

Amphibians and squamate reptiles from the latest early Pleistocene of Cueva Victoria (Murcia, southeastern Spain, SW Mediterranean): Paleobiogeographic and paleoclimatic implications

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ABSTRACT

The karstic filling of Cueva Victoria in southeastern Spain, dated from the latest early Pleistocene (ca. 1.1 Ma), is famous for providing primate fossil remains (*Theropithecus*) of typical African origin, in the general controversy on the antiquity of the first hominid settlements in Western Europe and their possible entrance into Europe through the Strait of Gibraltar. Cueva Victoria has also furnished the following fauna of anurans and squamate reptiles: cf. *Pelodytes* sp. (Pelodytidae), *Bufo* cf. *B. bufo* (Bufonidae), *Blanus cinereus* (Blanidae), *Tarentola* sp. (Geckonidae), *Chalcides* cf. *Ch. bedriagai* (Scincidae), *Timon* cf. *T. lepidus* and indeterminate small lacertids (Lacertidae), *Natrix maura*, *Coronella girondica*, *Rhinechis scalaris* and *Malpolon* cf. *M. monspessulanus* (Colubridae). This faunal association seems to suggest a mean annual temperature slightly fresher than nowadays (approximately 1°C less than at present in the area), with cooler winters but warmer summers and above all higher mean annual precipitations (+ 400 mm). The landscape may correspond to an open forest environment of a Mediterranean type, with some still water points.

KEYWORDS | Herpetofauna. Strait of Gibraltar. Spain. Early Pleistocene. Paleobiogeography. Paleoclimatology. Paleoeecology.

INTRODUCTION

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 enclosed lagoon adjacent to the Mediterranean Sea, called Mar Menor (Fig. 1).

The first mention of fossil remains presence in Cueva Victoria dates from 1976. The paleontologist J. Pons-Moyà made a first excavation campaign (Pons-Moyà and Moyà-Solà, 1979; Pons-Moyà, 1981, 1982, 1985). Then a team from the Institut de Paleontologia Miquel Crusafont de Sabadell (Barcelona) and the Spanish National Research Council (CSIC) comprising J. F. Villalta, E.

Carbonell, J. Agustí and S. Moyá described the cavity, part of the faunal remains, as well as some supposed lithic industry considered to be the first evidence of a hominine presence in the Iberian Peninsula (Alcalde et al., 1981; Carbonell et al., 1981; Agustí, 1982; Moyà-Solà and Menéndez, 1986). Finally, J. Gibert joined the project in 1984 and since then has organized numerous excavation campaigns in Cueva Victoria, working above all on highlighting the few remains attributed at the time to *Homo* sp. (Gibert, 2004a; Gibert et al., 2006, 2008).

The attribution of a phalanx to the genus *Homo* (Gibert and Pons-Moyá, 1984, 1985; Gibert et al., 1985, 1989, 1992a, 1999, 2002, 2006, 2008; Gibert and Pérez-Pérez, 1989; Pons-Moyá, 1985; Pérez-Pérez, 1989; Santamaria and Gibert, 1992; Palmqvist et al., 1996; Gibert, 2004a, 2004b) has contributed to the media coverage of the site in the context of the controversy regarding the presence of humans in the South of the Iberian Peninsula during the early Pleistocene. These remains have since been attributed by some authors to the African primate *Theropithecus* (Palmqvist et al., 2005; Martínez-Navarro et al., 2005, 2008).

In this paper, we briefly describe the amphibian and squamate reptile bone remains of Cueva Victoria in order to infer data on the paleoenvironment and paleoclimate in southeastern Spain at the end of the early Pleistocene.

GEOLOGICAL SETTING

The karstic complex is composed of 6 large rooms and various galleries (Ferrández et al., 1989). At the beginning of the 19th century, the mining of manganese led to the reopening of the cavity by two artificial entries. Most of the cavity's sediment has been removed by miners while digging out galleries. Only a little evidence of the Pleistocene layers has been preserved, mainly on the walls and in the roof of the cavity (Ferrández et al., 1989).

The stratigraphical sequence (Fig. 1) permits to understand the history and evolution of the cavity (Ferrández et al., 1989). The first deposits, a rather thick layer of laminated red clay (*terra rosa*) containing nodules of manganese and proceeding from the dissolution of Lower Triassic limestone, accumulate in the lowest areas when the

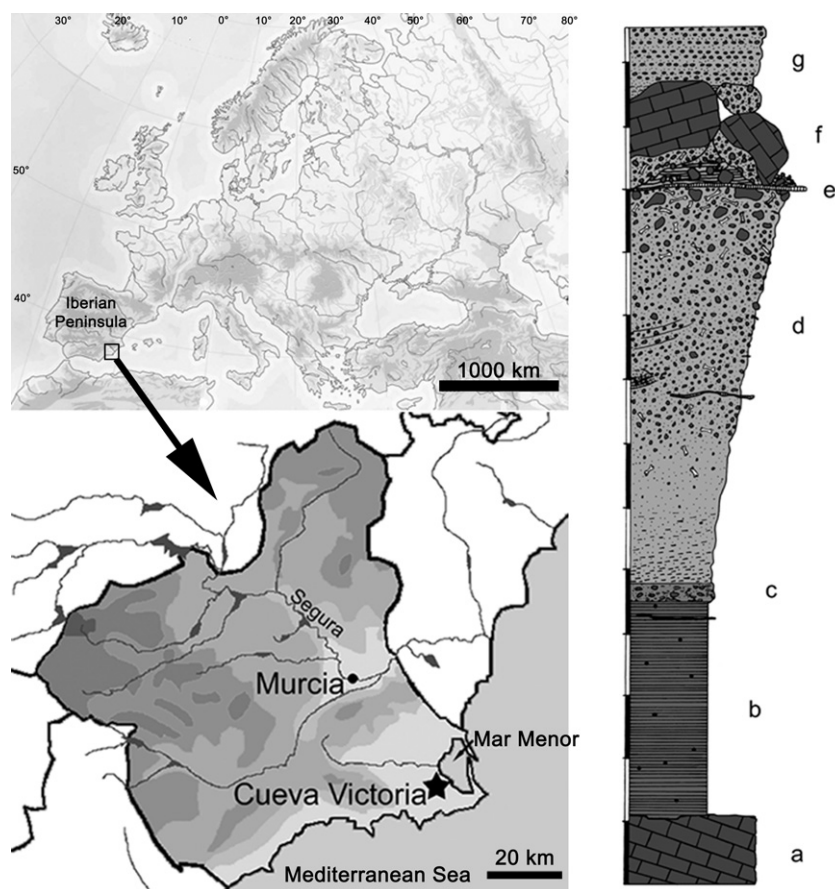


FIGURE 1 | Geographical location and simplified stratigraphy (redrawn from Ferrández et al., 1989; Gibert et al., 1992b, 1999, 2006) of Cueva Victoria (Murcia, Spain). a: Triassic limestone and dolomite; b: red clays (*terra rosa*) laminated with manganese nodules; c: reworked clays and first exogenous sediments; d: fossiliferous breccia; e: calcitic layers; f: material of the mining exploitation; g: recent sediments.

cavity was still closed. During the early Pleistocene, the cavity opens out and fills up with detrital material dominated by heterometrical breccias, coarse sands and clays, constituting the so-called fossiliferous breccia. The cavity at this time was used as hyena's den, as evidenced by the large amount of coprolites and gnawed and broken bones (Gibert et al., 1992b). The filling out of the cavity seems to have occurred before the end of the early Pleistocene (Gibert et al., 1992b). Finally, residues from the mining exploitation of manganese and recent sediment are present above the flowstone.

