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ARTICLE

MAIORICALACERTA RAFELINENSIS, GEN. ET SP. NOV. (SQUAMATA, LACERTIDAE), FROM THE EARLY PLIOCENE OF MALLORCA (BALEARIC ISLANDS, WESTERN MEDITERRANEAN SEA)

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ABSTRACT—Here we describe a new genus and species of Lacertidae, *Maioricalacerta rafelinensis*, gen. et sp. nov, a large-sized lizard with amblyodont teeth from the early Pliocene (Zanclean) of Mallorca (Balearic Islands, western Mediterranean Sea). The presence of amblyodont teeth separates *Maioricalacerta* from recent species of Lacertidae. *Maioricalacerta* differs from the amblyodont lacertids of the European Tertiary (*Quercycerta, Escampcerta*, *Mediolacerta*, *Pseudeumeces*, *Dracaenosaurus*, *Amblyolacerta*, and *Ligerosaurus*) in the anteroposterior and mediolateral widening of the teeth and in the wide lateral wall of the dentary, which is massive, relatively short, and robust. *Dracaenosaurus* displays a similar morphology of the dentary, but the number of teeth is lower and they are more amblyodont than in *Maioricalacerta*. The dentition observed in *Maioricalacerta* suggests that the diet of the species was related to a consumption of hard prey, perhaps molluscs. The length reduction of the dentary constitutes an evolutionary biomechanical advantage to consume this kind of prey as it improves jaw-closing force. However, its movement is likely to have been slower but potentially more accurate. The robustness of the dental structures in *Maioricalacerta* also contributes to enhance the resistance of the bone against the increased static pressure to which it is subjected during jaw closure. *Maioricalacerta* is the most Recent amblyodont lacertid known and the only one described from the Pliocene of Europe.

INTRODUCTION

In the Mediterranean islands, the fossil record of lacertid lizards is restricted to specimens referred to *Lacerta* and *Podarcis* from the lower Miocene–Holocene (e.g., Bailon, 2004; Delfino et al., 2011, and references therein). In the Balearic Islands (western Mediterranean Sea; Fig. 1), Quintana (1998) attributed some remains from the middle Miocene of Punta Nati 2, in Menorca, to a lacertid lizard, although Bailon (2004) subsequently stated that the attribution to this family is uncertain. Lacertids belonging to *Podarcis* are mentioned unambiguously from the Pliocene and Quaternary of several islands of the Balearic archipelago: *P. pityusensis* from Eivissa (Ibiza), and *P.* aff. *lilfordi* and *P. lilfordi* from Menorca and Mallorca (Bailon, 2004, and references therein). Previously, Boulenger (in Bate, 1918) reported some remains from breccias of probably Pleistocene age in Menorca, but they have never been adequately studied. He attributed these remains to belonging to the *viridis-ocellata* group (sensu Boulenger), then assigned them to *Lacerta* species that are currently referred to two distinct genera, *Lacerta* and *Timon*, respectively.

Extant lacertids inhabiting the Balearic Islands include two endemic species of the genus *Podarcis*, with a putative fossil record extending down to the Pliocene (*P. lilfordi* in the Gymnesic Islands [Mallorca, Menorca, and surrounding islets] and *P. pityusensis* in the Pityusic Islands [Eivissa, Formentera, and surrounding islets]) and several introduced species (*P. sicula* and *Scelarcis perspicillata* in Menorca, and *P. sicula* and *Psammodromus algirus* recently introduced in Mallorca; Vicens, 2005; Pinya and Carretero, 2011).

In this paper, we describe a new genus and species of amblyodont lacertid from the early Pliocene (Zanclean) deposits of Caló den Rafelino (Manacor, Mallorca). In Lacertidae, the presence of amblyodont teeth is a feature known to be acquired repeatedly and independently during different periods of the European Tertiary (Augé, 2005), but which has not been observed, until now, in Pliocene and Quaternary taxa or in an insular context.

Institutional Abbreviation—IMEDEA, Institut Mediterrani d'Estudis Avançats (Mediterranean Institute for Advanced Studies), Esporles, Balearic Islands, Spain.

Measurement Abbreviations—Hd, maximum height of the dentary; **Ht**, height of the tooth measured from base to tip in lingual view; **I**, anteroposterior width of the most amblyodont tooth (sensu Augé, 2005); **L**, length of dental series (sensu Augé, 2005) measured from the most anterior point of the dentary to the posterior extreme of the last tooth in lingual view; **N**, number of teeth; **TLd**, total length of the dentary; **Wt**, maximum anteroposterior width of the tooth in lingual view.

