

# Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family

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## ABSTRACT

The abundant remains from the Plio-Pleistocene fissure fillings of Monte Tuttavista (Orosei, Sardinia, Italy) allow identifying an acrodont lizard with anterior pleurodont teeth belonging to the family Agamidae. The morphology of the available skeletal elements does not significantly differ from that of the extant genera *Agama* and *Laudakia*. The poor knowledge of the comparative osteology of these genera hinders a confident identification of the remains that are simply referred to *Agama* s.l. (including both genera). In order to evaluate the contribution offered by palaeontology to the biogeography of the European agamids, an overview of their fossil record is presented. Agamids are present in about 40 European localities. The fossil record indicates that these lizards inhabited the continent since at least the early Eocene, with an apparent hiatus during the middle and late Eocene. The geographic range reached relatively high latitudes during the Paleogene (Belgium)

**KEY WORDS**

Lacertilia,  
 Agamidae,  
*Agama*,  
*Laudakia stellio*,  
*Uromastyx*,  
 Monte Tuttavista-Orosei,  
 lizard biogeography,  
 faunal dispersals,  
 anthropochorous fauna.

and Miocene (Germany and Ukraine), but since the Pliocene it was restricted to the Mediterranean regions only. The Plio-Pleistocene remains from Sardinia here described are among the youngest European evidences for the presence of these lizards outside the modern range. Curiously, there are no unambiguous Pleistocene remains even in the Balkans, the only European Mediterranean area in which agamids still live. The absence of post Pliocene remains in the Balkans could suggest that the restricted modern European range of *Laudakia stellio* is not the relict of a formerly larger range but that, if not of anthropochorous origin, the ancestors of extant populations dispersed relatively recently from the east.

**RÉSUMÉ**

*Les agamidés du Plio-Pleistocène de Sardaigne (Italie) avec un aperçu des données fossiles européennes de la famille.*

Les restes abondants des remplissages de fissures plio-pleistocènes de Monte Tuttavista (Orosei, Sardinie, Italie) permettent d'identifier un lézard acrodonte appartenant à la famille des Agamidae et qui présente une dentition antérieure pleurodonte. La morphologie des éléments squelettiques disponibles ne diffère pas de manière significative de celle des genres actuels *Agama* et *Laudakia* mais les connaissances limitées sur l'ostéologie comparative de ces deux genres ne permettent pas d'identifier avec certitude ces restes, qui sont ici référés au genre *Agama* s.l. (incluant les deux genres). Afin d'évaluer la contribution de la paléontologie sur la biogéographie des agamidés européens, une synthèse des données fossiles est présentée. Les agamidés sont identifiés dans environ 40 localités européennes. Le registre fossile indique que ces lézards occupaient le continent depuis au moins l'Éocène basal. Néanmoins, un hiatus important comprenant l'Éocène moyen et l'Éocène terminal a été mis en évidence. Leur distribution géographique a atteint des latitudes relativement hautes au cours du Paléogène (Belgique) et du Miocène (Allemagne et Ukraine), mais depuis le Pliocène leur répartition s'est restreinte aux régions méditerranéennes. Les restes plio-pleistocènes de Sardaigne ici rapportés constituent une des plus récentes preuves de la présence de ces lézards hors de leur répartition moderne. Curieusement, aucun reste pleistocène de ces lézards n'a encore été reporté sans ambiguïté en Europe, y compris dans les Balkans, la seule zone européenne dans laquelle les agamidés vivent actuellement. L'absence de restes post-pliocènes dans les Balkans suggère que la répartition européenne récente de *Laudakia stellio* n'est pas une relique d'une répartition ancestrale plus large mais que, excluant l'éventualité d'une origine anthropochorique, les ancêtres des populations actuelles se sont dispersés assez récemment depuis les régions orientales.

**MOTS CLÉS**

Lacertilia,  
 Agamidae,  
*Agama*,  
*Laudakia stellio*,  
*Uromastyx*,  
 Monte Tuttavista-Orosei,  
 biogéographie des lézards,  
 dispersions fauniques,  
 faunes anthropochoriques.

**INTRODUCTION**

The family Agamidae Spix, 1825 is a rather large, probably monophyletic (see Joger 1991; Honda *et al.* 2000, and literature therein), group of acrodont lizards that from a Late Cretaceous centre of origin likely placed in eastern Asia (Borsuk-Bialynicka & Moody 1984), or in the Gondwana (Macey *et al.* 2000), dis-

persed in most of the Old World. Nowadays agamids inhabit Africa, Asia, Australia and Europe (Pough *et al.* 2001). If compared with other lizard clades, agamids have a rather restricted European range at present (Gasc *et al.* 1997; Arnold & Ovenden 2002). They just reach the southeastern periphery of the continent with *Phrynocephalus* spp., *Trapelus sanguinolentus* (Pallas, 1814) and *Laudakia caucasia*



FIG. 1. — The European fossil record of Agamidae. Explanation of symbols:  $\diamond$ , Eocene;  $\triangle$ , Oligocene;  $\circ$ , Miocene;  $\square$ , Pliocene;  $\square$ , Plio-Pleistocene; the approximate European modern range of *Laudakia stellio* (Linnaeus, 1758) is represented by the empty ellipses. The present ranges of *Phrynocephalus*, *Trapelus* and *Laudakia caucasia* (Eichwald, 1831) are not shown in the figure. See Appendix for more information about the localities and the identified taxa. One locality, Rema Aslan (Greece), is not shown on the map because its location has not been identified.

(Eichwald, 1831), or inhabit a small area in continental Greece (Thessaloniki area) plus few islands (Corfu, Cyclades archipelago and few Greek islands close to Asian Turkey) as in the case of *Laudakia stellio* (Linnaeus, 1758) (see Fig. 1). According to Xyda (1983), the area inhabited by this species close to Thessaloniki could represent a relict of a formerly wider range, but the populations of at least one of the mentioned islands are considered to be of anthropochorous origin (Corfu in the Adriatic sea; Razzetti *et al.* 2006, and literature therein). Introduced specimens of other agamids, like *Agama agama* Linnaeus, 1758, have been sporadically mentioned for continental and insular Italy (Razzetti & Sindaco 2006) as well as Malta (Schembri & Schembri 1984).

