Youngest Agamid Lizards from Western Europe (Sierra de Quibas, Spain, Late Early Pleistocene)

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Youngest agamid lizards from Western Europe (Sierra de Quibas, Spain, late Early Pleistocene)

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Here we report a new Early Pleistocene record of agamid lizards (Agamidae indet.) from the Spanish locality of Quibas (ca. 1.3–1.0 Ma), which represents the latest evidence of the family in Western Europe. Up to now, the family Agamidae was considered to have disappeared in this region at 1.8 Ma. This new record implies the survival of agamid lizards for a large part of the Early Pleistocene in the southernmost Iberian Peninsula, probably because of favourable climatic and environmental conditions. Consequently, the formerly detected Pliocene / Pleistocene boundary is no longer recognisable in the evolution of the herpetological assemblages in Western Europe.

Introduction

Squamate faunas from Western Europe are known to become progressively impoverished during the Pliocene and the beginning of the Pleistocene, probably associated with the intensification of glaciation pulses in the northern hemisphere (Bailon 1991; Blain 2005, 2009; Bailon and Blain 2007). 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; ca. 2.6 Ma) some Gekkonidae, the scincid *Trachylepis* (formerly *Mabuya*), scolecophidian snakes, Erycinae and oriental vipers disappeared from Western Europe, whereas during the same period other thermophilous groups (Agamidae, Blanidae, some Anguidae, and some Colubridae) underwent a southward withdrawal. At the same time, some species (*Hierophis viridiflavus*, *Zanemis* aff. *longissimus*, *Coronella* cf. *austriaca*, and *Vipera* "*berus*") coming from Central Europe arrived in France, as registered at the Montoussé 5 locality (Bailon 1991). The last "exotic squamates" supposed to have disappeared from Western Europe were the Agamidae (at the end of the late Villanyian; ca. 1.8 Ma) and the anguid *Dopasia* (at the end of the Early Pleistocene; ca. 1.3 Ma) (Blain 2005, 2009; Bailon and Blain 2007; Agustí et al. 2009; Blain and Bailon 2010; Blain et al. 2011). The description by Delfino et al. (2008) of a single dentary from the latest Early Pleistocene or the earliest Middle Pleistocene of Cava XI-Canidae in Monte Tuttavista (Orosei, Sardinia, Italy) suggested a late-surviving agamid lizard in Western Europe, but these authors suggest caution over its age.

New excavations from 2002 to 2007 at Sierra de Quibas (Murcia, southeastern Spain) led by Miguel Ángel Mancheño from the University of Murcia have delivered an abundant and diverse herpetofauna. This material is currently under study, and will no doubt add new taxa to the previous faunal lists (Montoya et al. 1999, 2001; Carlos-Calero et al. 2006a, b; Alba et al. 2011; Piñero-García 2012), providing new information on the squamates that lived in the south of the Iberian Peninsula at the end of the Early Pleistocene. Here the agamid fossil remains from this locality are described for the first time.

Institutional abbreviations.—IPHES, Institut Català de Paleoecologia Humana i Evolució Social, Tarragona, Spain.

Other abbreviations.—EC, "Entrada Cueva".

Geological and chronological setting

The paleontological site of Quibas (Abanilla, Murcia) is located in the SE portion of the Sierra de Quibas, in the spot called Collado del Rey, in an abandoned quarry, at an altitude of approximately 669 meters above sea level (Fig. 1). The Sierra de Quibas is a 6 km long and 2.5 km wide carbonate massif oriented NE-SW, which is mainly composed of Jurassic limestone and dolomite from the Subbetic region (Rodríguez-Estrella et al. 2004). This massif was affected by considerable karstic activity during the Plio-Pleistocene, resulting in numerous exokarstic and endokarstic structures (Durán et al. 2004), which are infilled by chemical precipitates and/or by mixed detritic sediments. The fossiliferous sediments from the Quibas site constitute the Pleistocene karstic infilling of several cavities situated inside the dolomite of the Lower Lias. Most of the fossils come from a 5 m wide and 9 m high gallery (known as "Entrada Cueva") that extends more than 30 m in length, and displays several collateral branches separated by calcitic speleothems (Durán et al. 2004; Rodríguez-Estrella et al. 2004). In the Quibas-EC site, a 6 m thick stratigraphic sequence of reddish detritic sediments crops out in the wall crevices of a small abandoned limestone quarry (see Montoya et al. 1999 for further details on the stratig-

