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To cite this article: Andrej Čerňanský, Arnau Bolet, Johannes Müller, Jean-Claude Rage, Marc Augé & Anthony Herrel (2017): A new exceptionally preserved specimen of *Dracaenosaurus* (Squamata, Lacertidae) from the Oligocene of France as revealed by micro-computed tomography, *Journal of Vertebrate Paleontology*, DOI: [10.1080/02724634.2017.1384738](https://doi.org/10.1080/02724634.2017.1384738)



To link to this article: <https://doi.org/10.1080/02724634.2017.1384738>

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A NEW EXCEPTIONALLY PRESERVED SPECIMEN OF *DRACAENOSAURUS* (SQUAMATA, LACERTIDAE) FROM THE OLIGOCENE OF FRANCE AS REVEALED BY MICRO-COMPUTED TOMOGRAPHY

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ABSTRACT—The best-preserved material of *Dracaenosaurus croizeti*, an almost complete and previously unpublished skull with a few associated postcranial bones (stylopodium, zeugopodium, and cervical vertebra), is described. The material comes from the locality of Cournon, a late Oligocene site in south-central France. Micro-computed tomography applied to this specimen revealed previously unknown internal osteological characters. Among lacertids, this taxon represents a notable phenomenon: it is an extreme durophagous specialist. Many of the newly observed cranial character states reflect the lifestyle of this lizard, because animals with a hard-shelled diet display a specialized cranial morphology associated with more massive cranial muscles. One unique character for Lacertidae is observed: the parietal-supraoccipital contact is formed by a ventrally deep parietal crest that fits into a bifurcate ascending process of the supraoccipital. In fact, such a connection represents the opposite to the connection in modern members of Lacertidae. Phylogenetic analysis recovered *Dracaenosaurus* inside Gallotiinae, a clade that would consist of the mainly Oligocene genera *Pseudeumeces* and *Dracaenosaurus*, the Miocene genus *Janosikia*, and the extant *Psammodromus* and *Gallotia*. Our study supports previous phylogenetic results and provides an example of the achievement of large size in mainland members of the stem of *Gallotia*, previously exemplified by *Janosikia* and *Pseudeumeces*. The extreme amblyodonty of *Dracaenosaurus* also confirms the view that herbivory in *Gallotia* is derived and may be the result of insularity.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Čerňanský, A., A. Bolet, J. Müller, J.-C. Rage, M. Augé, and A. Herrel. 2017. A new exceptionally preserved specimen of *Dracaenosaurus* (Squamata, Lacertidae) from the Oligocene of France as revealed by micro-computed tomography. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2017.1384738.

INTRODUCTION

The lizard clade Lacertidae includes over 300 small- to medium-sized living species (Uetz et al., 2007). These lizards are broadly distributed in Eurasia and Africa, forming the dominant reptile group in Europe (Arnold et al., 2007). They make up a monophyletic group (Mayer and Benyr, 1994) consisting of two lineages: Lacertinae and Gallotiinae (see, e.g., Arnold et al., 2007). The origin of Lacertidae is thought to be in Europe (Arnold et al., 2007), where the fossils considered closest to the lacertid crown are also found (Borsuk-Bialynicka et al., 1999; Čerňanský and Augé, 2013). A European origin is also supported

by Paleogene finds of the stem clade from Germany, France, and Belgium (Čerňanský and Smith, 2017). According to Vidal and Hedges (2009), Lacertidae diverged from their sister lineage before the Mesozoic/Cenozoic boundary, although their fossil record is unknown in the Mesozoic and doubtful in the Paleocene (Rage, 2013). On the other hand, fossils of this clade are well documented in the post-Paleocene Cenozoic of Europe (e.g., Roček, 1984; Augé, 2005; Čerňanský, 2010; Čerňanský et al., 2015). Most finds are, however, represented by disarticulated elements. This has resulted in significant gaps in our knowledge of their evolution and the relationships of extinct forms to modern lineages.

The age of the lacertid crown group has been investigated using different methods. Albumin immunology suggested a divergence time of Gallotiinae and Lacertinae about 30–35 Ma (Mayer and Benyr, 1994). More recently, Čerňanský et al. (2016a) stated, based on remains of *Janosikia*, that the split

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between the *Gallotia* and *Psammodromus* lineages occurred in the Oligocene. This suggests that the origin of crown Lacertidae is most likely more ancient than the Oligocene. A Paleogene date would be consistent with the presence of crown or near-crown lacertids (e.g., *Plesiolacerta lydekkeri*) as early as the middle Eocene of France (see Čerňanský and Augé, 2013), and specimens in Baltic amber (*Succinilacerta succinea*) with exquisite scale preservation of middle–late Eocene age (Borsuk-Białynicka et al., 1999). The latter taxon shares a number of apomorphic external features with Lacertidae, but its exact relationship with the crown group is uncertain (see Borsuk-Białynicka et al., 1999). A Paleogene age was also suggested by Hipsley et al. (2009, 2014).