Despite being fairly discontinuous both in terms of chronology and geography, the European fossil record indicates a different scenario (Figure 1 summarizes all the available taxon-locality of the European fossil agamids; data presented in the

Appendix). Agamids were already present in the early Eocene of western and northwestern Europe and after an apparent hiatus, they reappeared later in the Oligocene of France (Augé & Smith 1997; Rage 1997). The Miocene record is rather widespread across the continent, from France to Ukraine (nearly reaching a 50°N during the Tortonian). During the Pliocene all the data come from localities in the Mediterranean area. Surprisingly, there are no unquestionable Pleistocene remains.

Bailon & Blain (2007: 55) recently proposed that “the disappearance of the last Agamidae [in western Europe] corresponds to a fall of the mean annual temperature below 15°C”, before the beginning of the Pleistocene.

In terms of diversity, all the fossil record is characterized by a great morphological uniformity that hinders a precise taxonomic identification. With the exceptions of some Paleogene remains referred to the extinct taxa *Quercygama galliae* (Filhol, 1877),

*Tinosaurus europeocaenus* Augé & Smith, 1997, and *Uromastyx europaeus* (de Stefano, 1803), most of the remains are identified as *Agama* Daudin, 1802, *Laudakia* Gray, 1845 or *Stellio* Laurenti, 1768, or even simply at family rank. Actually, the referral of fossil remains to the mentioned genera probably reflects the attempt to indicate similarity of the fossil remains with the extant *Laudakia stellio*, whose unstable nomenclature frequently changed since its original description (for an accurate summary, see Almog *et al.* 2005). The separation of *L. stellio* from the genus *Agama* suggested by Moody (1980; with the name *Stellio stellio*) seems not to be convincingly supported by osteological characters that can be applied to the fossil remains, usually represented by isolated cranial and vertebral skeletal elements. If it is so, a correct identification of the fossil material showing a close resemblance with the extant agamid inhabiting the Mediterranean Basin should be better formalized as *Agama* s.l. (comprehensive of genera *Agama* and *Laudakia*). At least until when the diagnosis of *Laudakia* and *Agama* will include osteological characters that could be traced on the fossil remains.

## MATERIAL AND METHODS

### NEW FOSSIL MATERIALS

The material is housed in the collections of the “Soprintendenza ai Beni Archeologici delle Province di Sassari e Nuoro” at Nuoro with the accession code “OR” (Orosei) followed by an “H” (Herpetology), the number of the quarry and a progressive number for each remain. In the following list, no distinction is made between perfectly preserved specimens and fragments.

Material (L, left; R, right; tbb, tooth bearing bone):

- Cava VI (3) – antica [519 remains]: maxilla: 16 R, 29 L; dentary: 48 R, 47 L; tbb: 75; trunk vertebra: 179; caudal vertebra: 125;
- Cava XI – Canidae [one remain]: dentary: 1 L;
- Cava VII – blocco strada [four remains]: dentary: 1 L; tbb: 3.

Due to the presence in the site “Cava VI (3) – antica” of several skeletal elements of a green lizard (*Lacerta* sp.) of size comparable to that of the agamids, it has not

been possible to identify several fragmentary lizard vertebrae; therefore, it is likely that the number of agamid vertebrae from “Cava VI (3) – antica” is slightly higher than that here reported.

Note that the presence of a single skeletal element of an agamid lizard in “Cava XI – Canidae” is here considered as potentially due to contamination (see below).

### THE AGE OF THE NEW MATERIALS

The whole faunal assemblage from Monte Tuttavista (Orosei) has been mentioned for the first time by Cordy (1997) and then preliminarily described by Abbazzi *et al.* (2004) and Rook *et al.* (2004a). To date, only few mammals have been the topic of a detailed report (Rook *et al.* 2004b; Abbazzi *et al.* 2005; Marcolini 2005; Marcolini *et al.* 2006a, b; Palombo *et al.* 2006; Angelone *et al.* 2008). The fossil remains come from different fissure fillings of the same karst network. The age of each fissure has been tentatively proposed on the basis of the faunal assemblage it contains; it varies from late Pliocene to late Pleistocene. According to the biochronological scheme of the Plio-Pleistocene terrestrial mammals of Sardinia recently defined by Palombo (2006), “Cava VI – antica” and “Cava VII – blocco strada” belong to the “Capo Figari/Orosei 1” subcomplex (latest middle or late Pliocene to early Pleistocene), while “Cava XI – Canidae” belongs to the younger “Orosei 2” subcomplex (latest early Pleistocene to earliest middle Pleistocene).

## SYSTEMATIC PALAEOLOGY

Order SQUAMATA Oppel, 1811  
Suborder LACERTILIA Owen, 1842  
Family AGAMIDAE Spix, 1825  
Genus *Agama* Daudin, 1802

*Agama* s.l.