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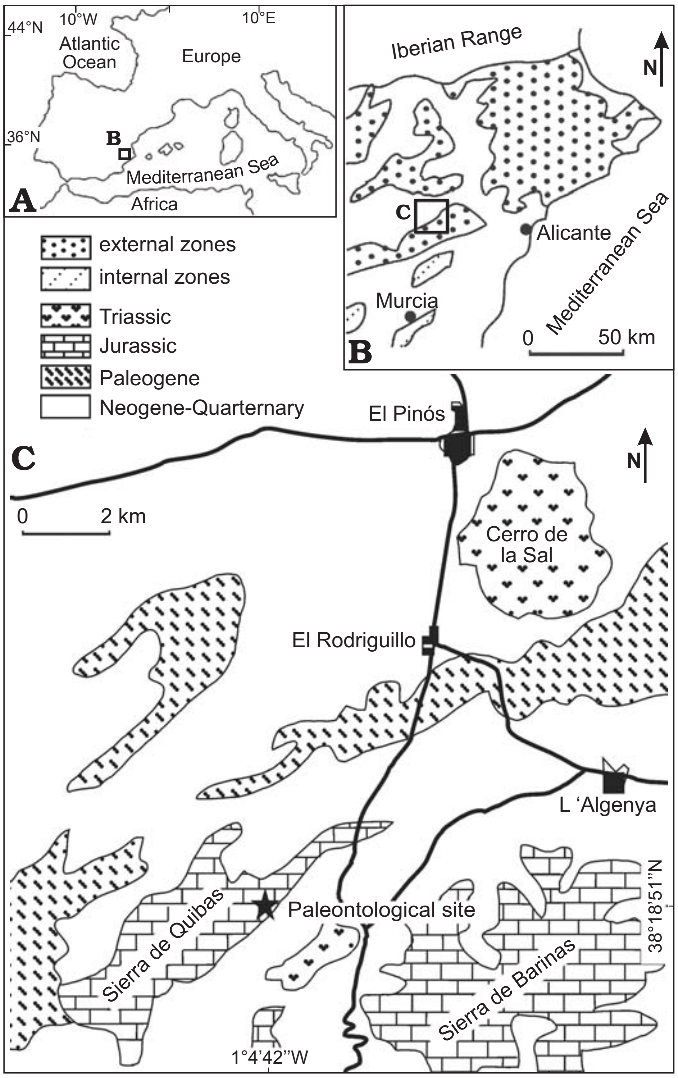

Fig. 1. Map of Western Europe (**A**), the location of Quibas paleontological site (**B**), geological map of the Quibas area (**C**) (modified from Montoya et al. 1999, 2001).

raphy). Six detritic layers have been distinguished, being mainly composed of clay, silt, and more or less cemented breccia. Magnetostratigraphic correlation indicates that the fossiliferous sediments correspond to the Late Matuyama subchron of reversed polarity (Carlos-Calero et al. 2006a, b), between 1.770 and 1.070 Ma. In a first biochronological approximation for Quibas-EC, specimens of *Equus altidens granatensis* (an equine known from the end of the Early Pleistocene to the beginning of the Middle Pleistocene) and of the rodents *Castillomys rivas rivas* and *Eliomys intermedius*, together with the arvicoline *Arvicola deucalion*, suggested an Early Biharian age, between 1.3 and 1.0 Ma, most probably closer to 1.3 Ma (Montoya et al. 1999, 2001). The rodents from earlier excavation campaigns (2002–2007) include *Apodemus mystacinus*, *Castillomys rivas*, *Allophaiomys* sp., and *Eliomys quercinus* (Piñero-García 2012). The presence in level III of a primitive form of *Allophaiomys* with Mimomian characteristics, together with *A. mystacinus* and *C. rivas* populations that are larger than those from the Fuente Nueva 3 site (dated at 1.2 Ma approximately; Agustí and Madurell 2003; Duval et al. 2012), suggest an age between 1.1 and 1.2 Ma for this level (Piñero-García 2012). Consequently the fossil agamid remains from Quibas-EC described here, and from the base of the sequence, may have an age slightly older and probably close to 1.3 Ma.