CHRONOLOGY OF CUEVA VICTORIA

According to the latest revisions, the faunal association of Cueva Victoria consists of an indeterminate teleost fish, 23 species of birds (Gibert et al., 2006), a tortoise (*Testudo hermanni*; García-Porta, 2001), and a number of small mammals (*Crocidura kornfeldi*, *Erinaceus* cf. *E. europeus*, *Allophaiomys chalinei*, *Allocricetus bursae* ssp., *Apodemus* aff. *mystacinus*, *Castillomys crusafonti rivas*, *Eliomys quercinus* ssp., *Hystrix* aff. *major*, *Myotis emarginatus*, *Rhinolophus mehelyi*, *Miniopterus* sp., *Rhinolophus hipposideros*, *Myotis myotis*; Alcalde et al. 1981; Agustí 1982; Sevilla García, 1988) and large mammals (*Theropithecus* sp., *Canis etruscus*, *Vulpes* sp., *Xenocyron lycaoides*, *Panthera onca gombaszoegensis*, *Puma pardoides*, *Homotherium crenatidens*, *Meganthereon* cf. *M. cultridens*, *Pachycrocuta brevirostris*, *Ursus* cf. *U. etruscus*, *Lynx spelaea*, *Mustela* sp., *Hippopotamus antiquus*, *Hemitragus bonali*, *Megaloceros savini*, *Ovibovini* indet. et *Bos/Bison* sp., *Dama* sp., *Stephanorhinus etruscus*, *Equus granatensis* and *Equus* sp., *Mammuthus meridionalis* and *Monachus* sp.; Pons-Moyá, 1982; Gibert et al., 1992c, 1999, 1995; Crégut-Bonnoure, 1999; Martínez-Navarro et al., 2005; Palmqvist et al., 2005).

Such a faunal association in Cueva Victoria indicates an early Pleistocene age, with the presence of characteristic large mammals such as *Canis etruscus*, *Pachycrocuta brevirostris*, *Ursus* cf. *U. etruscus*, *Stephanorhinus etruscus* or *Mammuthus meridionalis*. However, its position within the early Pleistocene has been a matter of debate. Earlier analysis of the fauna placed the site at the base of the early Pleistocene, in a position close to the site of Venta Micena in the Guadix-Baza Basin (Agustí et al., 1987). This assumption was based on the presence of an archaic rhinoceros species (*Stephanorhinus etruscus*), which was supposed to be less evolved than the rhinoceros from Venta Micena, assigned by Santafé-Llopis and Casanovas-Cladellas (1987) to *S. etruscus brachycephalus* (= *S. hundsheimensis*). By contrast, a middle

Pleistocene age has been proposed by Crégut-Bonnoure (1999) and van der Made (2004) on the basis of the evolutionary degree of some ruminants. Among the small mammals, the rodents and, more particularly, the arvicolids were of little help in these assessments, since the only species present was *Allophaiomys chalinei*, an endemic form that at the time was not reported for other localities. The archaic morphology of this species also supported an age close to the base of the early Pleistocene, yet later works have considerably expanded the range of this species. Accordingly, despite its archaic morphology, *A. chalinei* is present in levels close to the end of the early Pleistocene, such as TD6 in Gran Dolina de Atapuerca, with an age estimated at 800 ka by paleomagnetism (Parés and Pérez-González, 1999), Electron Spin Resonance (ESR) dating, and U-series analysis (Falguères et al., 1999), and biostratigraphy (Cuenca-Bescós et al., 1995, 1999; van der Made, 1998; García and Arsuaga, 1999). *A. chalinei* has also been found at the section of Cal Guardiola, in levels which are slightly lower than those containing *Iberomys huescarensis* (J. Agustí, personal observation). It therefore seems that, contrary to previous views, Cueva Victoria is more properly placed in the second half of the early Pleistocene and not at its base. Recent work by Gibert et al. (2006) has also provided paleomagnetic data that support this point of view. According to these authors, most of the section of Cueva Victoria belongs to a reverse polarity phase, which at the top changes to a normal one. This upper normal event at the top of the section cannot be correlated with Olduvai, which, according to the rodent content, is clearly younger than that of the early Pleistocene site of Dmanisi (Lordkipanidze et al., 2007). It is also improbable that it can be attributed to the Brunhes normal event, which would imply for Cueva Victoria an age similar to the base of the Gran Dolina de Atapuerca section, while the rodent content is clearly different and most probably older (according to the results from Cal Guardiola and the evolutionary degree of *Allophaiomys chalinei* from the two sites). Therefore, the normal chron at the top of Cueva Victoria can best be assigned to the base of the Jaramillo event, with an estimated age for this site of 1072 ± 2 ka (Oxygen Isotopic Stage 31; Horng et al., 2002). Accordingly, Cueva Victoria would be placed between the early Pleistocene archeo-paleontological sites of Fuente Nueva 3 and Barranco León in the Guadix-Baza Basin (Oms et al., 2000; Agustí and Madurell, 2003) and those of Gran Dolina de Atapuerca.

MATERIAL AND METHODS

The identified herpetofaunal remains consist of disarticulated bone fragments collected during the excava-

tion campaigns conducted by the teams of the Institut de Paleontologia Miquel Crusafont. This assemblage includes 257 fragments, comprising 5 elements of anurans (i.e. 1.95 %) and 252 of squamate reptiles (i.e. 98.05 %). They represent at least 2 species of anurans and 9 species of squamates. This material is stored in the collection of the Museu de Geologia de Barcelona (MGB). It was studied as part of a Ph.D. thesis (Blain, 2005) and listed in the catalogue of the paleoherpetofaunal collection of the MGB (Blain and Bailon, 2006). We must point out that this material was first observed by an unknown researcher and attributed, in part, at genus or family level as reported on a few index labels.

The bones were assigned to different taxa following the criteria given by the systematic literature (see below), using for purposes of comparison the collections of dry skeletons of the Museo Nacional de Ciencias Naturales, Madrid, of the Facultad de Ciencias of the University of Granada, of the Laboratoire d'Anatomie Comparée of the Muséum national d'Histoire naturelle, Paris, of the Laboratoire départemental de Préhistoire du Lazaret, Nice, as well as our personal collections. Accounts of the distribution and habitat of present species mainly proceed from Pleguezuelos and Martínez-Rica (1997), Salvador (1997a), Salvador and Pleguezuelos (2002) and Pleguezuelos et al. (2004). The taxonomic nomenclature basically follows Montori et al. (2005), Frost et al. (2006) and Arnold et al. (2007).

All measurements have been made with a digital Measurescope Kappa MFK-II on a Wild M8 binocular to the nearest 0.01 mm or with scaled drawings.

SYSTEMATIC PALEONTOLOGY

Class: Amphibia GRAY, 1825

Order: Anura FISCHER VON WALDHEIM, 1813

Family: Pelodytidae BONAPARTE, 1850

GENUS *Pelodytes* BONAPARTE, 1838

cf. *Pelodytes* sp.

Figures 2A and B

Among the material, 2 small-sized and slender radio-ulnae match well with genus *Pelodytes* representatives. Anterior and posterior ends have a similar width and the *collum antibrachii* is little narrowed and rather long. The *olecraneum* is high and the *capitulum* not much prominent. Such a set of characteristics permit to establish a link between the fossils and *Pelodytes* or, to a lesser extent to *Hyla*.

At present, in the region of Murcia, the common parsley frog [*P. punctatus* (DAUDIN, 1802)] is the only representative of the Pelodytidae and is represented by a few sporadic populations which constitute the southernmost limit of the distribution area of the species (Barbadillo, 2004a, b). It is a Franco-Iberian species characteristic of mid- and low-lying areas, which lives in sandy soils and beneath stones in the vicinity of water and shows a strong tendency to dwell in cave habitats, taking refuge in substratum fissures, cavities or caves at great depth (Sánchez-Herráiz and Barbadillo, 1997).