### DESCRIPTION

#### *Maxilla*

Due to the absence of a single complete maxilla, the description of the morphology of this element is possible thanks to the high number of fragments or partly complete elements. The most complete

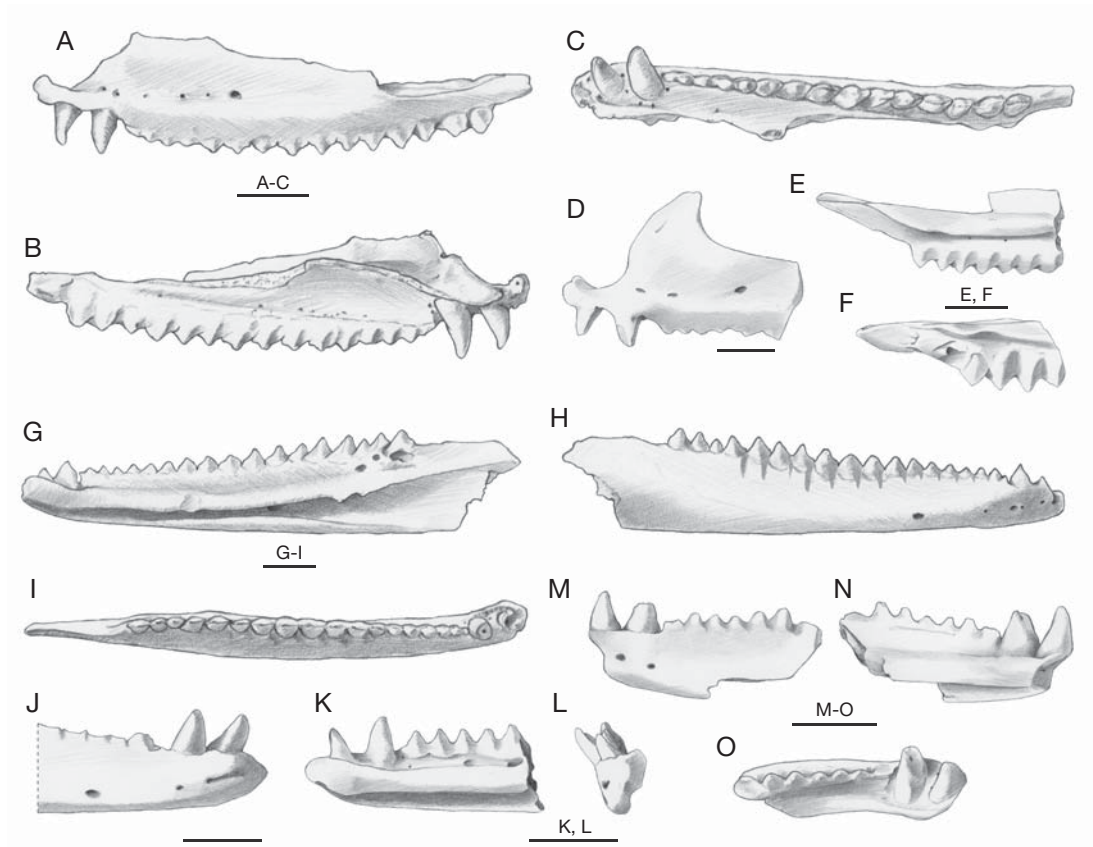


FIG. 2. — *Agama* s.l. from Monte Tuttavista (Plio-Pleistocene, Sardinia): **A-C**, left maxilla in lateral, medial and ventral views respectively (OR H VI 3/1); **D**, fragmentary left maxilla in lateral view (OR H VI 3/2); **E**, fragmentary left maxilla in medial view, note the length of the zygomatic process (OR H VI 3/3); **F**, same (OR H VI 3/4); **G-I**, right dentary in lateral, medial and dorsal views respectively (OR H VI 3/5); **J**, detail of the anterior region of a right dentary in lateral view showing well-preserved pleurodont teeth (OR H VI 3/6); **K, L**, fragmentary right dentary in medial and anterior views respectively (OR H VI 3/7); **M-O**, fragmentary left dentary in lateral, medial and dorsal views respectively (OR H XI/1). Scale bars: 2 mm.

maxilla, OR H VI 3/1 (Fig. 2A-C), is 16.3 mm long (the tip of the zygomatic process is broken off and therefore the original length was slightly higher). All the well-preserved maxillae are characterized by two anterior pleurodont teeth followed by at least 15 or 16 acrodont teeth. The orientation of the pleurodont teeth is approximately parallel to the external vertical wall while the acrodont tooth row is distinctly oriented medioventrally. The pleurodont teeth are located one anteriorly to and the other just under the beginning of the external vertical wall. They are well-spaced, monocuspidated, conical, pointed, slightly bent in posteromedial direction and, if well preserved (like in the case of OR H VI 3/1), apically

provided with a mesiodistal keel. The acrodont teeth are not spaced (the posterior ones are even overlapped to the anterior part of the following tooth) and triangular in shape. The main cusp is in some cases flanked mesially and distally by a much smaller cusp. Teeth are provided with an evident mesiodistal keel which separates a nearly flat labial surface from a variably swollen lingual surface. The base of these teeth is slightly developed also on the medial surface of the bone and therefore should be better defined as pleuroacrodont (Evans *et al.* 2002). The anterior acrodont teeth are small in size and variably worn (in one case they are nearly completely flattened by usage) while the central and posterior ones are larger

(the size increases in backward direction), massive and partly overlapping; in several cases the posterior end of a tooth is labially overlapped to the anterior end of the following tooth (that is therefore lingually placed). The mesiodistal keel of the posterior teeth is therefore not parallel to the main axis of the tooth row but slightly inclined (anteromedially directed proximally and posterolaterally directed distally). Elongated wear facets are clearly visible on the lingual surface of all the acrodont teeth; these facets are always developed on both sides of the swollen lingual surface of each tooth and in some cases nearly reach each other toward the midline of the triangular tooth. There are no foramina along the acrodont tooth row but some foramina are present around the base of the pleurodont teeth. On the external surface, up to six foramina are aligned at the base of the prefrontal process; the largest is invariably the last one (usually corresponding to the sixth acrodont tooth). The prefrontal process is never entirely preserved. However, judging from the preserved portions, it can be stated that it is smooth, anteroposteriorly narrow but tall and that the anterior margin is usually rather steep (Fig. 2D) and subvertical at the base, at least in some cases. Above the line of foramina, a shallow anteroposteriorly depression is always present. The premaxillary process is distinctly developed not only in anterior but also in dorsal direction; if not damaged, the premaxillary process has a well-developed anterior surface for the suture with the premaxilla. On the dorsal surface of the external vertical wall, there is a distinct step at the end of the orbital margin (therefore corresponding to a step in the missing jugal). The zygomatic process is broken off in most of the cases; when present (Fig. 2E, F) it is long at least as the space occupied by the last four or five teeth. On the inner surface of the bone, the horizontal lamina is developed in mediadorsal direction reaching the maximum development approximately at the level of the sixth acrodont tooth. At least two foramina are developed in the groove produced by the dental shelf and the vertical wall.

