conditions linked with the Messinian Salinity Crisis stimulated

the propagation of steppe taxa (*sensu lato*), that these climatic changes were doubtless favorable to the extension from the east of fauna and flora typical of Eurasian steppes, and that dispersals throughout the Mediterranean area may have been greatly favored by the increase in emerged lands due to the partial desiccation of the Mediterranean Sea (Blondel and Aronson, 1999; Suarez Cardona et al., 1992). In short, it has been suggested that these events at the end of the Miocene provided the environmental basis for the formation of the first Iberian steppes, and that they likewise stimulated the entrance and dispersal of steppe taxa coming from North Africa and the steppe areas of southern Eurasia. According to the molecular data (Stöck et al., 2006), this is probably the case for *B. viridis* s.l. which suggest a dispersal into western Europe and the western Mediterranean Islands for extant populations prior to the Early Pliocene (around 5 Ma), very probably due to (or favored by) the Messinian Salinity Crisis. Nevertheless a closely related form to *B. viridis* s.l. (*B. aff. viridis*) is still present in the Early and Middle Miocene of France (Bailon and Hossini, 1990).

Three scenarios are possible:

- the dispersal of the *B. viridis* s.l. in western Europe dates from the Latest Miocene (as stated by Stöck et al. (2006)), favored by the desiccation of the Mediterranean Sea, which created new routes for vertebrate fauna. Subsequently its distribution area was progressively reduced and withdrawn to its present-day distribution; in the Iberian Peninsula it survived owing to the particular ecological and/or climatic particularities of the semi-arid landscapes until the end of the late Early Pleistocene in Barranco León D (ca. 1.3 Ma), Cueva Victoria (ca. 1.1–1.2 Ma) and Almenara-Casablanca 3 (ca. 1.1 Ma). According to the study of mitochondrial relationships within the *B. viridis* s.l. (Stöck et al., 2006), Balearic populations (*B. balearicus*) are closer to the central European and Asia Minor populations (*B. viridis* and *B. variabilis*) than to the North-African *B. boulengeri*, so that probably the Late Miocene dispersal event came from Asia;
- although there was a first dispersal in western Europe during the Latest Miocene (and because no fossils of green toads have been found in the Earliest Pleistocene), the late Early Pleistocene Spanish green toads may have been associated with a second dispersal event from central Europe (*B. balearicus* or *B. viridis sensu stricto*) or, less probably, from North Africa (*B. boulengeri*) via the Strait of Gibraltar. For the moment no palaeontological data reveal whether there was a relation between the Iberian and the North-African populations known as early as the Late Pliocene (Bailon, 2000) or with the central European populations known since the Late Miocene and Pliocene (MN13 to MN16) of Italy, Greece, Turkey, Hungary and Poland (compiled in Sanchíz (1998)). Nevertheless, the African hypothesis cannot be disregarded according to a recent study using mitochondrial and nuclear markers (Stöck et al., 2006), which suggests that Sicilian green toad populations (newly named *B. siculus*) were more closely related to the North-African *B. boulengeri* than to the European green toads, and that the split may have occurred after the Middle Pliocene (3.6 Ma) (i.e.

independent of the Messinian Crisis), when the Strait of Sicily became a major biogeographical barrier, with some 140 km of sea-water today between Tunisia and Sicily;

- the Early Pleistocene Spanish fossils of *B. viridis* s.l. may come from a Mio-Pliocene autochthonous European population that had survived until the end of the Early Pleistocene in the South of the Iberian Peninsula. Although it is quite difficult for the moment to support this hypothesis, the presence of a supraorbital tectum on the frontoparietal seems to be an archaic characteristic only found on the European Miocene and Pliocene fossils (Bailon and Hossini, 1990; Špinar et al., 1993; Venczel, 1997, 2001).