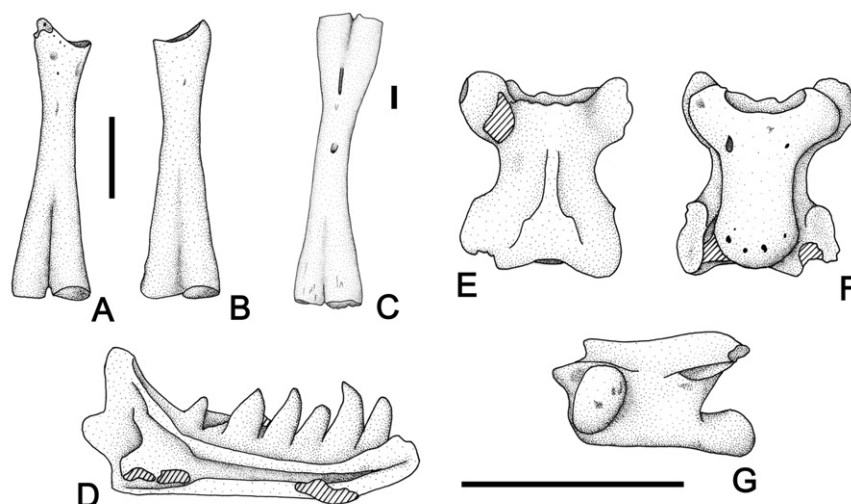


FIGURE 2 | cf. *Pelodytes*, A and B) radioulna, medial and lateral views. *Bufo* cf. *bufo*, C) tibiofibula, lateral view. *Blanus cinereus*, D) left dentary, medial view. E, F and G) trunk vertebra, dorsal, ventral and left lateral views. Scales = 2 mm.

Family: Bufonidae GRAY, 1825GENUS *Bufo* LAURENTI, 1768*Bufo cf. B. bufo* (LINNAEUS, 1758)

Figure 2C

Bufo nids are represented in Cueva Victoria by two vertebrae and one tibiofibula. The tibiofibula shows the general morphology of genus *Bufo* representatives: relatively short and robust, with well-developed proximal and distal extremities. The robustness, as well as the size (total length = 25 mm), of the element are consistent with *B. bufo*, this species being the largest bufonid in Western Europe.

The vertebrae are medium-sized, and their general morphology matches well with genus *Bufo* representatives. They are procoelous, with a short neural arch, and the transverse processes are cylindrical and directed transversally, which is characteristic of a posterior vertebra (V₆-V₇). The centrum of the vertebrae is developed, and the lateral walls are short and relatively robust.

The common European toad (*B. bufo*) has a large Eurasian range. At present in the region of Murcia, the species occurs sporadically along the Mediterranean seashore (Lizana, 2004). In arid areas, it has the tendency to search for more humid and cooler microhabitats (Gosá and Bergerandi, 1994) and, during its breeding season, it selects quiet or low energy water, preferably permanent and with vegetation (Lizana, 2004).

Class: Reptilia MCCARTNEY, 1802**Order:** Amphisbaenia GRAY, 1844**Family:** Blanidae KEARNEY, 2003GENUS *Blanus* WAGLER, 1830*Blanus cinereus* (VANDELLI, 1797)

Figures 2D-G

The Mediterranean worm lizard (*B. cinereus*) is represented in Cueva Victoria by 2 dentaries and 2 trunk vertebrae.

The dentaries are short and robust, bearing sub-pleurodont and monocuspid teeth. The anterior teeth are cylindrical and inclined anteriorly whereas the central and posterior teeth are cone-shaped, with a wide base and a posteromedially directed apex. The dentaries have 8 dental positions, the fourth tooth being the shortest whereas the first, third and fifth ones are the highest. The Meckel's groove is open along all its length. The splenial seems to be much reduced or absent because there is no impression visible on the ventral edge of the dental shelf.

The trunk vertebrae are procoelous, with a cotyle and a condyle flattened dorsoventrally. They show a dorsoventrally flattened neural arch, with a concave posterior end and a well-marked interzygapophyseal constriction. The neural spine is reduced, and in lateral view the synapophyses are globular and egg-shaped, which is characteristic of posterior trunk vertebrae. The ventral surface of the centrum is flat, with slightly convex margins. The prezygapophyses and postzygapophyses are well-developed and inclined upward.

The overall morphology of the dentaries and vertebrae does not differ from those of *B. cinereus*, the only current representative of the family in Western Europe.

B. cinereus is a western Mediterranean species restricted to the Iberian Peninsula with the exception of the North. Its presence is generally associated with areas with high environmental moisture, where it occurs in all vegetal cover types with loose or sandy humid grounds (Salvador, 1997b). In the region of Murcia, it is present in the interior mid-lying areas, but is absent from the western mountainous area and avoids all the arid conditions of the coastal area (López, 2004).

Order: Lacertilia OWEN, 1842

Among the material, 22 fragments (mainly dentaries and maxillae) have been attributed only at the level of the order.

Family: Gekkonidae OPPEL, 1811GENUS *Tarentola* GRAY, 1825*Tarentola* sp.

Figures 3A-E

The genus *Tarentola* is represented by 5 maxillae, 12 dentaries and 1 trunk vertebra.

The presence of numerous pleurodont, isodont, densely packed, cylindrical, thin, straight, monocuspid teeth, as well as of a dental shelf of the maxilla that is considerably extended on the medial side, constitutes a set of characteristics only found in gekkonids (Hoffstetter, 1946; Augé, 1986; Bailon, 1991). In lateral view, the best preserved maxilla possesses a well-developed prefrontal process, without any ornamentation and bearing 7 foramens. Attribution of maxillae to *Tarentola* is based principally on the presence of a robust and more or less horizontal premaxillary process, whereas in *Hemidactylus turcicus* (LINNAEUS, 1758) this process shows a dorsal angulation that is more pronounced (Schleich, 1987; Bailon, 1991).