#### *Dentary*

The dentaries are markedly slim and elongated, with a nearly straight ventral edge if seen in lateral view. The best-preserved dentary OR H VI 3/5 (Fig. 2G-I),

is 19.1 mm long but it is posteriorly broken off and anteriorly eroded. As for the maxillae, there are no complete dentaries and the above-mentioned specimen is the only one with an entirely preserved tooth row (length of the region with acrodont teeth is 12.9 mm). In this specimen, the two pleurodont teeth (partly broken off) are followed by 17 acrodont teeth. The shape of the pleurodont teeth (see also dentary fragments in Figure 2J-O) does not differ from the one already described for the maxillary teeth; also the position and shape of the acrodont teeth are similar, but the lingual surface is less swollen than the labial one. The overlapping pattern is analogous, with posterior acrodont teeth a little labially overlapped to the following one. Another similarity concerns the wear facets but in the case of the dentary they develop considerably in ventral direction reaching the external bony surface of the dentary, forming evident long V-shaped grooves (Fig. 2H). The anterior acrodont teeth of the dentaries are approximately symmetric while the posterior ones are posteriorly inclined. In the few well-preserved dentaries, the anterior acrodont teeth are not completely worn as it happens in one fossil maxilla or in the dentaries of living agamids. On the medial surface, the symphyseal area is not clearly delimited but seems to have an oval shape. Few irregular foramina can be present at the base of the pleurodont teeth and in the longitudinal groove at the base of the acrodont tooth row. The Meckel's groove opens along the entire length of the dentary: it is rather narrow in the anterior half of the dentary and slightly larger in the posterior half; under the last three or four teeth, the groove becomes narrower because of a blade-like ventrally directed expansion (partly broken in the specimen depicted in Figure 2G) of the dorsal rim of the groove itself. The foramen for the inferior alveolar nerve (intramandibular foramen according to Bailon 1991) opens inside the groove, at the level of the 10th or 11th acrodont tooth. On the external surface, there are usually five aligned foramina distributed from the tip of the dentary to the level of the sixth or seventh acrodont tooth. The coronoid process, not completely preserved in any of the available dentaries, is dorsally thin (blade-like), moderately long, gently sloping, but

clearly posterodorsally oriented. There are no evident scars left by the coronoid. The angular process is invariably broken off.

#### Vertebrae

Several vertebrae come from the cervical, dorsal and caudal region. All the vertebrae are procoelous.

**Cervical and dorsal vertebrae (Fig. 3).** In anterior view, the cotyle is oval (dorsoventrally flattened). The neural canal is proportionally wide. The neural arch is triangular and devoid of zygosphenes. The prezygapophyseal facets are dorsolaterally tilted. In dorsal view, the neural arch does not cover completely the centrum, of which the anteriorly convex edge is usually visible. The anterior edge of the neural arch is U- or V-shaped. Prezygapophyseal facets are oval-shaped and anterolaterally directed. The neural spine nearly reaches the anterior edge of the neural arch. Despite the presence of a moderate interzygapophyseal constriction, the neural arch has a rather wide appearance. The postzygapophyses surpass the posterior edge of the neural arch, which is modestly concave. In posterior view, the neural canal is wide. The neural arch is rather low and with straight lateral edges. The condyle has a shape that varies from oval to roundish. In ventral view, the dorsal rim of the cotyle overhangs the ventral one. The synapophyses are evident and laterally protruding. The centrum is triangular, anteroposteriorly compressed in the anterior trunk (cervical) vertebrae and more elongated in the posterior ones. The centrum ventral surface can be nearly flat or weakly convex, showing the presence of a modest, wide and smooth keel latero-anteriorly delimited by the hint of a groove. A couple of sub-central foramina can be present. In lateral view, the synapophyses are well defined, roundish or oval-shaped and placed at the level of the ventral rim of the cotyle or behind it. The ventral rim of the centrum is flat or moderately concave. Due to incompleteness of the neural spines, it is not possible to assess their dorsal development: the only exception shows a short neural spine of which the caudal edge does not surpass the posterior rim of the postzygapophyses. The few vertebrae with a hint of hypapophysis located just behind the cotyle come

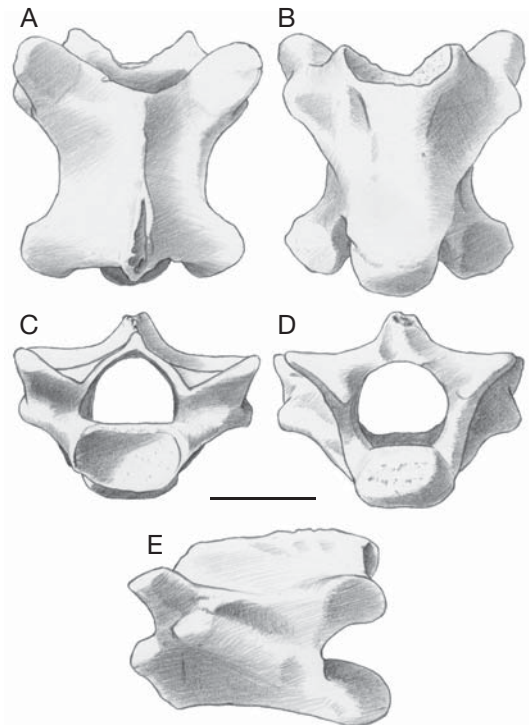


FIG. 3. — *Agama* s.l. from Monte Tuttavista (Plio-Pleistocene, Sardinia), OR H VI 3/8, trunk vertebra in dorsal (A), ventral (B), anterior (C), posterior (D) and left lateral views (E) respectively. Scale bar: 2 mm.

from the cervical sector. The maximum centrum length of a dorsal vertebra is of about 4 mm (but sensibly smaller on average).