Systematic palaeontology

Reptilia Laurenti, 1768

Squamata Oppel, 1811

"Lacertilia" Owen, 1842

Family Agamidae Spix, 1825

Agamidae indet.

Fig. 2.

Material.—IPHES QB-06-EC-H/1, one right maxilla (Fig. 2A); IPHES QB-06-EC-H/2, one left dentary (Fig. 2B); IPHES QB-06-EC-H/3, one right dentary (Fig. 2C); IPHES QB-06-EC-H/4 and 5, two fragments of dentaries; IPHES QB-06-EC-H/6, one trunk vertebra (Fig. 2D); IPHES QB-06-EC-H/7, one anterior caudal vertebra (Fig. 2E); IPHES QB-06-EC-H/8-10, three posterior caudal vertebrae from Quibas, late Early Pleistocene.

Description.—The fossil maxilla and dentaries, all incomplete, are characterized by an acrodont dentition (Fig. 2A, B) ankylosed against the medial wall and floor of the shallow dental gutter. The shearing portion is triangular and compressed mediolaterally, with the lateral surface more flattened than the medial surface. The teeth are variably packed and the overlapping part of a tooth is medial to the posterior part of the preceding tooth. Only one dentary preserves the two more anterior teeth, and these are pleurodont and caniniform (Fig. 2C). The fragment of maxilla (Fig. 2A) represents the postero-medial part of the bone and preserves six acrodont triangular, slightly overlapping teeth.

All dentaries are fragmentary. The longest fragment (Fig. 2B) corresponds to the posterior part of the bone, bearing seven acrodont teeth morphologically similar to those of the maxilla, although somewhat larger and better individualized. In lateral view, some small interdental grooves produced by jaw occlusion are visible. The ventral limit of the bone is slightly convex. No labial foramen is visible. In medial view, the dental gutter is nearly straight and shallow all along the medial surface of the dentary. The Meckelian canal is open for all its length and it narrows anteriorly. Posteriorly, the subdental shelf (sensu Rage and Augé 2010) forms a small bony expansion. This blade-like expansion is broken, but seems to be built from the fusion of the splenial with the dentary, commonly seen in Agamidae (Bailon 1991). The coronoid process of the dentary, posteriorly directed, is relatively long and robust and presents a rather well developed concave and antero-posteriorly elongated medial surface of insertion for the coronoid. The dentary preserving the anterior part of the bone (Fig. 2C) bears two anterior pleurodont, large and conical teeth of rather similar size, though the posterior tooth looks slightly larger than the anterior one. The Meckelian canal forms at its anterior part a narrow longitudinal groove ventral to the mandibular symphysis. The subdental shelf is