Anatomical Abbreviations—dp, dorsal process; **dr**, dental ridge; **if**, infraorbital foramen; **ipc**, impression of the anterolateral process of the coronoid; **lf**, labial foramina; **mf**, mandibular foramen; **Mg**, Meckel's groove; **mme**, medial maxillary edge; **ms**, mandibular symphysis; **pp**, posterior process; **sbs**, subdental shelf;

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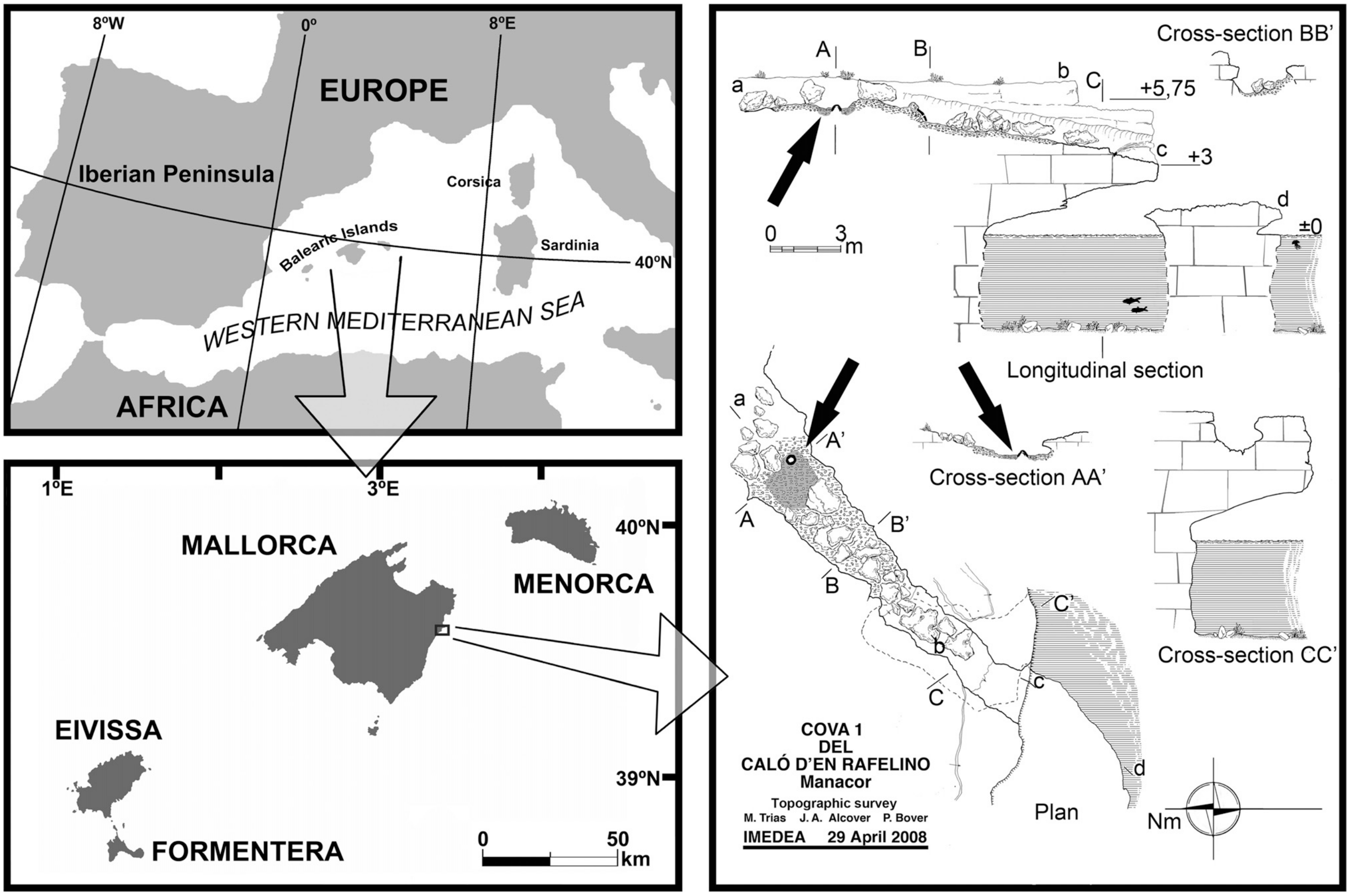

FIGURE 1. Locality map (left) and topographic survey (right) of the paleontological deposit from Caló den Rafelino. Arrows and gray-shaded area indicate the exact location of the fossiliferous breccia.

sd, sulcus dentalis; **sf**, splenial facet; **sps**, supradental shelf; **t5**, 5th tooth; **t9**, 9th tooth; **t13**, 13th tooth.

GEOLOGIC, PALEONTOLOGICAL, AND CHRONOSTRATIGRAPHIC SETTINGS

The fossiliferous bone breccia yielding the fossils described herein is located on the east coast of the island of Mallorca, close to Caló den Rafelino, in the municipality of Manacor. It consists of hardened red limestones of a collapsed cave gallery excavated in the upper Miocene Reef Complex. The fossils are concentrated in a small area, with an extent of about 1 m^2 (Fig. 1).

Stratigraphic and paleontological evidence points to an early Pliocene (Zanclean) chronology for Caló den Rafelino site (Bover et al., 2007, 2010; Bailon et al., 2010; Quintana et al., 2010; Agustí et al., 2012; Rofes et al., 2012), although a late Messinian age cannot be definitively excluded. The infilling should have been restricted to a very short period, after the upper Tortonian–lower Messinian and prior to the Piacenzian. An earliest early Pliocene age has been suggested as the most probable age for the site, based on the affinities of the obtained taxa (see Bover et al., 2010).

The faunal assemblage of Caló den Rafelino has not been recorded previously in Mallorca. In addition to the lizard studied herein, it contains remains of five mammals (a caprine *Myotragus palomboi*; a lagomorph *Hypolagus balearicus*; a shrew *Nesiotites rafelinensis*; a large-sized cricetid *Tragomys macpheei*; and a glirid of the genus *Hypnomys*), several reptiles (*Vipera* sp. of the Oriental Vipers Complex, *Vipera* cf. *natiensis*, a colubroid snake, a tortoise, an anguid, and the lacertid described here), a bird, and some fish teeth (Bover et al., 2007, 2010; Bailon et al., 2010; Quintana et al., 2010; Agustí et al., 2012; Rofes et al., 2012). Currently, Caló den Rafelino represents the only known Mallorcan vertebrate deposit from the earliest early Pliocene.