**Caudal vertebrae (Fig. 4).** Caudal vertebrae are characterized by roundish cotyles and condyles, elongated centra devoid of autotomic plane and of fused chevron bones. The anterior caudal vertebrae preserve the proximal portion of robust and apparently long lateral processes (one per side), with a base dorsoventrally flattened, perpendicularly oriented to the main axis of the centrum and slightly pointing ventrally. The process-bearing vertebrae have a reduced neural spine represented by a ridge on most of the neural arch, but developed at the back of the neural arch as a robust spine pointing in dorsocaudal direction. The lateral processes and the neural spine decrease in size in backward direction

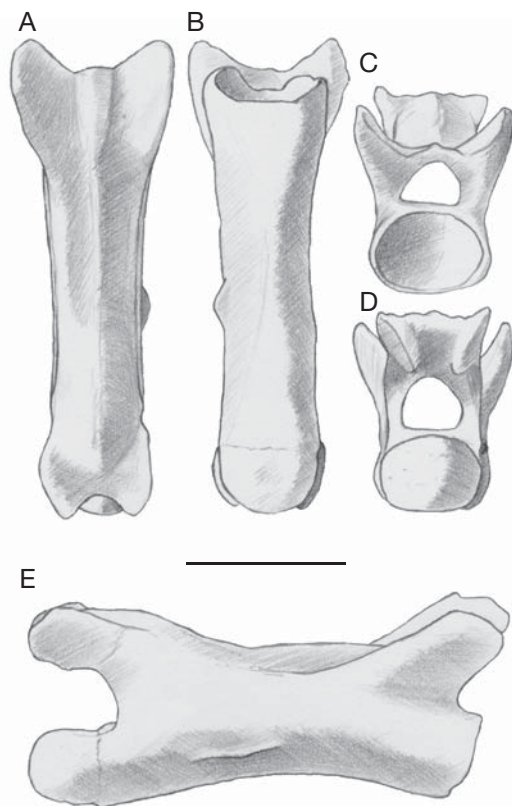


FIG. 4. — *Agama* s.l. from Monte Tuttavista (Plio-Pleistocene, Sardinia), OR H VI 3/9, posterior caudal vertebra in dorsal (A), ventral (B), anterior (C), posterior (D) and right lateral views (E) respectively. Scale bar: 2 mm.

along the tail and are not present in many of the fossil posteriormost vertebrae, where just a sagittal thin ridge is visible (as in the specimen depicted in Figure 4). The maximum centrum length of an anterior caudal vertebra is about 4.5 mm, the one of a posterior vertebra is about 5 mm.

#### REMARKS

The heterodont dentition characterized by pleurodont and acrodont teeth, unambiguously identifies the family Agamidae. Chameleons have a rather similar dentition but the anterior pleurodont teeth are missing and the acrodont teeth are usually more spaced, more labio-lingually symmetric (without an inflated surface) and located more apically than those of agamids (for a discussion of the differences

among these two groups see Moody & Rocek 1980; Bailon 1991; Blain 2005, and literature therein). The comparative osteology of agamids is incompletely known (the few exceptions are represented by Siebenrock 1895; El-Toubi 1947; Duda 1965; Ananjeva 1980, 1981, 1998; Moody 1980; Baig 1992) and the available information is hardly applicable to the fossil remains. Even if a confident allocation at genus level has to be considered as tentative at least, some considerations can be developed.

The referral of the remains from Monte Tuttavista to *Phrynocephalus* Kaup, 1825 and *Trapelus* Cuvier, 1817, agamid genera presently inhabiting the periphery of Europe, can be excluded on the basis of remarkably different tooth numbers and/or different morphology of the prefrontal process and external vertical wall (see Ananjeva 1980, 1981, 1998; Moody 1980).

Blain (2005) recently allocated at genus level (*Laudakia* sp.) an agamid dentary from the late Pliocene of Vallirana (Spain) mostly on the basis of the morphology of this element and acrodont teeth counts. The dentary from this locality possesses 14 teeth, a number which is congruent to that of the dentaries from Seynes and Medas islands (14 or 15 teeth) reported by Bailon (1991) and with that indicated by Baig (1992) for the *Laudakia*-group (*Stellio*-group for the mentioned author), with the exception of *L. tuberculata* (Gray, 1827) that has 15-18 teeth. However, the teeth counts reported by Blain (2005: 243) for extant species do not match with those seen on the limited comparative material at our disposal. Blain reports the presence of 13 acrodont teeth in *A. agama* while the only specimen at our disposal (adult male from Kenya; M. Delfino pers. coll. no. 305) hosts 22 acrodont teeth. The morphological differences pointed out by Blain seem to be based on limited comparative material and not taking into account the ontogenetic variability. Cooper *et al.* (1970, and literature therein) report remarkable ontogenetic changes in terms of teeth counts (ontogenetic change from nine to 19 acrodont teeth in the dentaries of agamids) suggesting that this character can be applied only to large samples of fossil material and not to isolated findings. It is worth noting that the number of acrodont teeth has not been included among



the several cranial characters identified by Moody (1980) for the phylogenetic analysis of the agamids: the author explicitly writes that “characterization of agamid species and genera by number of acrodont teeth is difficult because of the radically different-sized anterior and posterior teeth and because of the enlargement of the anterior pleurodont teeth which erodes several of the anterior acrodont teeth” (Moody 1980: 62). The identification as cf. *Laudakia* sp. of the agamid fossils from another Spanish site, Casablanca-Almenara, reported by Blain (2005), is not based on any character that is exclusively present in the extant species of this genus; therefore such characters will be not further discussed here.