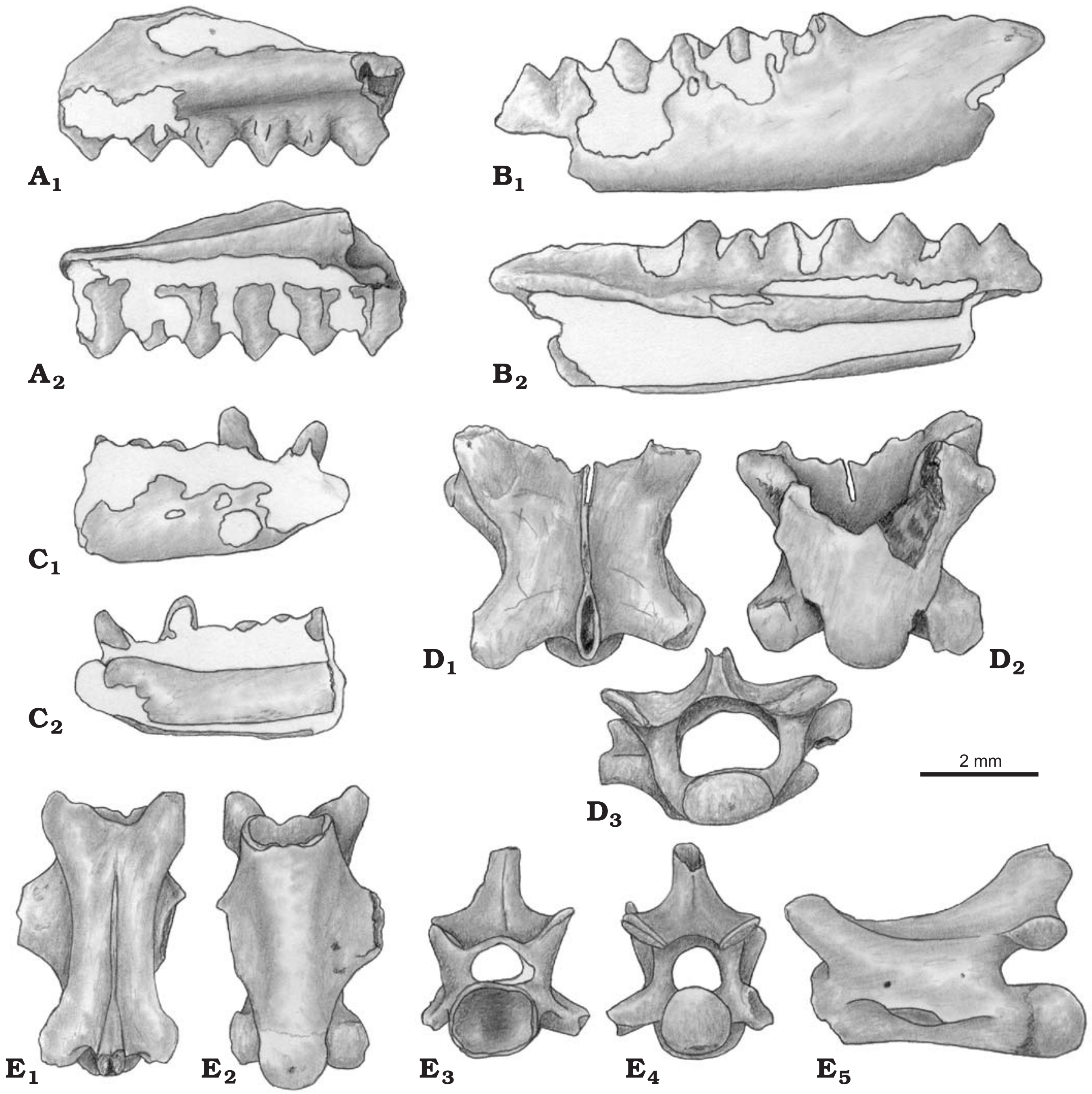

Fig. 2. Agamidae indet. from the late early Pleistocene of Sierra de Quibas, Murcia, southeastern Spain. **A**. IPHES QB-06-EC-H/1, right maxilla in lateral (A_1) and medial (A_2) views. **B**. IPHES QB-06-EC-H/2, left dentary in lateral (B_1) and medial (B_2) views. **C**. IPHES QB-06-EC-H/3, right dentary in lateral (C_1) and medial (C_2) views. **D**. IPHES QB-06-EC-H/6, trunk vertebra in dorsal (D_1), ventral (D_2), and posterior (D_3) views. **E**. IPHES QB-06-EC-H/7, anterior caudal vertebra in dorsal (E_1), ventral (E_2), anterior (E_3), posterior (E_4), and left lateral (E_5) views.

wide with a moderately convex ventral margin, and anteriorly, it constitutes the medial limit of the dental gutter.

The only available trunk vertebra (Fig. 2D) is procoelous, with a neural arch indented anteriorly. The centrum is triangular and moderately widened anteriorly. A haemal keel is absent. The prezygapophyses and postzygapophyses are rather small but well individualized. As long as wide, this vertebra has relatively dorso-ventrally flattened condyle and cotyle. In lateral view, the globular synapophyses are more or less egg-shaped. The neural spine, although broken, seems to have been relatively high, strong and reached the anterior margin of the neural arch.