METHODOLOGY

Storage of the Material Studied

The material obtained from the deposit is currently curated at the Institut Mediterrani d'Estudis Avançats in Esporles (IMEDEA).

Methods

X-ray Microtomography and 3D Visualization—We used a Viscom X8050-16 micro-computed tomography (μCT) scanner at the Centre for Microtomography of the University of Poitiers (France) to scan the fossil material. The X-ray source consists of a microfocus Viscom 150 kV open tube. The scans were performed at 90 kV and 0.248 mA (power: 22.3 W) for the present experiment. We used a detector composed of an image intensifier with a camera of 1004 × 1004 pixels and a pixel size of 147 μm. The geometry was set to obtain a 24.4 μm voxel size in the reconstructed three-dimensional (3D) images. The reconstruction was performed using the software imageJ (available from http://rsb.info.nih.gov/ij) and FDK algorithms of DigiCT version 2.4.3 (Digisens, with pluging: SnapCT, acceleration in GPU). The data set for a jaw consists of 1200 projections taken over 360°, and 32 integrations by projection. 3D images were produced in 16 bit and subsequently converted into 8-bit voxels for visualization. 3D processing and rendering was obtained after semiautomatic segmentation of the cranial skeleton using generate surface and volume rendering in AVIZO 7.01 (VSG, SAS, Merignac, France; http://www.vsg3d.com).

Measurements—Measurements have been taken with an electronic digital calliper (accuracy 0.01 mm) on bone projections using a camera lucida.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA Linnaeus, 1758
Order SQUAMATA Oppel, 1811
Family LACERTIDAE Batsch, 1788
Genus *MAIORICALACERTA*, gen. nov.

Type and Only Species—*Maioricalacerta rafelinensis*, sp. nov.

Diagnosis—As for type and only species (see below).

Etymology—After the Latin words for Mallorca, 'Maiorica,' and lizard, 'lacerta.'

MAIORICALACERTA RAFELINENSIS, sp. nov.
(Figs. 2, 3)

Holotype—IMEDEA 90107. Left dentary missing the posteroventral and posterior portions (Fig. 2).

Paratypes—IMEDEA 90109 (right dentary fragment), 90105, 90106 (left maxillae fragments), 90260 (caudal vertebra).

Locality and Horizon—Caló den Rafelino, Manacor, Mallorca, Spain; earliest early Pliocene.

Etymology—The specific name refers to the name of the deposit, Caló den Rafelino.

Diagnosis—Large-sized lacertid. Differs from all Recent lacertids by having amblyodont teeth. Differs from all European Tertiary amblyodont lacertids (*Quercycerta*, *Escampcerta*, *Mediolacerta*, *Pseudeumeces*, *Dracaenosaurus*, *Amblyolacerta*, and *Ligerosaurus*) by displaying a markedly thicker lateral wall of dentary and amblyodont teeth transversally widened. Differs from all lacertids except *Dracaenosaurus* by the presence of a shorter, more massive, and deeper dentary. Differs from *Quercycerta*, *Escampcerta*, *Mediolacerta*, and *Amblyolacerta* by its relatively larger amblyodont teeth and from *Dracaenosaurus* by its relatively smaller amblyodont teeth. Differs from *Quercycerta*, *Escampcerta*, and *Mediolacerta* by having a smaller number of teeth and from *Dracaenosaurus* by its greater number of teeth.

DESCRIPTION

Dentary

Two dentaries of *Maioricalacerta rafelinensis* have been obtained, IMEDEA 90107 (holotype) and 90109. IMEDEA 90107 is a short, massive, robust dentary with an arched profile. Measurements: TLd = 19.15 mm (this length appears to correspond to the dental length); Hd (as measureable; see Fig. 2) = 6.77 mm; ratio Hd/TLd = 0.35.

In lingual view, the subdental table (sensu Rage and Augé, 2010) is subhorizontal and medially extended through a dorsally concave and a poorly developed subdental shelf (sensu Rage and Augé, 2010). Anteriorly, the medial edge of the subdental shelf is thick and vertical, but from the 8th tooth position its height declines posteriorly and its medial edge appears rounded medially from the 11th tooth onwards. The splenial should be well developed because a continuous and well-marked splenial facet has been left on the mid-ventral edge of the subdental shelf, in the area between the posterior limit of the 5th and the anterior limit of the 11th tooth position.

Meckel's groove remains largely exposed medially, although tapers anteriorly and its anterior extremity is covered by the mandibular symphysis at the level of the 4th tooth position. The mandibular foramen is located at the level of the 11th tooth position. The ventral limit of the dentary is distinctly curved and has a rounded, massive, and robust medioventral edge.