Moody (1980) considered as a valid character for his phylogenetic analysis of the agamids the position of the Meckel’s groove at the symphysis (if remains on the medial surface of the dentary – *Stellio* 57:0 – or if rotates to the ventral edge – *Agama* 57:1). Assuming that this character differentiates *Agama* from *Laudakia*, it could be used to identify the fossil remains from the Pliocene of Europe. According to his character matrix, all the analyzed species of *Agama* (*A. agama*, *A. atra* Daudin, 1802, *A. hispida* Kaup, 1827) have a Meckel’s groove which rotates ventrally, while all the analyzed species of *Laudakia* (*Stellio* in his work; *L. stellio*, *L. tuberculata*) have a groove which remains on the medial surface of the dentary (Moody 1980: appendix D). Surprisingly, on page 55 he states that “the groove rotates to the ventral edge as it rounds the symphysis in *Agama* [and] *Stellio* [= *Laudakia*]”. The limited modern comparative material available for the present study does not show any significant difference among *L. stellio* (adult male from Corfu, M. Delfino pers. coll. no. 245), *A. agama*, *A. bibroni* Dumeril & Bibron, 1851 (adult specimen from Morocco, M. Delfino pers. coll. no. 275) and the few fossil dentaries from Monte Tuttavista that preserve the symphyseal region (a weak difference could concern the fact that in the fossils the symphysis is slightly more developed in medial direction). In all these cases, it seems that the groove is developed on the medial surface and never significantly rotates ventrally as it approaches the symphysis.

A further relevant character could be the orientation of the coronoid process of the dentary which is slightly posterodorsally oriented in the comparative modern specimen of *L. stellio* and in the few fossil remains from Sardinia, but slightly posteroventrally oriented in the comparative specimens of *A. agama* and *A. bibroni*. The orientation of this process has been also taken into consideration by Moody (1980; character 62; the process is called “retroarticular process”) but in the character matrix the status is reported to be the same for *Agama* and *Laudakia* (process projected posteriorly in a horizontal plane or curve dorsally; 62:0). Hence, the validity of this character for the identification of the members of these two genera should be confirmed on a wider sample of modern comparative skeletons (both in terms of number of species and of number of specimens for each species).

In conclusion, despite the fossil material from Sardinia here described resembles the only available comparative specimen of *L. stellio* in terms of maxillary and dentary acrodont teeth counts (the comparative specimen has 15 maxillary and 16 – or 17? – dentary acrodont teeth), shape of the coronoid process and position of the ventral lamina on the Meckel’s groove dorsal rim (that reduces the largeness of the groove posteriorly to the 14th acrodont tooth), a precise generic identification is here considered hazardous due to absence of any reliable osteological character allowing the distinction of *Laudakia* from *Agama*. The agamids from Monte Tuttavista are therefore formally referred to *Agama* s.l., which includes both these genera.

## DISCUSSION

THE FOSSIL AGAMIDS FROM MONTE TUTTAVISTA  
Despite the fact that they have been simply identified at genus rank, without even indicating a precise genus, the agamid remains from Monte Tuttavista represent the best-preserved and most abundant fossil evidence of this lizard family in the Mediterranean area. Broadly speaking, the herpetofauna from this locality can be considered as one of the most informative of the Mediterranean Plio-Pleistocene, being made up by 14 taxa (four amphibians and

10 reptiles) represented by roughly 15 000 already identified remains (Abbazzi *et al.* 2004). The same fissures with the agamids, also yielded, among others, cave salamanders (*Speleomantes* sp.), green lizards of moderate size (*Lacerta* sp.), worm lizards (*Amphisbaenia* indet.) and vipers (*Vipera* gr. *V. aspis* (Linnaeus, 1758)). All the listed taxa, except the cave salamanders, are now extinct in Sardinia. There are no clues about why all these taxa disappeared from the island, mostly in the cases in which they (or related taxa) survived on the neighbouring mainland (it can be the case of the green lizards and the vipers) but also in the case of taxa which still inhabit other Mediterranean peninsulas.

The contemporaneous presence of agamids, which are usually considered as proxies of arid and sunny environments, and of cave salamanders, which being characterized by the absence of lungs are tied to an interstitial life in rather humid environments, is only apparently contrasting and leads to suppose the presence of a fissured rocky substrate with interstitial moisture, placed in a typical Mediterranean environment (approximately as the karstic area in which the quarries are located nowadays).

The agamids from Monte Tuttavista were likely superficially similar to the mentioned genera *Agama* and *Laudakia*, but the sample of remains is large enough to state with confidence that the size of these lizards was slightly smaller than that of modern *L. stellio* since there are no remains suggesting a snout-vent length larger than about 90–100 mm. Moreover, on the basis of the most common element (the dentary) it is possible to indicate that the minimum number of individuals from “Cava VI – 3 antica” is of 48 specimens (assuming that there are no dentary fragments belonging to the same skeletal element).

The presence of a fragmentary left dentary (Fig. 2M–O) in the Pleistocene fissure “Cava XI – Canidae” could represent the first and only European evidence for a Pleistocene fossil agamid. However, it is here preferred to conservatively not exclude the possibility of an allochthonous fossil (due to the geometric relationships among this and the other fissures, and therefore to possible contamination prior or during the collection of the sediments). Future sampling of this fissure will hopefully clarify this issue.

#### ITALIAN FOSSIL AGAMIDS

The only other published evidence for agamid lizards in Italy is represented by a dentary and two maxillary fragments from the late Miocene of Cava Monticino (peninsular Italy; Delfino 2002), whose morphology is conform to those of *Agama* and *Laudakia* (at least on the basis of the poor present knowledge of the comparative anatomy of these taxa). Moreover, few unpublished fragmentary teeth bearing bones and vertebrae have been recently identified in the late Pliocene assemblage of Montagnola Senese (Delfino pers. obs.).