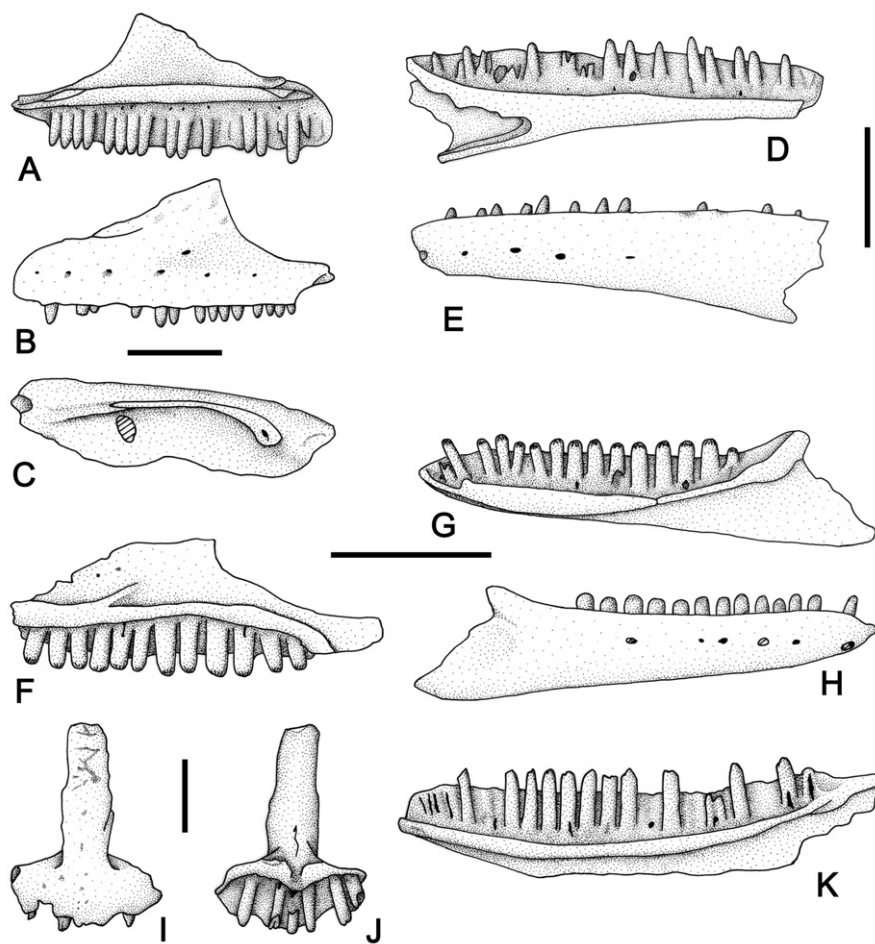


FIGURE 3 | *Tarentola* sp., A, B and C) right maxilla, medial, lateral and dorsal views. D and E) left dentary, medial and lateral views. *Chalcides* cf. *bedriagai*, F) right maxilla, medial view. G and H) right dentary, medial and lateral views. *Timon* cf. *lepidus*, I and J) premaxilla, anterior and posterior views, indeterminate small lacertid. K) right dentary, medial view. Scales = 2 mm.

The fragments of dentaries show the presence of a Meckel's groove that is entirely surrounded by the dentary. Tooth characteristics are identical to those described for the maxilla. The size, robustness and general morphology of these dentaries do not show any major difference with respect to current Iberian representatives of *T. mauritanica*.

The only vertebra has an amphicoelous centrum that is transversally convex in ventral view and with a concave ventral edge in lateral view. The neural arch shows a deep anterior notch, and the interzygapophyseal constriction is little pronounced. All these characteristics permit attribution to geckonids.

The study of *T. mauritanica* mitochondrial DNA has suggested that only one haplotype characterizes the current populations of the Iberian Peninsula, Italy, Minorca, Crete and Tunisia. This may demonstrate that the current distribution of the species may be linked to a recent expansion from

the North of Africa due to human activities during the historic period (Harris et al., 2004a). However, some genetically distinct lineages in southeastern and central Spain seem to be native (Harris et al., 2004b). Even though the few fossil remains of Cueva Victoria do not present any major difference in relation to modern representatives of *T. mauritanica*, prudence permits an attribution at genus level only. We should bear in mind at this point that fossil bones attributed to *T. mauritanica* have already been cited in the studied area, proceeding from the late early Pleistocene locality of Sierra de Quibas (Montoya et al., 1999, 2001).

The Moorish Gecko (*T. mauritanica*) is a circum-Mediterranean species which, in the Iberian Peninsula, lives preferentially in coastal areas of the South and East and enters inland along major fluvial valleys mainly avoiding mountainous areas (Martínez-Rica, 1997). Its favourite habitat is the Mediterranean scrubland. In the region of Murcia, the species is relatively common with a few minor exceptions (Hódar, 2004).

Family: Scincidae OPPEL, 1811GENUS *Chalcides* LAURENTI, 1768***Chalcides* cf. *Ch. bedriagai*** (BOSCA, 1880)

Figures 3F-H

In Cueva Victoria, 6 maxillae and 23 dentaries have been carefully attributed to Bedriaga's skink.

The maxillae bear pleurodont, isodont, cylindrical and monocuspid teeth with a blunt apex. The anterior teeth possess a width/height ratio ($=l/h$, *sensu* Barbadillo, 1989) equal to 0.39, whereas the most posterior teeth are shorter ($l/h > 0.5$) and slightly backward-leaning. In lingual view, every tooth apex shows a variably visible ornamentation, with delicate vertical striation limited ventrally by a transversal groove. In lateral view, the dental crest is straight and the prefrontal process is relatively high and without any ornamentation.

In medial view, the dentaries possess a Meckel's groove that is open along all its length. In lateral view, unlike in Lacertidae, the coronoid does not leave any impression on the dentary. The best preserved dentary bears 17 dental positions and teeth with the same morphology as on the maxillae. The first 8 anterior teeth are thin and high ($l/h = 0.20$) and slightly forward-leaning, then the 9th to 16th teeth are vertical, shorter and more robust than the preceding one ($l/h = 0.29$), and the last tooth is very short ($l/h = 0.42$). The morphology and proportion of the teeth do not differ from those of the modern species *Chalcides bedriagai*, which is characterized by the presence of 17 dental positions and by teeth with a width/height ratio (l/h) equal to 0.3 (Barbadillo, 1989; H.A. Blain and S. Bailon, personal observations). By contrast, in the only other representative of the genus in the Iberian Peninsula *Chalcides striatus* (currently absent from the region of Murcia), the dentary is characterized by 20 dental positions and by shorter and more robust anterior teeth ($l/h = 0.4$), with other teeth that are slightly more slender ($l/h = 0.23$).

Bedriaga's skink is an endemic Iberian species, which occurs over most of the Iberian Peninsula with the exception of the northernmost part. It lives principally in meadows, brushwood and forest glades, where loose soils are rich in refuges (Pollo, 2004). In the region of Murcia, its presence seems to be restricted to two coastal nuclei: the first one located near the city of Cartagena and the other one on the border with the province of Almeria (Pollo, 2004).

Family: Lacertidae OPPEL, 1811GENUS *Timon* TSCHUDI, 1836***Timon* cf. *T. lepidus*** (DAUDIN, 1802)

Figures 3I and J

Among the remains attributed to Lacertidae, the ocellated lizard (*Timon lepidus*) is represented in Cueva Victoria by 3 big-sized premaxillae (maximal width of the premaxillary shelf > 4.5 mm). The lateral margins of the posterodorsal process are slightly leaf-shaped (*sensu* Barahona and Barbadillo, 1997), and the external surface bears a smooth ornamentation. The best preserved premaxilla has 9 dental positions. All these characteristics, according to Barahona and Barbadillo (1997), permit an attribution to juvenile or sub-adult specimens of *T. lepidus*.

The ocellated lizard is a southern European species that is relatively widespread and common in the South of its distribution area. Mainly associated with Mediterranean biotopes, it lives in rocky areas and open scrublands, avoiding areas with a dense vegetal cover (Mateo, 1997). It is very common in the region of Murcia, with the exception of a few mountainous areas in the North-West (Mateo, 2004).

Indeterminate small lacertids

Figure 3K

In Cueva Victoria, 14 maxillae, 30 dentaries, 1 trunk vertebra, 2 sacral vertebrae and 1 hemipelvis have been attributed to indeterminate small lacertids.

All the dentaries are small-sized (length of the dental shelf, *sensu* Barahona and Barbadillo, 1997 < 6 mm), excluding in principle the species *Timon lepidus*, *Acanthodactylus erythrurus* (SCHINZ, 1833) and *Psammmodromus algirus* (LINNAEUS, 1758), the size of which is larger in adults (Barahona and Barbadillo, 1997). The best preserved dentaries are long and low. The medial edge of the dental shelf is relatively thin. The teeth, in number of more than 20, are thin, cylindrical, mainly bicuspid and project beyond the dental crest approximately 1/3 of their total height. Such characteristics rule out attribution to the genus *Acanthodactylus* WIEGMANN, 1834, which possesses more robust and high dentaries (Barbadillo, 1989; Blain et al., 2007), but are more concordant with the current representatives of *Psammmodromus hispanicus* FITZINGER, 1826 and *Podarcis hispanica* (STEINDACHNER, 1870).