The tooth row (dental series, sensu Augé, 2005) seems to have been composed of 13 teeth of a pleurodont implantation type. The first four teeth are missing and the 5th tooth retains only its lower half. The 6th tooth is cylindrical and its apex is rounded and bears a small central cusp from where a series of fine radial striations originates. From the 7th tooth onwards, the teeth gradually widen anteroposteriorly, and the 9th, 10th, and 11th teeth have an amblyodont aspect (sensu Hoffstetter, 1944) and possess a blunt and rounded apex. The 9th and 10th teeth are complete and their Ht is 4.03 mm, whereas Wt is 1.77 and 2.25 mm respectively, and the Wt/Ht ratio is 0.44 for the 9th tooth and 0.56 tooth for the 10th tooth.

Posteriorly, the dental series is damaged, but the tomograms obtained (Fig. 2) clearly show the presence of two teeth smaller than the others and a tooth bud seems to be among them. The interdental spaces are narrow and mostly filled with cement. The dental foramina are not observed at the base of the teeth, instead there are small circular depressions. Cement fills the base of the teeth only very slightly and does not clog the sulcus dentalis. Only the 4th to 8th tooth positions seem to correspond to areas of tooth replacement.

The labial surface of the dentary is convex outward and devoid of dermal relief. Six labial foramina are arranged in line on the dorsal half of this face. Posterodorsally, at the level of the final tooth position, the bone has a series of longitudinal prints produced by the insertion of the anterolateral process of the coronoid on the dentary. The dental ridge is relatively straight except for the posterior edge of the 11th tooth where it tilts posterodorsally. The teeth surpass the dental crest over approximately one-quarter of its total height.

In occlusal view, the longitudinal axis of the dentary is fairly straight and has only a small medial bulge in its anterior extreme. The teeth are slightly compressed anteroposteriorly, and as a result the amblyodont teeth have a suboval shape in outline, with the transversal axis slightly greater than the longitudinal one. The 5th tooth, which is transversely broken, has a thick layer of dentin and its pulp cavity is reduced. In the amblyodont teeth 9 and 10, the radial striations converge towards a light central and longitudinal delicate crest, whereas in tooth 6 they converge on a central cusp (see above). Medially, the subdental shelf is reduced and the sulcus dentalis is narrow, very shallow, and not always visible. Laterally, teeth and interdental cement are closely linked to the parapet of the dentary.

In posterior view, fracturing of the bone reveals the section of the lateral wall of the dentary. It is remarkably thick (being approximately one-third of the section of the dentary in this part) and the bone structure is dense.

The different tomograms confirm the presence of a wide lateral wall in the dentary. The mandibular canal displays a moderate development when compared with the size of the dentary. A dense internal vascular network can also be observed and a wide dentine layer is present on the teeth (Fig. 2).

IMEDEA 90109 is a fragment of the right dentary with four amblyodont teeth (Fig. 3C). Its size is markedly smaller than the holotype (it probably belongs to a subadult or a juvenile).

Maxilla

Two fragments of left maxillae (IMEDEA 90105 and 90106) belong to two adult individuals of similar size (Fig. 3). A large