## 6. Palaeoecological implications

As underlined by Sanchíz (1997), extinction, whether absolute or only in a defined territory, is not probabilistically predictable in relation to ecological or physiological parameters for fossils. In 1989, living *B. viridis* was mentioned in the province of Murcia (Dicenta et al., 1989), but further investigations have not confirmed its presence. As a consequence, because neither living green toads nor fossils from after the Middle Pleistocene have been recorded from the Iberian Peninsula, it is very probable that *B. viridis* s.l. became locally extinct in Spain.

During the Middle Pleistocene transition (MPT), the Earth's climatic system is known to have experienced a major change related to intensification of the Northern Hemisphere glaciation, with a significant shift toward more intense glacial conditions, which occurred between 1250 and 700 ka. The emergence of low-frequency, high-amplitude, quasi-periodic (100-kyr) glacial variability during the Middle Pleistocene in the absence of any significant change in orbital forcing indicates a fundamental change internal to the climate system. Its onset was accompanied by decreases in sea surface temperatures in the North Atlantic and tropical-ocean upwelling regions and by an increase in African and Asian aridity and monsoonal intensity (Clark et al., 2006). On lands the MPT corresponds to a major rearrangement of mammalian communities (e.g. Croitor and Brugal, 2010; Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2005, 2010; Palombo, 2010). Nevertheless, semi-arid steppe environments seem to have occurred in southeastern Spain throughout the Middle and Late Pleistocene, and the climate was not very harsh even during glacial periods (e.g. Carrión et al., 2010; López-García, 2008). And even if some late Early Pleistocene localities suggest mean annual precipitations to have been higher than today in southeastern Spain (Agustí et al., 2009; Blain et al., 2007, 2008a, in press), a period of aridity is well recorded during summer that favored the existence of semi-arid open landscape (Blain et al., in press). So why did the green toads from the Iberian Peninsula disappear?

Another hypothesis can be made. It seems that today in southeastern Spain the natterjack toad *B. calamita* has a preference for arid environments and in particular is more likely to be found in areas with very low climatic stability (Romero and Real, 1996). So might the disappearance of *B. viridis* from the Iberian Peninsula be due to a competition for habitat with *B. calamita*? Romero and Real (1996)



show that in the south of the Iberian Peninsula *B. bufo* has a different distribution from *B. calamita* with respect to certain climatic and environmental parameters. Moreover, they suggest that the evolution of these parameters has an influence on the competitiveness of toads. As *B. calamita* shows the greater adaptability under an unpredictable climate, might it have exerted a pressure on *B. viridis* leading to its complete disappearance?

*B. calamita* currently lives in a large part of Europe from the Iberian Peninsula to Byelorussia and Ukraine at the east and Estonia at the north. It is lacking south of the Alps and Carpathian as well as in Mediterranean Islands (like the Balearic Islands for example) (Pleguezuelos et al., 2002). Its earliest fossil occurrence is reported from the Late Miocene of Spain in Concud, Mansuetos (MN12 (Sanchíz, 1977, 1998)) and from the Pliocene of Spain and France in Sète (MN15), Islas Medas (MN16) and Montoussé 5 (MN17) (Bailon, 1991; Sanchíz, 1998). It is noticeable that in Cueva Victoria, Barranco León D and Almenara-Casablanca 3, the presence of *B. calamita* is very scarce, whereas *B. bufo* is always represented, though only from a few remains. At the same time, in other Pleistocene localities from northern Spain in the Sierra de Atapuerca, more than 50,000 bufonid fossil remains have so far been studied in the Sima del Elefante (ca. 1.2 Ma (Blain et al., 2010; Cuenca-Bescós et al., 2010; Rodríguez et al., in press)) and in Gran Dolina (ca. 0.9 to 0.2 Ma (Blain et al., 2008b, 2009)), and no evidence of *B. viridis* has been found; *B. calamita* is far less the more abundant and *B. bufo* varyingly represented but with a much lower abundance.