The caudal vertebrae are elongated and show a centrum that is transversally convex and slightly constricted in its central part. The neural spine is rather long, thin and low and is prolonged posteriorly by an interzygapophyseal tip that does not reach the posterior limit of the postzygapophyses. No autotomy line is visible. In the anterior caudal vertebra (Fig. 2E), the incomplete transverse processes are only represented by their

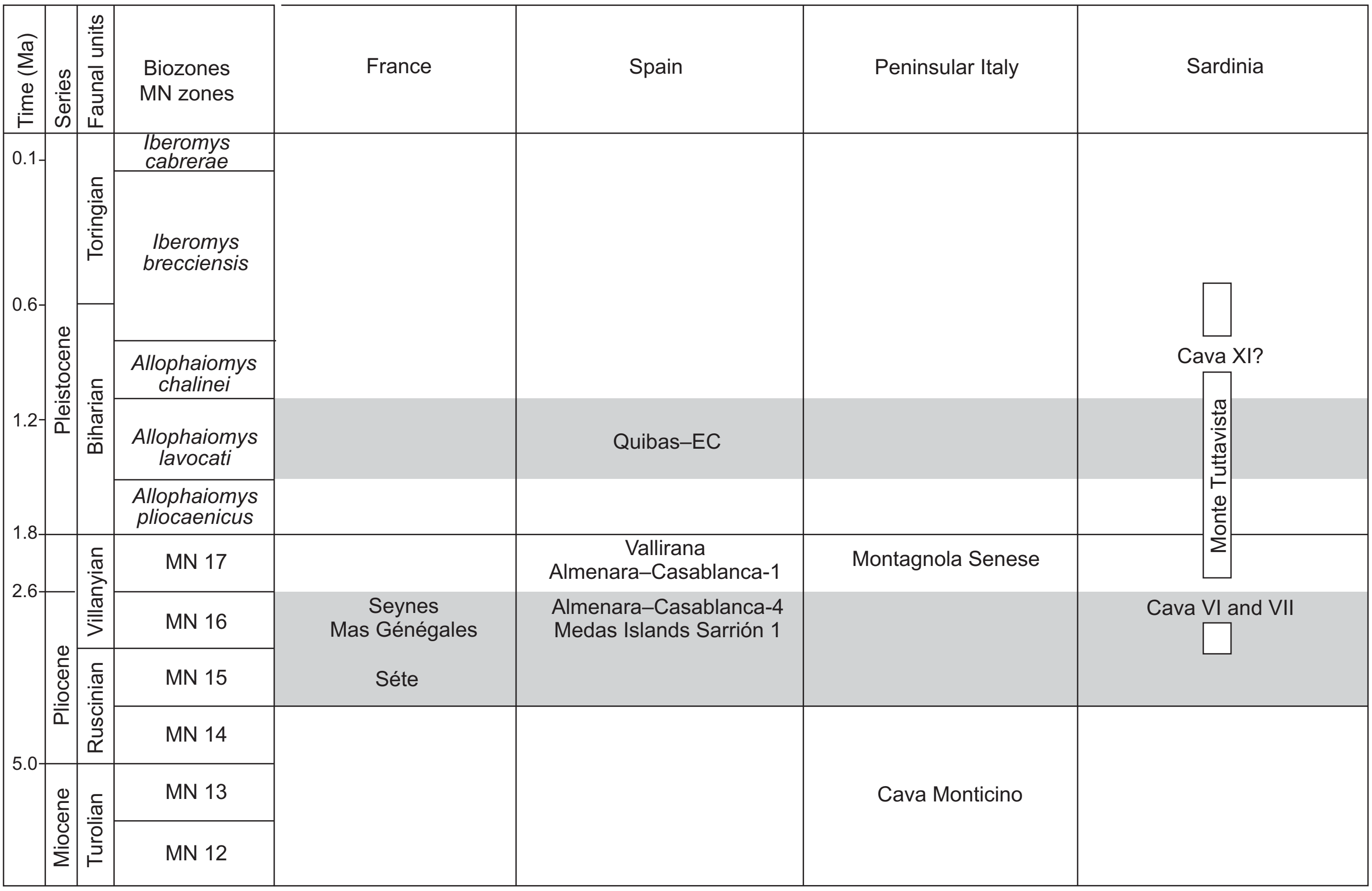

Fig. 3. Chronological synthesis of the latest Miocene, Pliocene, and Pleistocene records of the family Agamidae in Western Europe (data mainly from Delfino et al. 2008). The grey strips represent the two periods of extinction of Western and Central European herpetofauna during the Pliocene and Pleistocene (Bailon 1991; Blain 2005, 2009; Bailon and Blain 2007; Ivanov 2007). MN, Mammal Neogene Biozonation.

bases on the centrum. In the three fossil posterior caudal vertebrae, no transverse process is visible.