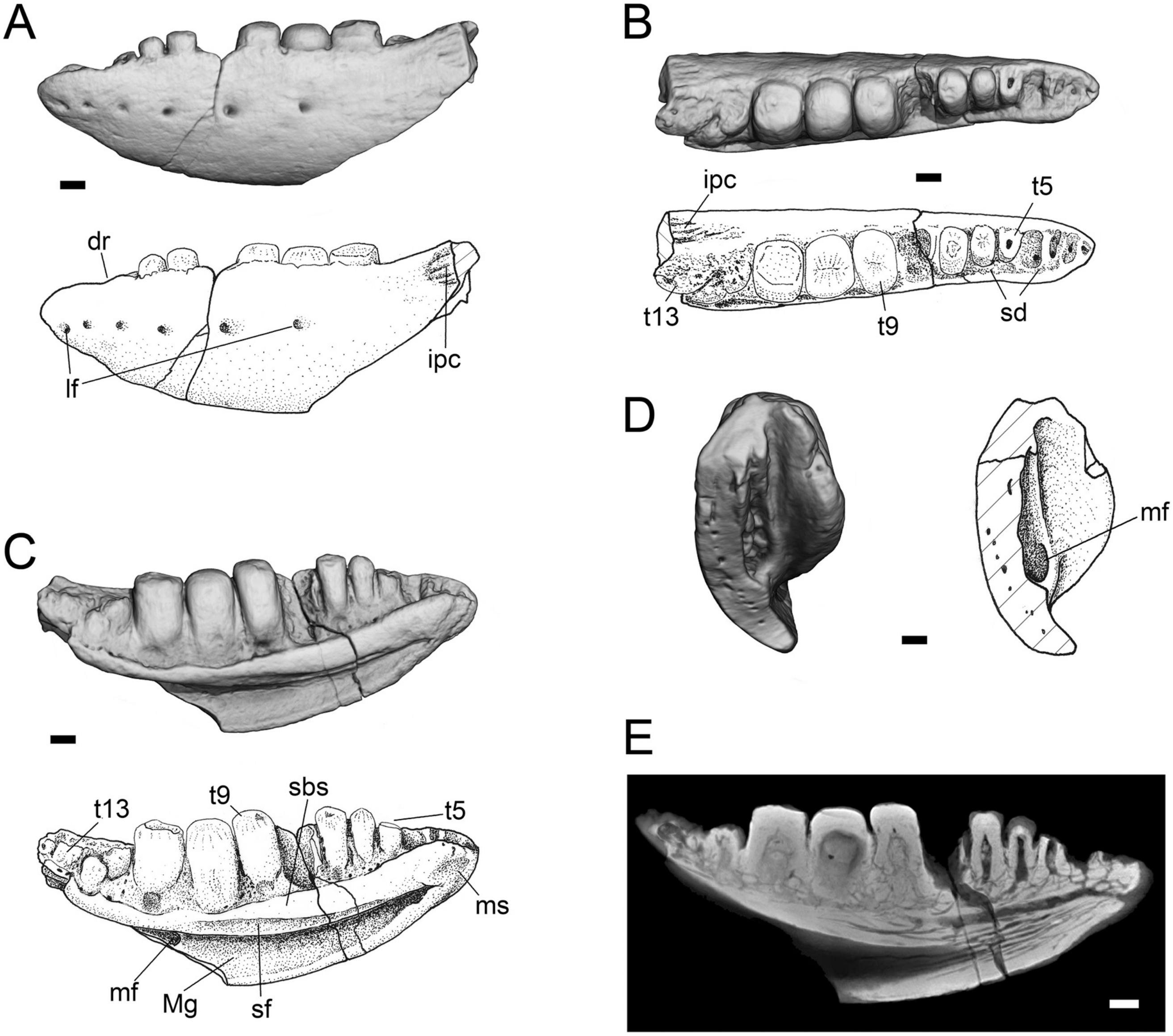

FIGURE 2. *Maioricalacerta rafelinensis*, gen. et sp. nov., left dentary (IMEDEA 90107). Volume rendering in **A**, labial; **B**, occlusal; **C**, lingual; and **D**, posterior views; **E**, anteroposterior cross-section of dentary, a tomogram. All scale bars equal 1 mm.

part of the tooth row can be identified, except in its anterior portion.

In medial view, the supradental table (sensu Rage and Augé, 2010) is dorsally convex and medially prolonged by a supradental shelf that is slightly more developed than the subdental shelf of the dentary and characterized by a rounded and relatively thin medial edge. The sulcus dentalis is narrow but somewhat deeper than the dentary. Anterior to the infraorbital foramen, the dorsal side of the supradental table is subhorizontal, whereas posteriorly its insertion area with the anterior branch of the jugal has a deep longitudinal groove on the posterior process.

Specimen IMEDEA 90106 is a central and posterior fragment of maxilla (Fig. 3A). It has five amblyodont teeth, the central one being the most prominently developed. The Wt/Ht ratios of each tooth, from anterior to posterior, are 0.57, 0.54, 0.65, 0.75, and 0.75, respectively. This series was possibly completed posteriorly by a much smaller tooth.

The specimen IMEDEA 90105 is a central and anterior fragment of a maxilla missing the anterior end (Fig. 3B). This fragment has five cylindrical monocuspid anterior teeth, followed by a currently empty tooth position originally occupied by an amblyodont tooth, and by three amblyodont teeth, among which the central tooth is the most prominently developed.

As in the case of the dentary, the interdental spaces are narrow and largely filled with cement. The estimated number of teeth in a complete maxilla ranges between 11 and 13.

In dorsal view, the infraorbital foramen is large and divided (IMEDEA 90106) or partially divided (IMEDEA 90105) by a

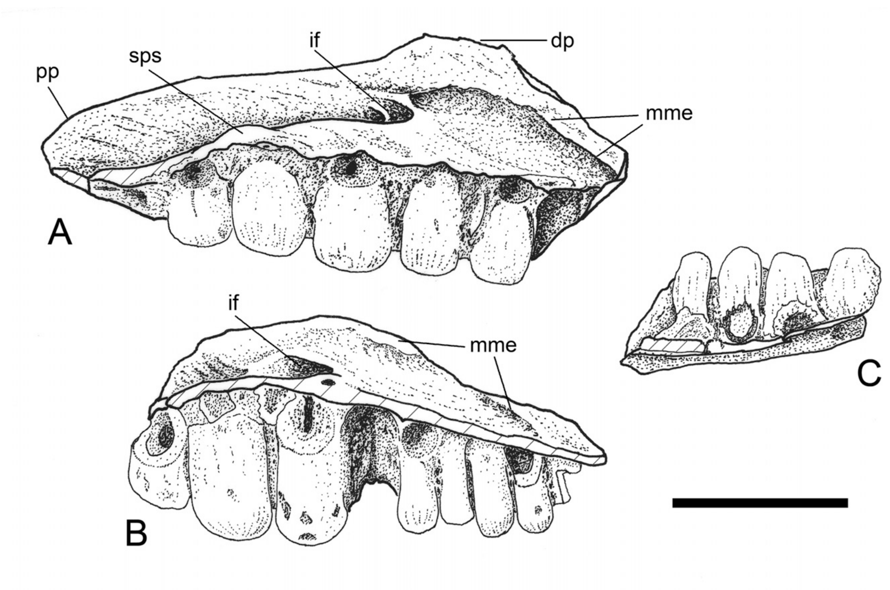

FIGURE 3. *Maioricalacerta rafelinensis*, gen. et sp. nov. **A**, fragment of left maxilla (IMEDEA 90106), lingual view; **B**, fragment of left maxilla (IMEDEA 90105), lingual view; **C**, fragment of right dentary (IMEDEA 90109), lingual view. Scale bar equals 5 mm.

transverse septum. The medial maxillary edge (= carina maxillaris, sensu Müller, 1996) is well marked and constitutes an arch placed at the base of the dorsal process of the maxilla. Anteriorly, this edge is obliquely extended onto the dorsal part of the subdental table (IMEDEA 90105), whereas posteriorly the arch formed by the edge may be closed (IMEDEA 90106) or open (IMEDEA 90105). The dorsal process is broken in both maxillae and displays areas of breakage with rounded and polished edges, indicating a probable tumbling of the fossil material.