At present, *Podarcis hispanica* and *Psammmodromus hispanicus* are present in the region of Murcia (Sá Sousa and Pérez Mellado, 2004; Carretero et al., 2004). These small lacertids are heliophilous species with a marked preference for open scrublands (Pleguezuelos, 1989).

Order: Serpentes LINNAEUS, 1758

Among the material, 48 elements (mainly incomplete vertebrae) have been attributed only at the level of the order and 8 elements to “Colubrinae”.

Family: Colubridae OPPEL, 1811

“Natricinae” type (trunk vertebrae with hypapophysis)

GENUS *Natrix* LAURENTI, 1768*Natrix maura* (LINNAEUS, 1758)

Figures 4A-E

N. maura is represented in Cueva Victoria by one trunk vertebra.

The vertebra possesses a sigmoid-shaped, short and robust hypapophysis with a pointed distal end. The neural arch is vaulted posteriorly, the condyle and cotyle are small and circular, and one of the parapophyses conserves a thin parapophyseal process. In ventral view, the centrum is slightly transversally concave and its lateral margins are poorly marked. In *N. natrix* (LINNAEUS, 1758), by contrast, the parapophyseal process is more robust, the hypapophysis end is more rounded, and the centrum is generally flat (Szyndlar, 1984).

The viperine snake (*N. maura*) has a large Iberian range, where its presence seems to be linked mainly with the existence of water (rivers, lakes, swamps...) (Santos et al., 1997). In the region of Murcia, it seems to be absent from the western part. As with *P. punctatus* and *B. cinereus*, this absence may be due to the pronounced ari-

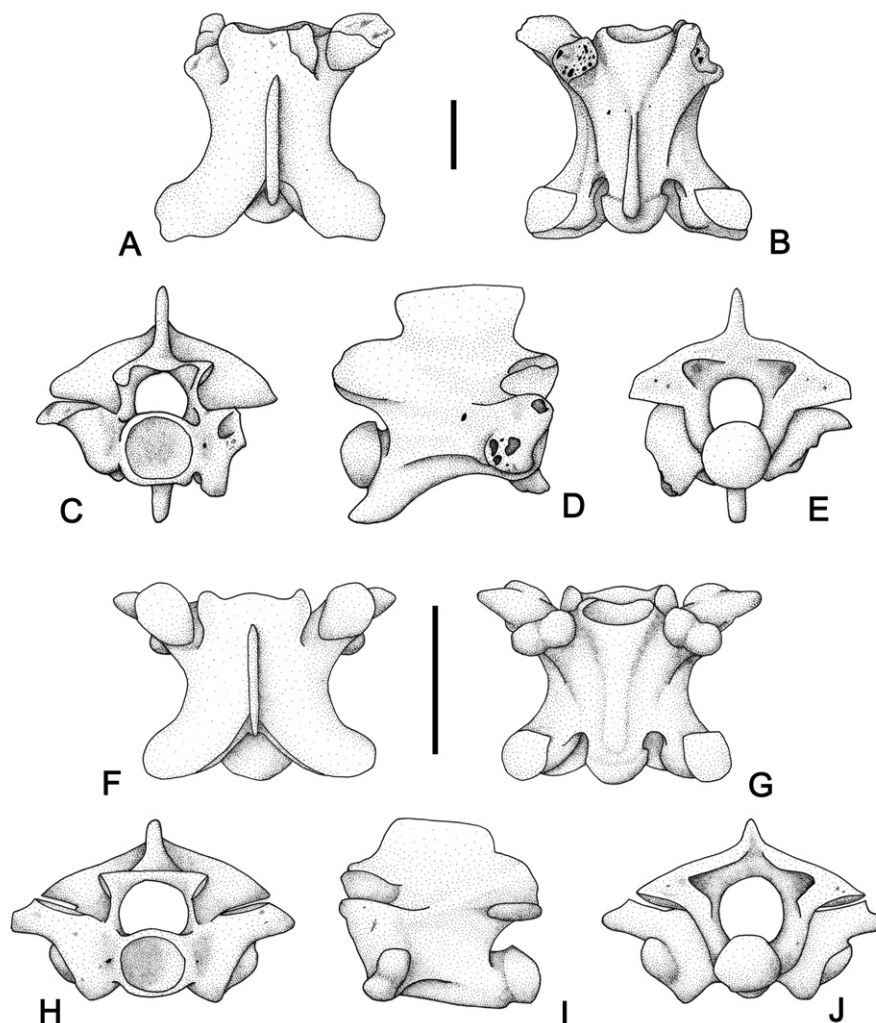


FIGURE 4 | *Natrix maura*, A-E) trunk vertebra, dorsal, ventral, anterior, right lateral and posterior views. *Coronella girondica*, F-J) trunk vertebra, dorsal, ventral, anterior, left lateral and posterior views. Scales = 2 mm.

dity of the coastal area of the province of Almeria (Salvador and Pleguezuelos, 2002).

“Colubrinae” type (trunk vertebra without hypapophysis)

GENUS *Coronella* LAURENTI, 1768

Coronella girondica (DAUDIN, 1803)

Figures 4F-J

GENUS *Malpolon* FITZINGER, 1826

Malpolon cf. *M. monspessulanus* (HERMANN, 1804)

Figures 5A-E

GENUS *Rhinechis* MICHAELLES, 1833

Rhinechis scalaris (SCHINZ, 1822)

Figures 5F-J

“Colubrine” snakes are only represented in Cueva Victoria by vertebrae: 10 trunk vertebrae are attributed to *C. girondica*, 39 trunk vertebrae to *Malpolon* cf. *monspessulanus* and 1 cervical vertebra and 21 trunk vertebrae to *Rh. scalaris*.

The size of the trunk vertebrae is highly variable: the small-sized trunk vertebrae attributed to *C. girondica* ($2.05 < \text{centrum length (CL)} < 4.04$ mm) correspond to sub-adult and adult specimens, whereas the trunk vertebrae attributed to *Rh. scalaris* ($1.13 < \text{CL} < 6.41$ mm), and *M. monspessulanus* ($1.64 < \text{CL} < 5.00$ mm) may correspond to juvenile or sub-adult specimens.

In the light of biometrical results obtained from modern specimens (Blain, 2005), the trunk vertebrae of *C. girondica* have ratios $\text{CNW}/\text{NAW} < 0.47$ and $\text{CNW}/\text{CL} < 0.43$ (Table 1 and Fig. 6). As in genus *Coronella* representatives, the neural arch is dorso-ventrally flattened. Attribution to *C. girondica* rests on the morphology of the