Actually, Schleich *et al.* (1996: 23) wrote that “there are records of *Uromastyx* in southern Italy (Estes 1983) and probably of other NAF [= North African] reptiles in the Neogene of southeastern Spain that may be explained by migrations during the Messinian”. The reference mentioned by Schleich and co-authors does not contain any indication of Italian *Uromastyx* remains, nor at that time (or even in 1996) were agamid remains from Italy known (Delfino 2002). Possibly, at the origin of such datum is the report by an Italian author on an Italian magazine of a fossil putative *Uromastyx* from a cave with an Italian name. Mangili (1980) reported the presence of *Uromastyx aegyptia* (Forskål, 1775), formerly called *U. spinipes* (Boulenger, 1885), in the Pleistocene of the Simonelli Cave, Crete. The author stated that “the morphology of the tibia of the *Agama* is remarkably different from that of the fossil specimen; in particular the value of the length, in the ratio of the total length to the transverse dimensions, is remarkably high and the bone appears rather slender on the whole, the proximal epiphyso-metaphyseal complex moreover shows a remarkable backward flexion” (Mangili 1980: 121). Moreover, the author explicitly indicated that the size of the fossil tibia exceeds those of *Laudakia stellio* (then *Agama stellio*). Since the material has not been figured and it is not presently available for study, it is not possible to assess the validity of such identification, nor to confirm the referral of the remain to “? *Agama* sp.” as uncritically reported by Caloi *et al.* (1986, 1988). Due to the fact that Mediterranean islands were inhabited by large sized lacertids during the Pleistocene (Kotsakis 1977; Böhme & Zammit-Maempel 1982; Delfino 2002),

it is here proposed to identify this fossil at order rank (*Lacertilia* indet.) waiting a formal revision. Therefore, such datum has not been taken into account in the review of the European agamid remains presented in this paper.

#### ON THE EUROPEAN FOSSIL RECORD AND MODERN RANGE OF AGAMID LIZARDS

The only agamid presently inhabiting the European Mediterranean region is *Laudakia stellio* whose range largely extends to the East reaching Asia Minor and northeastern Africa (Gasc *et al.* 1997). The extremely “insular-like” restricted European distribution (defined as a zoogeographic paradox by Džukić & Kalezić 2004) could be the result of a progressive shrinkage of the range or the product of a relatively recent dispersal from the east. Progressive range shrinkage from NW to SE during the Late Neogene and Quaternary is a well-known pattern for many reptile genera (Delfino *et al.* 2003, and literature therein) and agamids could be taken as a further confirmation. However, a direct phylogenetic link between the agamids which populated western Europe during the Pliocene and the extant populations of *Laudakia* in the Balkans cannot be proved on a sound, morphological, basis. An alternative hypothesis, that the modern populations were isolated since the Pliocene or the beginning of the Pleistocene, conflicts with the low divergence of the European populations whose subspecific status has been questioned until recently (Almog *et al.* 2005; Crochet *et al.* 2006; but note that this issue has not been explored with a phylogeographic approach).

On the other hand, despite the fact that the absence of evidence should not be considered as an evidence of absence, it is tempting to underline that the remarkable lack of post-Pliocene remains of these rather large and easily recognizable lizards (so that their presence in the palaeontological or archaeological deposits can be hardly overlooked) from the entire Mediterranean area, and from the Balkans in particular, could support the option of a relatively recent dispersal.

These topics have been previously treated in the literature, but the lack of a critical evaluation of the original palaeontological data generated some sort of confusion. The origin and dispersal pattern of

genus *Laudakia* has been discussed by Baig (1992) who stated that “the fossil record shows that the ancestors of this group were widely distributed until the Miocene, in the west up to France and in the east up to eastern side of China [... and that] they remained on the surface of Earth until Pleistocene” (Baig 1992: 219). Such statement should be taken with caution because of the unreliability of the identification of the European fossil record discussed in the previous sections of this paper. Conversely, the recurrent and relatively recent (Pleistocene) dispersal of *L. stellio* in the Mediterranean islands, proposed by the same author, seems more likely, and it is supported not only by the present distribution, but also by the absence of relatively young fossils.

As for the origin of the Pliocene fossils from western Europe, Moody (1980: 245) affirmed that “several Plio-Pleistocene *Agama* sp. fossils from southern France extend the distribution of the genus into western Europe via the Iberian Peninsula (personal observation)”, that is to say from Africa to Iberian Peninsula. Disregarding that, as already discussed earlier, there are no unambiguous Pleistocene agamid remains in Europe, the identification at genus rank of the available fossil remains has to be considered as putative and therefore it is not known if the Pliocene agamids from western Europe (at least Spain and France) are of direct African origin or not.

#### FUTURE DEVELOPMENTS

Due to the fact that the Plio-Pleistocene reptiles of the Mediterranean area are strictly related with the modern species inhabiting the same area, if not belonging to the extant species themselves, the study of the fossil record can offer key evidences to understand the evolutionary history of the modern Mediterranean herpetofauna. Unfortunately, the *Agama-Laudakia* case presented in this paper is far from being isolated: the poor knowledge of the osteology of extant taxa limits significantly the resolution power of palaeontological studies (for the Italian herpetofauna, see Delfino 2004a). Examples of taxa with a present disjunct west-east distribution but with a continuous Pleistocene range are represented by the terrapin *Mauremys*

(Chesi *et al.*, 2007) and the amphisbaenian *Blanus* (Delfino 1997). In both cases, the Italian fossil record contributes to partly fill the gap in the present range but the comparative osteology of the Mediterranean members of these genera is largely unknown and does not allow the identification of the fossil remains at species rank, limiting the information provided by palaeontology (which is in fact providing a rather confusing taxonomic scenario). It is therefore desirable that future neontological taxonomic studies will also take into consideration the osteology of the isolated skeletal elements in order to stimulate the promising analysis of the fossil record.