In lateral view, IMEDEA 90106 displays traces of pustular dermal relief on the dorsal process. IMEDEA 90106 also has a posterior process that is moderately tall and with a slightly convex dorsal edge. Seven labial foramina are present in both specimens.

Caudal Vertebra

A single caudal vertebra has been found (IMEDEA 90260). It is procoelous, moderately elongated, and bears a subcircular cotyle and condyle. Anteriorly, the vertebra has a zygosphene (sensu Hoffstetter and Gasc, 1969) with vertical walls and a notched roof, whereas posteriorly the zygantrum is composed of a dorsomedial extension of the postzygapophysis. The neural spine has a robust posterodorsal tip and the transverse processes are simple and flattened. The vertebral centrum is convex in transverse section and displays a wide hemal keel and has a length of approximately 3.5 mm. A hypothetical autotomy plane cannot be observed. The general morphology of this vertebra corresponds to that usually observed in the 2nd caudal vertebrae of extant lacertids (e.g., *Timon* and *Lacerta*; pers. observ.). The relatively large size of this vertebra can be tentatively attributed to the Mallorcan remains described above.

COMPARATIVE ANALYSIS

The attribution of *Maioricalacerta* to the family Lacertidae is based on the simultaneous presence of the following combination of characters: (1) an arched dentary, with concave tooth row, subdental shelf, and ventral edge; (2) Meckel's groove medially open and regularly tapering from back to front; (3) well-developed and continuous splenial facet on the medioventral edge of the subdental shelf; (4) anteriorly, the splenial facet reaches an anterior position, close to the mandibular symphysis, whereas posteriorly it ends just in front of the mandibular fossa; (5) absence of a notch and a spina splenialis on the ventral edge of the subdental shelf; (6) the subdental and supradental tables are horizontal; (7) presence of subdental and supradental shelf and sulcus dentalis, although not well developed; (8) presence of a posterodorsal impression on the lateral side of the dentary indicating the insertion zone of the anterior process of the coronoid on the dentary; (9) medial maxillary edge (= carina maxillaris, sensu Müller, 1996) well developed and prolonged on the dorsal area of the supradental table; (10) cylindrical teeth with pleurodont implantation and replacement areas located at the base; and (11) interdental cement present but without filling the sulcus dentalis. In addition, the procoelous caudal vertebra tentatively referred to this taxon is also consistent with the morphology observed in extant lacertids.

None of the characters cited above can be considered as apomorphies of Lacertidae, because each one of them can be observed in different hierarchical levels and clades within Squamata. Although apomorphies of Lacertidae are cited by Estes et al. (1988), none of them concerns the dentaries, maxillae, or vertebrae. Arnold et al. (2007) admit that the synapomorphies used to define Lacertidae are generally not observable in fossils. Nevertheless, the simultaneous presence of all of them is an exclusive character combination that defines Lacertidae (see Estes, 1983; Augé, 1993, 2005; Augé et al., 2003; character matrices and polarities in Evans and Barbadillo [1998] and Augé and Smith [2002]).

Maioricalacerta differs from extant Lacertidae in the presence of a reduced number of teeth, a markedly amblyodont dentition, and in the presence of a shorter and more robust dentary. Among extant lacertids, only *Timon* displays widening of the teeth during ontogeny (Estes and Williams, 1984; Mateo, 1988; Mateo and López-Jurado, 1997; Castroviejo and Mateo, 1998), but it never reaches the growth observed in the fossil from Caló den Rafelino. Heterodont dentition and the presence of teeth with molariform trends have been described in insular Quaternary taxa (*Lacerta*, n. sp., from the middle Pleistocene of Corsica [Salotti et al., 1997; Bailon, 2004], *Lacerta siculimelitensis* from the middle–late Pleistocene of Malta and Sicily [Böhme and Zammit-Maempel, 1982; Estes, 1983; Kotsakis, 1996; Bailon, 2004], and their related continental taxa from the early Pleistocene of Italy [Delfino and Bailon, 2000; Delfino, 2001]), but in those cases the teeth are not really amblyodont. Additionally, as happens in the extant species, the tooth rows of these fossils have a greater number of teeth and the dentary is more slender than in *Maioricalacerta*. *Gallotia*, an endemic lacertid from the Canary Islands that can reach a large size and is adapted to a predominantly herbivorous diet, displays completely different teeth and dentary morphology from *Maioricalacerta* (pers. observ.).