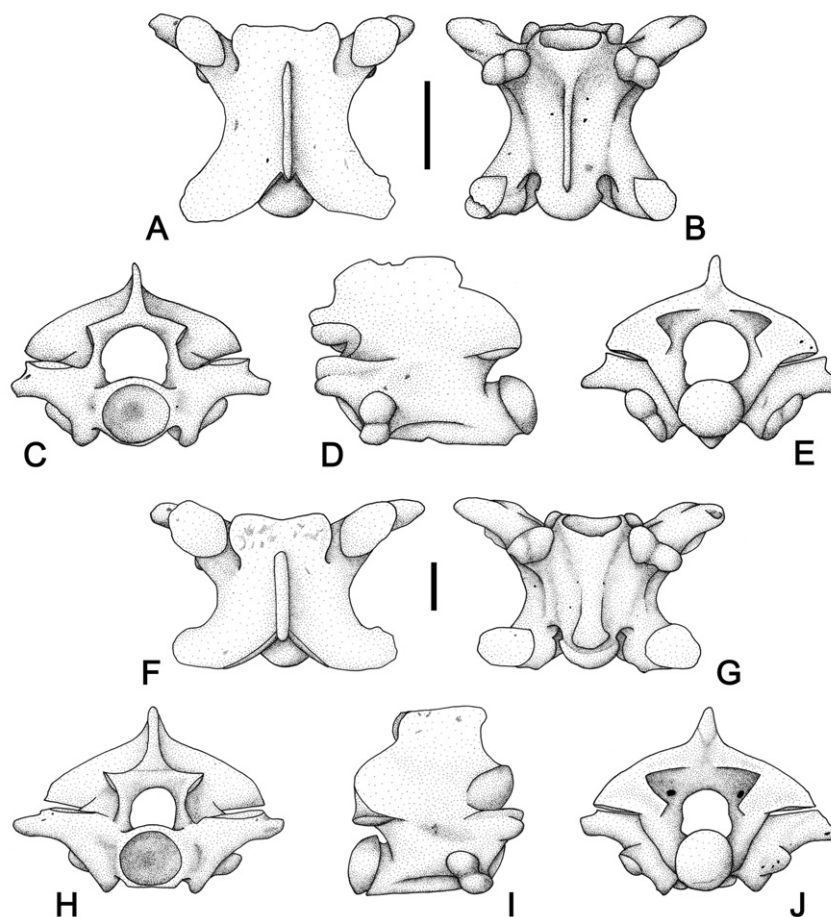


FIGURE 5 | *Malpolon* cf. *monspessulanus*, A-E) trunk vertebra, dorsal, ventral, anterior, left lateral and posterior views. *Rhinechis scalaris*, F-J) trunk vertebra, dorsal, ventral, anterior, right lateral and posterior views. Scales = 2 mm.

TABLE 1 | Measurements (in mm) and ratios of trunk vertebrae of “colubrines” of Cueva Victoria. Abbreviations: see Figure 6.

<i>Coronella girondica</i>	n	mean	median	SD	min.	max.
CL	10	2.73	2.46	0.75	2.05	4.04
NAW	10	2.45	2.29	0.61	1.78	3.48
PR-PO	10	3.32	3.03	0.88	2.42	4.87
PO-PO	7	3.67	3.46	0.76	2.85	4.98
PR-PR	9	4.13	4.18	1.02	3.00	5.43
CNW	10	1.06	0.99	0.31	0.78	1.62
CNW/NAW	10	0.43	0.43	0.03	0.39	0.47
PR-PR/PR-PO	9	1.24	1.24	0.09	1.11	1.36
PR-PR/NAW	9	1.67	1.68	0.07	1.56	1.79
CL/NAW	10	1.11	1.11	0.07	1.02	1.24
PO-PO/NAW	7	1.60	1.56	0.07	1.55	1.71
CNW/CL	10	0.39	0.38	0.02	0.36	0.42
<i>Rhinechis scalaris</i>						
CL	16	3.91	4.33	1.92	1.13	6.41
NAW	16	3.67	3.87	1.81	1.11	5.99
PR-PO	15	5.00	6.26	2.44	1.35	8.12
PO-PO	14	6.53	7.62	3.10	1.70	10.12
PR-PR	11	7.41	9.11	3.08	1.84	10.15
CNW	16	1.78	1.91	0.77	0.53	2.68
CNW/NAW	16	0.50	0.49	0.05	0.44	0.60
PR-PR/PR-PO	11	1.30	1.29	0.06	1.17	1.40
PR-PR/NAW	11	1.71	1.71	0.08	1.56	1.81
CL/NAW	16	1.07	1.05	0.07	0.96	1.26
PO-PO/NAW	14	1.65	1.67	0.10	1.42	1.81
CNW/CL	16	0.47	0.47	0.05	0.38	0.58
<i>Malpolon monspessulanus</i>						
CL	37	3.60	3.61	0.75	1.64	5.00
NAW	37	2.58	2.59	0.55	1.20	3.64
PR-PO	35	4.29	4.32	0.94	1.95	6.28
PO-PO	25	4.26	4.36	0.98	2.07	6.42
PR-PR	22	4.24	4.50	0.91	2.13	5.29
CNW	37	1.29	1.33	0.25	0.70	1.79
CNW/NAW	37	0.50	0.50	0.03	0.43	0.58
PR-PR/PR-PO	22	1.08	1.09	0.04	1.00	1.14
PR-PR/NAW	22	1.80	1.79	0.06	1.66	1.88
CL/NAW	37	1.40	1.38	0.08	1.29	1.54
PO-PO/NAW	25	1.74	1.75	0.07	1.58	1.88
CNW/CL	37	0.36	0.36	0.03	0.28	0.43

proximal portion of the prezygapophysis (generally more slender in *C. girondica* than in *C. austriaca*) and the relative size of the parapophysis in relation to the diapophysis (Szyndlar, 1984; H.A.Blain and S.Bailon, personal observations).

The trunk vertebrae attributed to *Malpolon* cf. *M. monspessulanus* have a ratio PR-PR/PR-PO<1.15 and an elongated centrum (1.29<CL/NAW). Morphologically, the angle between the main axes of the prezygapophyseal articular surfaces seems to be wider in *C. girondica* and *Rh. scalaris* than in *Hemorrhois hippocrepis* (LINNAEUS, 1758) and *M. monspessulanus*. Moreover, in ventral view, the haemal keel seems to be relatively slim along all its

length with well-defined lateral edges in *M. monspessulanus* and *H. hippocrepis*, whereas in *C. girondica* and *Rh. scalaris* the haemal keel is wider with indistinct lateral edges (Bailon, 1986; Barroso Ruiz and Bailon, 2003).

The trunk vertebrae attributed to *Rh. scalaris* show the general morphology of the species: prezygapophyseal articular surfaces that are large and circular or sub-rectangular, and a haemal keel that in ventral view is wide with indistinct lateral edges and sometimes slightly spatulated. They possess ratios PR-PR/NAW<1.81 and PO-PO/NAW<1.81, which differ from *H. hippocrepis* (Table 1 and Fig. 6).

A recent study of the mitochondrial DNA of *M. monspessulanus* (Carranza et al., 2006) has suggested a recent origin dating back to the beginning of the late Pleistocene in the Maghreb for all the current representatives of *M. monspessulanus* in the Iberian Peninsula. Nevertheless, this study does not exclude the possibility of previous populations during the Pliocene and the early Pleistocene, as suggested by paleontological data (Bailon, 1991; Blain,

2005). In this way, Pliocene and early-middle Pleistocene fossil remains attributed to this species may correspond to earlier populations, suggesting that there were one or various previous colonization events from Africa

The southern smooth snake (*C. girondica*) is a ubiquitous species, occurring in the whole Iberian Peninsula. It is a thermophilous ophidian, typical of plateaus and medium-