## CONCLUSION

More than 500 remains from the Plio-Pleistocene fissure fillings of Monte Tuttavista, Sardinia, testify for the presence of an agamid lizard slightly smaller than *Laudakia stellio*, the only agamid which still inhabits the European Mediterranean region. Their morphology is similar to that of *Laudakia* and *Agama*, two genera that were formerly grouped together and whose recent distinction is not based on osteological characters applicable to the fossil material. However, even if presently referred to *Agama* s.l., these Sardinian remains represent the most informative agamid material from the Plio-Pleistocene of Europe and will provide significant information when the comparative osteology of the two above-mentioned genera will be known more in detail. A positive identification of the Plio-Pleistocene remains from Spain, France and Italy could significantly contribute to understand the last stages of the agamid evolution in Europe, that is to say if direct dispersals from northwest Africa or Middle East occurred. Even though the fossil record indicates an extended (Eocene-Recent) permanence of agamids in Europe, there is no evidence for a continuous local evolution and the absence of unquestionable Pleistocene remains in the entire European Mediterranean area could suggest that the modern populations of the continental and insular Greece dispersed relatively recently from the east.

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## APPENDIX

List of the European localities with fossil agamids (see Figure 1).

**Belgium**

**B1**, Dormaal (*Tinosaurus europeocaenus*; early Eocene, MP 7; Augé & Smith 1997).

**France**

**F1**, Condé-en-Brie (*T. europeocaenus*; early Eocene, MP 8+9; Augé 1990; Augé & Smith 1997); **F2**, Avenay (*T. europeocaenus*; early Eocene, MP 8+9; Augé 1990; Augé & Smith 1997); **F3**, Mutigny (*T. europeocaenus*; early Eocene, MP 8+9; Augé 1990; Augé & Smith 1997); **F4**, Sézanne (*T. europeocaenus*; early Eocene, MP 8+9; Augé 1990; Augé & Smith 1997); **F5**, La Plante 2, Phosphorites du Quercy (*Uromastyx europaeus*, Early Oligocene, MP 22; Augé & Smith 1997); **F6**, Mas de Got B, Phosphorites du Quercy (*U. europaeus*, Early Oligocene, MP 22; Augé & Smith 1997); **F7**, Roqueprune, Phosphorites du Quercy (?*Quercygama galliae*; Early Oligocene, MP 23; Augé & Smith 1997); **F8**, Rigal-Jouet, Phosphorites du Quercy (Agamidae indet., Late Oligocene, MP 25; Augé & Smith 1997); **F9**, Garouillas, Phosphorites du Quercy (*Quercygama galliae*; Late Oligocene, MP 25; Augé & Rage 1995; Augé & Smith 1997); **F10**, Coderet (Agamidae indet., Late Oligocene, MP 30; Augé & Smith 1997); **F11**, “Allier” (Agamidae indet.; Late Oligocene; Hoffstetter 1955; Augé & Smith 1997); **F12**, “Lyonnais” (Agamidae indet.; Miocene; Hoffstetter 1955; Augé & Smith 1997); **F13**, La Grive (Acrodonta; Miocene; Augé & Smith 1997); **F14**, Seynes (*Agama* sp.; middle Pliocene, MN 16; Bailon 1991); **F15**, Sète (*Agama* sp.; early Pliocene, MN 15; Bailon 1987, 1991); **F16**, Mas Génegas II and IX (*Agama* sp.; early/middle Pliocene, MN 15/16; Bailon 1991).

**Germany**

**D1**, Burtenbach 1b (b. Thannhausen) (Agamidae indet.; early Miocene, MN 5; Böhme & Ilg 2007); **D2**, Furth 460 m (Agamidae indet.; middle Miocene; Böhme & Ilg 2007); **D3**, Laimering 3 (aff. *Stellio* sp. – Agamidae indet.; middle Miocene, MN 6; Böhme & Ilg 2007); **D4**, Unterempfenbach 1b (Agamidae indet.; early Miocene, MN 5; Böhme & Ilg 2007).

**Greece**

**Gr1**, Maramena (*Agama* sp.; late Miocene-earliest Pliocene?, MN 13–14?; Richter 1995; Böhme & Ilg 2007); **Gr2**, Ano Metochi 3 (*Agama* s.l.; Late Miocene, MN 13; Delfino 2004b); **Gr3**, Kastoria (*Agama* s.l.; middle-late Pliocene?; Delfino 2004b); **Gr4**, Maritsa A, Rhodes (*Agama* s.l.; early Pliocene, MN 14; Delfino 2004b); **Gr5**, Tourkbounia 1 (*Agama* s.l.; middle Pliocene, MN 16; Delfino 2004b); **Gr6**, Vevi (*Agama* s.l.; early Pliocene, MN 15; Delfino 2004b); **Gr7**, Rema Aslan 1 – not located – (*Agama* s.l.; Mio-Pliocene; Delfino 2004b).

**Italy**

**I1**, Cava Monticino (*Agama* s.l.; Late Miocene, MN 13; Delfino 2002); **I2**, Monte Tuttavista (*Agama* s.l.; Plio-Pleistocene; Abbazzi *et al.* 2004; this paper); **I3**, Montagnola Senese (*Agama* s.l.; late Pliocene, MN 17; Delfino personal observation).

**Portugal**

**P1**, Silveirinha (cf. *Tinosaurus* sp.; early Eocene, MP 7; Rage & Augé 2003).

**Romania**

**Ro1**, Tasad (Agamidae indet.; middle Miocene, MN 8; Böhme & Ilg 2007).

**Spain**

**S1**, Medas Islands (*Agama* sp.; middle Pliocene, MN 16; Bailon 1991); **S2**, Casablanca-Almenara 1 and 4 (cf. *Laudakia* sp.; from latest middle Pliocene, MN 16–17; Blain 2005); **S3**, Cova Bonica (Agamidae indet.; middle-late Pliocene, MN 16–17; Blain 2005); **S4**, Vallirana (cf. *Laudakia* sp.; late Pliocene, MN 17; Blain 2005); **S5**, Sarrión 1 (Cerro de los Espejos) (*Agama* sp.; middle Pliocene, MN 16; Böhme & Ilg 2007).

**Switzerland**

**Ch1**, Rümikon (*Agama* sp.; middle Miocene, MN 6; Böhme & Ilg 2007).

**Ukraine**

**Ua1**, Gritsev (Agamidae indet.; late Miocene, MN 9; Böhme & Ilg 2007).