In this regard, articulated finds of lacertid fossils, which otherwise are mostly fragmentary, are crucial for understanding the evolution of the clade. Besides the aforementioned *Succinilacerta*, the second notable exception is *Dracaenosaurus croizeti* Gervais, 1848–1852, from the Oligocene of Marcoin, south central France. Apart from additional finds of numerous isolated tooth-bearing bones (e.g., Hoffstetter, 1944; Augé, 2005), the cranial morphology is so far only known from two articulated, incompletely preserved skulls (see Müller, 2004). *Dracaenosaurus* is a Paleogene lacertid presenting an extremely amblyodont dentition (see, e.g., Augé, 2005) likely related to a durophagous diet. The occurrence of this taxon is not restricted to France, but it is also recorded from Germany (Čerňanský et al., 2016b), showing a broad European distribution during the Oligocene. It is often compared (and said to be closely related) to *Pseudeumeces cadurcensis*, a less specialized form found in some of the same and other contemporaneous localities. The holotype of *Pseudeumeces cadurcensis* has been recently located at the American Museum of Natural History (New York) after being lost for more than a century (see Bolet et al., 2017). Here we describe a previously unstudied skull that represents the third and best-preserved skull of *Dracaenosaurus croizeti* using micro-computed tomography. Several postcranial elements are described for the first time as well.

Institutional Abbreviation—MNHN—Muséum national d’Histoire naturelle, Paris, France.

THE COURNON LOCALITY

The locality of Cournon is located a few kilometers east of Clermont-Ferrand, in south-central France. Oligocene vertebrates were found there during the 19th century and were reported as coming from Cournon, although they quite likely came from several sites and even from different beds. Several quarries, which are potentially fossiliferous sites, indeed occur north of the village of Cournon. The exploitation of the quarries was likely abandoned before the 20th century, and the fossiliferous beds are no longer accessible. Thaler (1972) noted that the collection of fossils from Cournon was more than a hundred years old. No fossil was likely recovered from the historical sites after the 19th century. According to Giraud (1902), the vertebrates were preserved in a bed of whitish, marly limestone. Vertebrate finds are composed mainly of mammals: Lavocat (1951) reported 32 species of mammals from Cournon. However, Thaler (1972) questioned the origin of some taxa. Despite the uncertain provenance of some fossils, Thaler (1965) estimated that the fauna was sufficiently homogenous and significant to use Cournon as the reference locality for a mammalian zone in the late Oligocene. The mammal fauna of a new site in the Cournon area, Cournon-les-Soumérois, confirmed the stratigraphic information provided by the old collections (Brunet et al., 1981). Although yielded by a level (green marls) distinct from the bed that produced at least most of the old material, the

geological age of the new assemblage is similar to that indicated by the historical collection. In the European reference levels system, Cournon is included in the standard level MP 28 (Schmidt-Kittler, 1987), i.e., it is regarded as late, but not latest, Oligocene. According to Mertz et al. (2007), MP 28 corresponds to a 24.9–24.5 Ma time interval. The Oligocene beds of Cournon are of lacustrine origin. Therefore, most vertebrates were transported there.

Giraud (1902) reported a few non-mammalian vertebrates, including two lizard species, from Cournon. The lizard taxa corresponded to *Lacerta antiqua* Pomel, 1853, which is regarded as a nomen dubium (Estes, 1983), and *Dracaenosaurus croizeti* (see below). The single specimen, a mandible, allocated to *Lacerta antiqua*, could not be located in the collections, but four specimens from Cournon belonging to *Dracaenosaurus croizeti* are present in the collections of the MNHN. Three of them (MNHN.F.COR4–MNHN.F.COR6) were studied by Müller (2004) and the fourth, MNHN.F.COR7, is described here. These specimens are embedded in a marly limestone that is white to light gray. This matrix corresponds to the bed that produced most of the fossils in the 19th century, and it secures the provenance of the four specimens.

MATERIALS AND METHODS

The skull of MNHN.F.COR7 is robustly built (Figs. 1, 2), elongate (almost twice as long as wide), and tall, even when allowing for some compression due to postmortem fossilization processes (Fig. 2). The anteroposterior length of the skull roof is 44 mm, and the total anteroposterior skull length is 46 mm (together with supratemporal processes of the parietal). The length corresponds well with the skull length (45 mm) of the material described by Müller (2004). The cranium is generally well preserved, except for the poor preservation of premaxilla and palate. Both lower jaws are almost complete, well preserved, and in place, but only the right one is in anatomical connection to the corresponding quadrate (the other quadrate is only partially preserved). Also, a few postcranial elements, including one vertebra and a partial forelimb, are preserved. The specimen was scanned using the micro-computed tomography (CT) facility at the Slovak Academy of Sciences in Banská Bystrica. The scanner used was a Phoenix v|tome|x L240 micro-CT with the following settings: VxSize = 0.03746667; Current = 160; Voltage = 180; Intime = 20000; Average = 3; Steps = 1800; Steps360 = 1800. The images were recorded over 360°. The CT data set was analyzed using VG Studio Max 2.2 and Avizo 8.1. The photographs of the entire specimen were taken with a Nikon camera. Detailed photographs were taken with a Leica M205 C binocular microscope with an axially mounted DFC 290 HD camera; software: LAS (Leica Application Suite) 4.1.0 (build 1264). The phylogenetic analysis was performed in PAUP* 4.0a150 (Swofford, 2002).