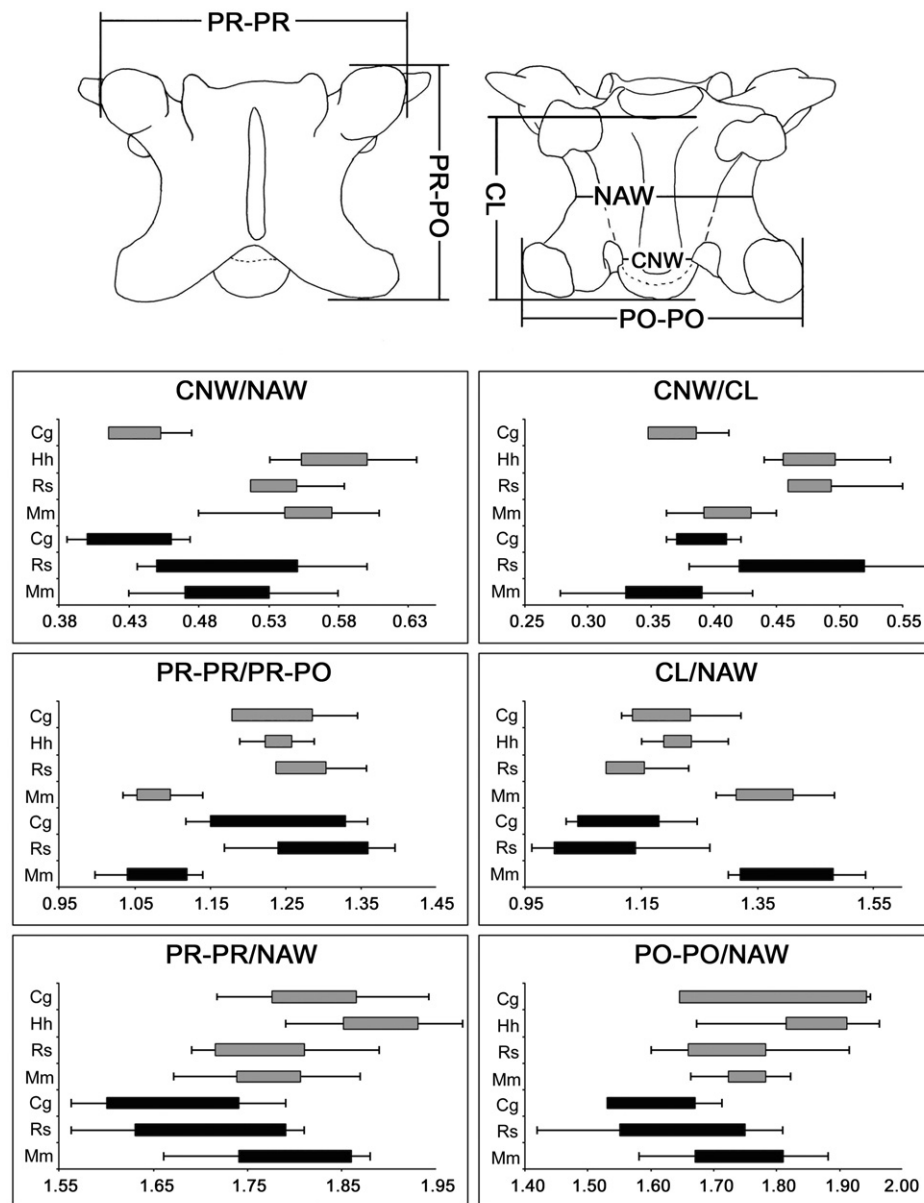


FIGURE 6 | Measurements of the “colubrine” snakes’ trunk vertebrae (from Szyndlar, 1984 and Blain, 2005) and biometrical ratios between the Cueva Victoria material (in black) and modern specimens (in grey) for *Coronella girondica* (Cg), *Hemorrhois hippocrepis* (Hh), *Rhinechis scalaris* (Rs) and *Malpolon monspessulanus* (Mm). Abbreviations: CL: centrum length; CNW: condyle neck width; NAW: centrum width; PO-PO: width between the outer edges of postzygapophyseal articular surfaces; PR-PO: length from the anterior edge of prezygapophyseal articular surface to the posterior edge of the postzygapophyseal articular surface; PR-PR: width between outer edges of prezygapophyseal articular surfaces. Data on recent specimens from Blain (2005).

lying mountainous areas, where it shows a preference for wooded areas and low and medium brushwood (Santos and Pleguezuelos, 2004). In the region of Murcia, it seems quite uncommon, in particular in a large western area where its populations occur as small isolated nuclei in the highest-lying areas (Santos and Pleguezuelos, 2004).

The Montpellier snake (*M. monspessulanus*) and the ladder snake (*Rh. scalaris*) have a large and homogeneous distribution in the Iberian Peninsula, although highly influenced by the Mediterranean bioclimatic region. In the region of Murcia, they seem to be absent from the mountainous areas of the North-West as well as along the western part of the coastal area (Blázquez and Pleguezuelos, 2004). *M. monspessulanus* avoids inland areas where mean annual temperatures are lower than 8–9°C and with more than 90 frosty days a year (Pleguezuelos, 1997). The males of this species have a vernal spermatogenic cycle that hinders the expansion of the species into areas with a too short warm period and with mean July temperatures lower than 22°C (Cheylan et al., 1981).

PALEOBIOGEOGRAPHICAL DATA

In the Region of Murcia, only the herpetofaunal assemblage of the early Pleistocene of the Sierra de Quibas had been studied up to now (Montoya et al., 1999, 2001). For this reason, the study of Cueva Victoria is of considerable interest with regard to what is known of amphibian and squamate reptile fossil assemblages in the South-East of Spain.

All the species cited in Cueva Victoria are currently present in the Region of Murcia. Nevertheless, Cueva Victoria for the first time provides evidence of the presence, in the early Pleistocene of Murcia, of a parsley frog (cf. *Pelodytes* sp.), Bedriaga's skink (*Ch. bedriagai*), the viperine snake (*N. maura*), the southern smooth snake (*C. girondica*) and the Montpellier snake (*M. monspessulanus*), and moreover confirms the presence of taxa already cited in Quibas, such as the common European toad (*B. bufo*), the Mediterranean worm lizard (*B. cinereus*), the genus *Tarentola*, the ocellated lizard (*T. lepidus*) and the ladder snake (*Rh. scalaris*).

Bearing in mind that according to genetic studies (mitochondrial DNA), the current populations of the Montpellier snake (*M. monspessulanus*) may have a recent origin dating from between 167,290 and 83,645 years ago (Carranza et al., 2006), fossil remains older than these datings may correspond, according to these authors, to populations that are now extinct.

According to the paleontological data known for the Iberian Peninsula, all these taxa seem to have been present at least since the late Pliocene (Bailon, 1991; Blain, 2005). The cooler and above all more humid conditions that occurred at the end of the early Pleistocene (ca. 1.0 Ma), as evidenced at other sites such as Almenara-Casablanca 3 (Castellón) and Cal Guardiola (Barcelona), suggest a southward withdrawal of certain thermophilous taxa such as the geckonids, which are absent from these two localities (Blain, 2005; Blain et al., 2007). Cueva Victoria permits us to confirm the presence of representatives of the genus *Tarentola* in the South of the Iberian Peninsula during this period.