In Lacertidae, the presence of amblyodont teeth is a feature known to be acquired repeatedly and independently during different periods of the European Tertiary (Augé, 2005), but has, until now, not been observed in Pliocene and Quaternary taxa. Described lacertids with amblyodont teeth are (a) the Eocene species *Quercycerta maxima* (middle Eocene, MP17; Augé, 2005) and *Escampcerta amblyodonta* (middle–late Eocene, MP17–MP19; Augé, 2005); (b) an Oligocene series of lacertids with increasing amblyodonty constituted by *Mediolacerta roceki* (MP23–MP30; Augé, 2005), *Pseudeumeces cadurcensis* (MP25–MP28 and maybe early Miocene; Hoffstetter, 1944; Estes, 1983; Rage, 1987; Rage and Augé, 1993; Augé and Rage, 2000; Augé, 2005; Augé and Hervet, 2009; Čerňanský and Augé, 2012), and *Dracaenosaurus croizeti* (MP28–MP30; Gervais, 1848–1852; Hoffstetter, 1964; Estes, 1983; Müller, 2004; Augé, 2005); and (c) the Miocene species *Amblyolacerta dolnicensis* (early–middle Miocene, MN2–MN6; Roček, 1984) and *Ligerosaurus pouiti* (early–middle Miocene, MN3–MN5; Augé et al., 2003).

In comparison with known amblyodont lacertid lizards, the degree of amblyodonty in *Maioricalacerta* allows its clear differentiation from *Quercycerta*, *Escampcerta*, *Mediolacerta*, and *Amblyolacerta*, which all display a lower degree of amblyodonty. *Dracaenosaurus* has markedly more amblyodont teeth than *Maioricalacerta*, whereas the Mallorcan fossil has similar values to *Pseudeumeces* and *Ligerosaurus*; the I/L ratio (sensu Augé, 2005) has similar values in the last three genera (0.12 in *Maioricalacerta*, 0.09–0.16 in *Pseudeumeces* [Augé, 2005], and 0.1 in *Ligerosaurus*). Additionally, the number of teeth observed in the dentary of *Maioricalacerta* (13) is within the variability observed in *Pseudeumeces* (10–16; Augé, 2005; Augé and Hervet, 2009; Čerňanský and Augé, 2012) and is slightly smaller than in *Ligerosaurus* (14 or 15; Augé et al., 2003), but it differs from *Quercycerta*, *Escampcerta*, and *Mediolacerta*, in which the number of teeth is greater than 18 (Augé, 2005) or from *Dracaenosaurus*, whose number of teeth is never more than eight (Müller, 2004; Augé, 2005). The number of teeth is unknown in *Amblyolacerta*. Nevertheless, *Maioricalacerta* displays a set of morphological characters that precludes any relationship with these other genera. *Maioricalacerta* has (a) large size, comparable only to *Quercycerta*; and (b) a comparatively short and high dentary with a more massive and robust appearance than most of the known taxa. Only *Dracaenosaurus* displays a similar dentary morphology and N/L ratio (sensu Augé, 2005) (*Maioricalacerta* has a value for the N/L index of 0.68, which lies within the values obtained for *Dracaenosaurus* [N/L between 0.4 and 1; Augé, 2005]); (c) in transverse section, the lateral wall of the dentary is thick and moderately convex in its posterior part; (d) the teeth of *Maioricalacerta* display widening in the anteroposterior direction but also slightly lateromedially. A very thick lateral wall of the dentary and the presence of teeth that are transversally widened seem to be two synapomorphies for *Maioricalacerta.* Although the latter character has been observed in other fossil and recent squamate taxa, mainly in some teiids such as the extant *Dracaena* and the fossil genus *Paradracaena* from the Miocene of South America (Estes, 1961, 1983; Dalrymple, 1979; Estes and Williams, 1984; Nydam et al., 2007; Pujos et al., 2009), it has not been reported in any lacertid until now.

The presence of amblyodont teeth in individuals of small size (probably belonging to juveniles) within the remains attributed to *Maioricalacerta* allows us to state that amblyodonty appeared relatively early in the ontogeny of the species, as happens in some teiids (*Dracaena* and probably the extinct *Paradracaena*) or scindids (*Tiliqua*) (Dalrymple, 1979; Estes, 1983; Estes and Williams, 1984; Pujos et al., 2009).

The fauna from Caló den Rafelino probably arrived in Mallorca during the main regressive episode of the Messinian (upper Miocene, between 5.6 and 5.32 Ma ago) (Bover et al., 2007, 2010; Bailon et al., 2010; Quintana et al., 2010), a period during which Mediterranean sea level dropped by about 1500 m (Clauzon et al., 1996; Krijgsman et al., 1999), establishing new connections between the mainland and Balearic Islands. No relationship between the faunal assemblage of the middle Miocene from Mallorca (Mein and Adrover, 1982; Adrover et al., 1985) and the fauna from Caló den Rafelino apparently exists, because the middle Miocene Mallorcan terrestrial fauna is composed only of an ochotonid lagomorph (*Gymnesicolagus gelaberti*) and three glirid rodents (*Carbomys sacaresi*, *Margaritamys llulli*, and *Peridyromys ordinasi*) that are not phylogenetically related to the early Pliocene fauna recorded in Caló den Rafelino or even in Mallorca (Bover et al., 2008). Thus, *Maioricalacerta* probably evolved from a mainland Miocene lacertid. Observed morphological differences between *Maioricalacerta* and the species with amblyodont teeth from the Miocene of France, *Ligerosaurus*, precludes a close phylogenetic relationship. We are consequently tempted to consider that the ancestor of *Maioricalacerta* probably was a lacertid with a more generalized tooth morphology, such as those of, e.g., *Amblyolacerta* or a member of the *Timon* complex (ocellated-lizard complex). Both European and African clades could have had biogeographic relationships with the Balearic Islands at the end of the Miocene (Paulo et al., 2008).