From an ecological point of view, some characteristics in common between Barranco León D, Cueva Victoria and Almenara-Casablanca 3 can be noted that may have favored the presence of *B. viridis* over other bufonids. These three localities are currently located in one of the aridest areas of the Iberian Peninsula, with low rainfall (<400 mm) and high summer temperatures. Moreover, the water available in the vicinity of these localities was very probably brackish (at least temporarily) in the large, shallow lake of Barranco León D (Anadón and Gabàs, 2009; Gibert et al., 2007), and in Almenara-Casablanca 3 and Cueva Victoria that were very near to the Mediterranean Sea (Figs. 1 and 4). It is common knowledge that *B. viridis* is one of the few Mediterranean anurans that tolerates brackish water to reproduce (El Hamouni et al., 2007; Sicilia et al., 2006), whereas *B. calamita* usually avoids such environments (Banks and Beebe, 1987; Gómez-Mestre, 2009). Such competition between *B. calamita* and *B. viridis* has never been studied (either in a laboratory or in the field), although it has been tentatively suggested in order to explain the eastern limits of *B. calamita* (Beebe and Rowe, 2000). Laboratory experiments are not rare for evaluating the competition between genus *Bufo* toad tadpoles (e.g. Banks and Beebe (1987); Katzmann et al. (2003)), but again no data are available between *B. calamita* and *B. viridis*.

A similar pattern may perhaps have occurred in the replacement of the Mongolian toad (*B. raddei*) by *B. viridis* in the East-European Platform. According to Ratnikov (1996), most of the reliable finds of *B. viridis* in the Russian Platform are restricted to the Upper Pleistocene–Holocene, whereas in the Late Pliocene–Middle Pleistocene *B. raddei* is found

persistently. In the Late Pliocene the Mongolian toad seems to have occupied a vast area including, besides its recent natural habitat, the southern Russian Platform, where it persisted up to the Middle Pleistocene. The green toad, inhabiting eastern Europe (since the Late Miocene [Sanchíz, 1998]), appeared in the Russian Platform only recently in the Late Pleistocene, when the area of the Mongolian toad had been reduced substantially. So far, however, no clear conclusions have been reached on this replacement that may suggest competition between these two toads.

## 7. Conclusions and perspectives

For the first time fossil remains of a green toad (*B. viridis* s.l.) are identified in the Early Pleistocene of the Iberian Peninsula, in three late Early Pleistocene localities: Barranco León D (ca. 1.3 Ma), Almenara-Casablanca 3 (ca. 1.1 Ma) and Cueva Victoria (ca. 1.1–1.2 Ma). They correspond to the last occurrence of the *B. viridis* group in the westernmost part of Europe.

Since no osteological differences have been established between the recently described extant species of *B. viridis* s.l. (e.g. *B. balearicus*, *B. siculus*, *B. boulengeri*, *B. viridis* and *B. variabilis*) no precise palaeobiogeographical relationships can be drawn for the Spanish fossils. However, the possible (although improbable) entrance of these toads via the Strait of Gibraltar is of particular relevance in the debate on the post-Messinian North Africa–Europe interchange. Moreover, the occurrence of a third species of bufonid toad during the Pleistocene in the south of the Iberian Peninsula raises some interesting ecological questions in relation to the local disappearance of the green toad, which can be hypothetically linked with the intensification of the Pleistocene glacial/interglacial climate dynamics (emergence of low-frequency, high-amplitude, quasi-periodic 100-kyr glacial variability) and/or with probable competition with another toad, *B. calamita*, which today in southeastern Spain shows a preference for arid environments and in particular is more likely to be found in areas with very low climatic stability.

As perspectives opened up by this work: an osteological revision of all the newly-named species of the *B. viridis* group is required in order to establish the relationship of the Spanish fossils with extant species; also, a revision of the bufonid fossil record in Spain since the Miocene and in particular in the Late Pliocene – Early Pleistocene is needed in order to clarify whether there were no, one or two dispersal events for green toads in western Europe.

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