PALEOCLIMATIC AND PALEOENVIRONMENTAL DATA

Quantitative study of the different species occurring in the locality of Cueva Victoria grouped together by ecological affinities shows the predominance of taxa from tem-

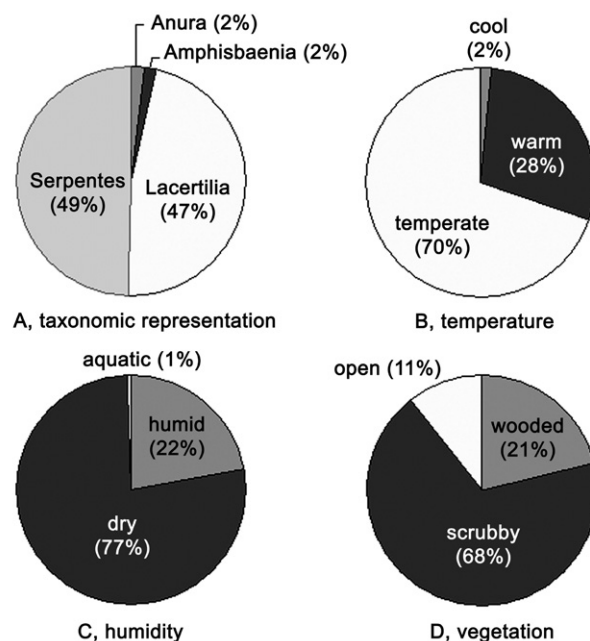


FIGURE 7 | Percentage of the amphibians and squamate reptiles from Cueva Victoria by climatic and environmental affinities. We have considered here some typical southern Iberian species as suggesting "warm" climatic conditions (*B. cinereus*, *Ch. bedriagai*, and *Tarentola* sp.), northern mid-European species as suggesting "fresher" climatic conditions (*B. bufo*), species with a large distribution in the Iberian Peninsula as suggesting "temperate" climatic conditions (cf. *Pelodytes*, *T. lepidus*, small lacertids, *N. maura*, *C. girondica*, *Rh. scalaris*, and *M. monspessulanus*), water edges species (*N. maura*), species suggesting a certain environmental humidity (cf. *Pelodytes*, *B. bufo*, *B. cinereus*, and *Ch. bedriagai*), species suggesting a dry environment (*Tarentola* sp., lacertids, *M. monspessulanus*, and *Rh. scalaris*), species suggesting a more wooded landscape (*B. bufo*, *B. cinereus*, and *Ch. bedriagai*), species suggesting a more open landscape (*Tarentola* sp.) and finally species suggesting a "scrubby" landscape (cf. *Pelodytes*, *T. lepidus*, small lacertids, *N. maura*, *C. girondica*, *Rh. scalaris*, and *M. monspessulanus*).

perate-warm/dry and scrubby environments (Fig. 7). The landscape may have been of an open Mediterranean type, certainly with the presence of oak groves, alternating, owing to the relief, between fresher and moister areas favourable to the parsley frog (cf. *Pelodytes* sp.), the common European toad (*B. bufo*), the Mediterranean slow worm (*B. cinereus*) and Bedriaga's skink (*Ch. bedriagai*) and more sunny, warm and dry areas favourable to the genus *Tarentola*, the lacertids and snakes. The presence of amphibians and in particular of the viperine snake (*N. maura*) suggests the existence of a small river or a permanent water point in the vicinity of the cavity.

The intersection of the recent distributions of species occurring in the locality (= common climatic range principle) provides a way of indicating its potential climatic conditions (Blain, 2005; Martínez Solano and Sanchiz, 2005). In Cueva Victoria, this intersection gives a total of 85 10x10 km UTM squares as represented in Fig. 8. The greatest concentration of these squares occurs in western Andalusia, which is currently under the influence of the Atlantic Ocean and is more humid than eastern Andalusia. The western part of the region of Andalusia that coincides with the intersection has a mean annual precipitation (MAT) higher than 600 mm and a moisture index (P/ETP) higher than 0.6 (www.juntadeandalucia.es/medioambiente). Such an intersection for Cueva Victoria suggests a mean annual temperature slightly lower than at present ($\text{MAT}_{\text{CuevaVictoria}} = 16.7 \pm 1.9^\circ\text{C}$, minimum = 11°C , maximum = 18.5°C ; presently $\text{MAT} = 17.7^\circ\text{C}$ at the meteorological station of San Javier, located nearly 15 km to the North of the cavity, recent data from Font Tullot, 2000) and mean annual precipitations higher than at

present ($\text{MAP}_{\text{CuevaVictoria}} = 716 \pm 241$ mm, min. = 300 mm, max. = 1500 mm; presently $\text{MAP} = 329$ mm in San Javier, recent data from Font Tullot, 2000). The mean temperature of the coldest month (MTC) for Cueva Victoria is equal to $9.0 \pm 2.3^\circ\text{C}$ (max. = 12.5°C , min. = 3°C ; at present 10.6°C in San Javier, recent data from Font Tullot, 2000) and for the warmest month (MTW) it is equal to $24.6 \pm 1.4^\circ\text{C}$ (max. = 27°C , min. = 19°C ; at present 23.9°C in San Javier, recent data from Font Tullot, 2000). This suggests that if the mean annual temperature is lower than at present, the summers stay warm with winters that are slightly cooler. However, the rainfall is clearly higher than at present in the studied area.

These results match well with the presence in Cueva Victoria of Hermann's tortoise (*Testudo hermanni* Gmelin, 1789; García-Porta, 2001), whose current distribution in the Iberian Peninsula (restricted to Catalonia) is characterized by a MAT higher than 14°C and a MAP lower than 700 mm (Cheylan, 1981; Llorente et al., 2004).

Finally, these interpretations are concordant with the reconstruction of the paleoclimate and paleoenvironment of other latest early Pleistocene localities in Spain such as Cal Guardiola (Barcelona) and Almenara-Casablanca-3 (Castellón), where the herpetofaunal assemblages have suggested a slightly lower MAT and higher MAP than at present (Blain, 2005; Blain et al., 2007).

CONCLUSIONS

The site of Cueva Victoria (Murcia), dating from the end of the early Pleistocene (ca. 1.1 Ma), has furnished the following fauna of amphibians and squamate reptiles: cf. *Pelodytes* sp. (Pelodytidae), *Bufo* cf. *B. bufo* (Bufonidae), *Blanus cinereus* (Blanidae), *Tarentola* sp. (Geckonidae), *Chalcides* cf. *Ch. bedriagai* (Scincidae), *Timon* cf. *T. lepidus* and indeterminate small lacertids (Lacertidae), *Natrix maura*, *Coronella girondica*, *Rhinechis scalaris* and *Malpolon* cf. *M. monspessulanus* (Colubridae).

Cueva Victoria provides the first citation during the early Pleistocene of Murcia of a Pelodytidae (cf. *Pelodytes* sp.), the Bedriaga's skink (*Ch. bedriagai*), the viperine snake (*N. maura*), the southern smooth snake (*C. girondica*) and the Montpellier snake (*M. monspessulanus*).

This herpetofaunal assemblage is likely to have been contemporaneous with slightly cooler and moister climatic conditions than those occurring at present in the area, and comparable to those of the current western Andalusia, and it suggests an open Mediterranean landscape, with some water points in proximity to the cave.

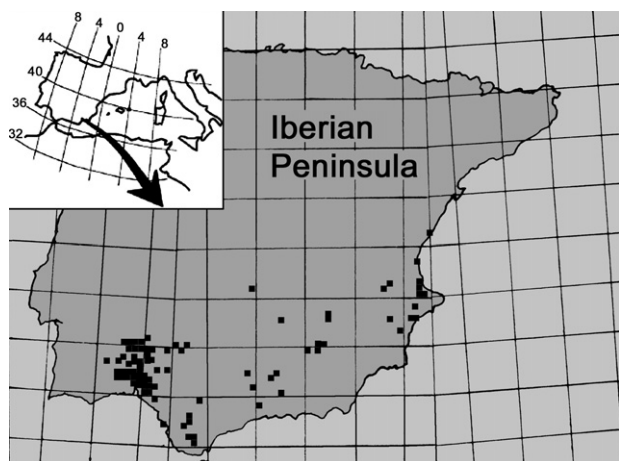


FIGURE 8 | Map of the Iberian Peninsula indicating the 10x10 km UTM squares where all the species represented in Cueva Victoria presently occur together (■). Square pattern corresponds to the UTM network (100x100 km). Data on recent distribution from Pleguezuelos et al. (2004).

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