MORPHOLOGICAL DESIGN, BITE PERFORMANCE, AND DIET OF *MAIORICALACERTA*

Most of the morphological changes observed in the evolution of the squamate skull are the result of the continuous combined action of a complex system of factors, including close links between the performance, behavior, and ecology of a species (Herrel et al., 2007; Herrel and Holanova, 2008). In this sense, some of the morphological characters observed in *Maioricalacerta* allow the inference of parameters related to diet and feeding behavior.

Most papers on Recent lizards show that the presence of amblyodont teeth is linked to a diet based on hard food items (durophagy), molluscs typically being an important component of the consumed prey (Dalrymple, 1979; Rieppel and Labhardt, 1979; Estes and Williams, 1984; Kosma, 2004). Furthermore, according to Hoffstetter (1944), Rage (1987), Augé et al. (2003), Müller (2004), Augé (2005), Augé and Hervet (2009), and Čerňanský and Augé (2012), the extinct *Pseudoeumeces*, *Ligerosaurus*, and *Dracaenosaurus* were also durophagous forms that probably fed on hard-shelled invertebrates. The morphological adaptations to durophagy likely allow consumers to occupy niches where there are few competitors.

Molariform and blunt teeth increase the contact surface with the food and allow greater resistance to the compressive forces applied during occlusion (Rieppel and Labhardt, 1979; Rensberger, 2000; Herrel and Holanova, 2008). On the other hand, the ridges and grooves observed in the cusps of the teeth of *Maioricalacerta* and in most of the amblyodont lizards (Dalrymple, 1979; Rieppel and Labhardt, 1979; Kosma, 2004; Augé, 2005; Pujos et al., 2009) constitute an additional reinforcement of the dental enamel because it allows the homogeneous distribution of the forces exerted during the adduction of the mandibles (Preuschoft et al., 1974). In addition, the ridges will tend to prevent slippage of the shell that is being crushed between the amblyodont teeth (Rieppel and Labhardt, 1979).

The presence of a shorter and more robust dentary in *Maioricalacerta* than in most other known lacertids likely induced a biomechanical advantage for the consumption of hard prey. Because the vertebrate mandible acts as a type 3 lever (Ostrom, 1964; Rieppel and Labhart, 1979; Augé, 1988; Herrel et al., 2002a, 2002b, 2004), the length reduction of the dental series implies a reduction of the jaw out-lever (sensu Herrel et al., 2002a, 2002b), and in case of a similar development of the adductor muscles of the mandible, the bite performance is comparatively greater. However, the short out-lever also implies that mandible closure would be slower in *Maioricalacerta* than in most extant and fossil lacertids with proportionally longer dentaries. Additionally, the great robustness of the different structures of the dentary observed in *Maioricalacerta* would likely have enhanced the resistance of the bone against the increased static pressure to which it was subjected during jaw closure. In *Dracaenosaurus*, the presence of the blunt teeth, a short tooth row, and a heavy, strongly curved mandible are also related to the development of a strong bite force (Müller, 2004).

Mediterranean insular environments are characterized by limitation of resources and an increase in intra- and interspecific competition. Consequently, amblyodont teeth would have been an important selective advantage for *Maioricalacerta* to widen its dietary strategies with the consumption of hard food items, such as molluscs with shells or beetles, even at juvenile stages. During the proposed chronology for the formation of the deposit (i.e., earliest early Pliocene; Bailon et al., 2010), there were warm and dry climatic conditions (e.g., Fauquette et al., 1999) that would have favored and accelerated this evolutionary process, because the shell of molluscs is known to be harder and wider in arid conditions (Sacchi and Testard, 1971), although such shells have not yet been found in the deposit.

CONCLUSIONS

The early Pliocene deposit of Caló den Rafelino has yielded remains of dentaries, maxillae, and a caudal vertebra of a large-bodied lacertid, *Maioricalacerta rafelinensis*, gen. et sp. nov. It is morphologically different from other extant lacertids because it displays a comparatively shorter and more robust dentary with a reduced number of teeth (13 in the dentary) and with amblyodont central and posterior teeth.

Among the amblyodont lacertids of the European Tertiary, *Maioricalacerta* displays a higher degree of amblyodonty than the Eocene *Quercycerta* and *Escampcerta*, the Oligocene *Mediolacerta*, and the Miocene *Amblyolacerta*. The degree of amblyodonty is, however, remarkably lower than in *Dracaenosaurus* (late Oligocene) and similar to that in *Pseudeumeces* (Oligocene and less probably early Miocene) and *Ligerosaurus* from the early–middle Miocene.

Maioricalacerta also displays a unique set of characters that allows it to be differentiated from other extant and extinct lacertids: great size, short and robust dentary with a wide lateral wall, and amblyodont teeth with a slight mediolateral widening. The two latter characters can be considered as autapomorphies of the genus.

The presence of wide teeth in small-sized individuals (juveniles) shows that amblyodonty appeared relatively early in *Maioricalacerta* ontogeny. Among Lacertidae, *Maioricalacerta* is the most recent lacertid with amblyodont teeth in the fossil record and is also the only island lacertid with truly amblyodont teeth.

Maioricalacerta may not be related to *Ligerosaurus*, but to a mainland form with a more generalized dentition that arrived in Mallorca during the Messinian Crisis. In insular conditions, amblyodonty might have been an important selective advantage because the diet could have been more durophagous.

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