Remarks.—The heterodont dentition characterized by pleurodont and acrodont teeth unambiguously identifies the family Agamidae (Moody 1980; Ananjeva 1981; Bailon 1991; Delfino et al. 2008; Baig et al. 2012). Chameleons have a rather similar dentition but the anterior pleurodont teeth are missing and the acrodont teeth are located more apically than in the agamids (Moody and Roček 1980). The fossil material from Quibas-EC resembles 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 derived in the same manner as in Agaminae (Maul et al. 2011).

Discussion

Agamids today inhabit Africa, Asia, Australia, and Europe (Pough et al. 2001; Zug et al. 2001). The only genera currently in Europe are *Stellagama*, *Trapelus*, and *Phrynocephalus* (Gasc et al. 1997; Baig et al. 2012), and these are only found in the southeastern periphery of the continent, in a small area in continental Greece (Thessaloniki area) plus a few islands (Corfu, Cyclades archipelago and few Greek islands close to Asian Turkey) (Gasc et al. 1997).

The earliest European agamid fossils are from the early Eocene of Western and Northern Europe and after an apparent hiatus, they reappear later in the Oligocene of France (Augé and Smith 1997; Augé 2005). During the Miocene records are rather widespread across the continent, from France to Ukraine (Delfino et al. 2008). Later, in the Pliocene, finds are restricted to localities in the Mediterranean area (Bailon and Blain 2007; Delfino et al. 2008).

Until now, the last records of fossil agamids in Western Europe came from the MN17 sites (formerly late Pliocene, now part of the Early Pleistocene) of Vallirana and Almenara-Casablanca-1 in Spain (Blain 2005, 2009; Bailon and Blain 2007) and Montagnola Senese in Italy (Delfino et al. 2008) (Fig. 3). Consequently it was assumed that the agamids became extinct in Western Europe at the former Pliocene/Pleistocene boundary, ca. 1.8 Ma (Bailon 1987, 1991; Blain 2005, 2009; Bailon and Blain 2007). Thereafter Delfino et al. (2008) described agamid remains from three new fissure fillings from Monte Tuttavista (Sardinia, Italy) of "Plio-Pleistocene" age, so now probably considered as

Early Pleistocene: Cava VI-antica, Cava VII-blocco strada, and Cava XI-Canidae. Of particular interest was the dentary found in Cava XI-Canidae, with an age established as “latest Early Pleistocene to earliest Middle Pleistocene”, since it would represent the most recent agamid in Western Europe. However, the authors warn that this record should be considered with caution as the presence of a single skeletal element of an agamid lizard might be due to contamination (Delfino et al. 2008). Thus, the agamid fossil remains in the Early Pleistocene of Quibas-EC at approximately 1.3 Ma provides new information on the timing of the local extinction of agamids in Western Europe.

Considering the progressive impoverishment of squamate faunas in Western Europe during the Pliocene and the beginning of the Pleistocene, the new evidence that agamid lizards survived the former Pliocene/Pleistocene boundary is important because it was the only family that was supposed to have became extinct in Western Europe at that time (Bailon and Blain 2007). Our new data suggests that squamate extinctions in Western Europe were similar to events in Central Europe (Ivanov 2007), where the former Pliocene / Pleistocene boundary is not recognisable in the evolution of herpetological assemblages. Two main herpetofaunal extinction events took place in Central Europe, the first during the Pliocene (MN15 and MN16) and the second in the early Biharian (1.4–1.6 Ma ago). The first extinction is marked by the last occurrences of *Albanerpeton pannonicum*, *Mertensiella mera*, *Latonia gigantea*, *Varanus marathonensis*, and *Natrix longivertebrata*; the second extinction by the loss of *Mioproteus wezei*, *Lacerta altenburgensis*, *Podarcis praemuralis*, *Pseudopus pannonicus*, and *Zanemis paralongissimus* (Ivanov 2007). In Western Europe, the latter extinction event is marked by the last occurrences of *Pseudepidalea viridis* sensu lato in Cueva Victoria at 1.1–1.2 Ma (Murcia, southeastern Spain; Blain et al. 2010), of the anguid *Dopasia* in Barranco León D at 1.3 Ma (Granada, southeastern Spain; Blain 2005, 2009; Bailon and Blain 2007; Agustí et al. 2009; Blain et al. 2011) and finally, of agamid lizards in Quibas-EC.

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