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811
 LACERTIFORMES Estes, de Queiroz, and Gauthier, 1988
 LACERTIDAE Oppel, 1811
 GALLOTIINAE Cano, Baez, López-Jurado, and Ortega, 1984
DRACAENOSAURUS Pomel, 1846
DRACAENOSAURUS CROIZETI Gervais, 1848–1852
 (Figs. 1–13)

Material—MNHN.F.COR7, an almost complete skull and a few postcranial elements in semianatomical connection or close association, partly embedded in the matrix.

Locality and Horizon—Cournon, Department of Puy-de-Dôme, France; upper Oligocene.

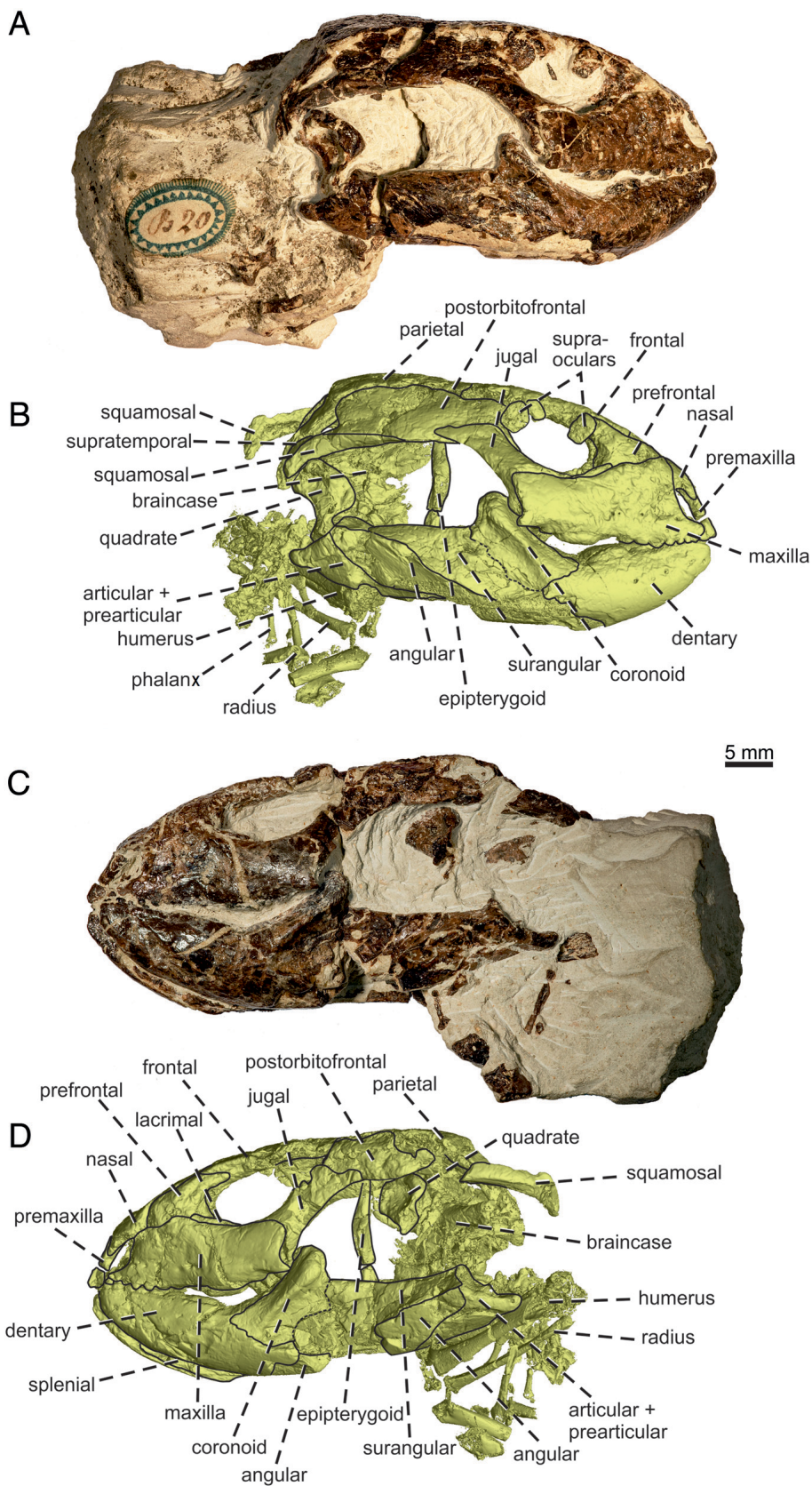


FIGURE 1. *Dracaenosaurus croizeti*, MNHN.F.COR7. **A**, right lateral view and **B**, micro-CT visualization. **C**, left lateral view and **D**, micro-CT visualization.

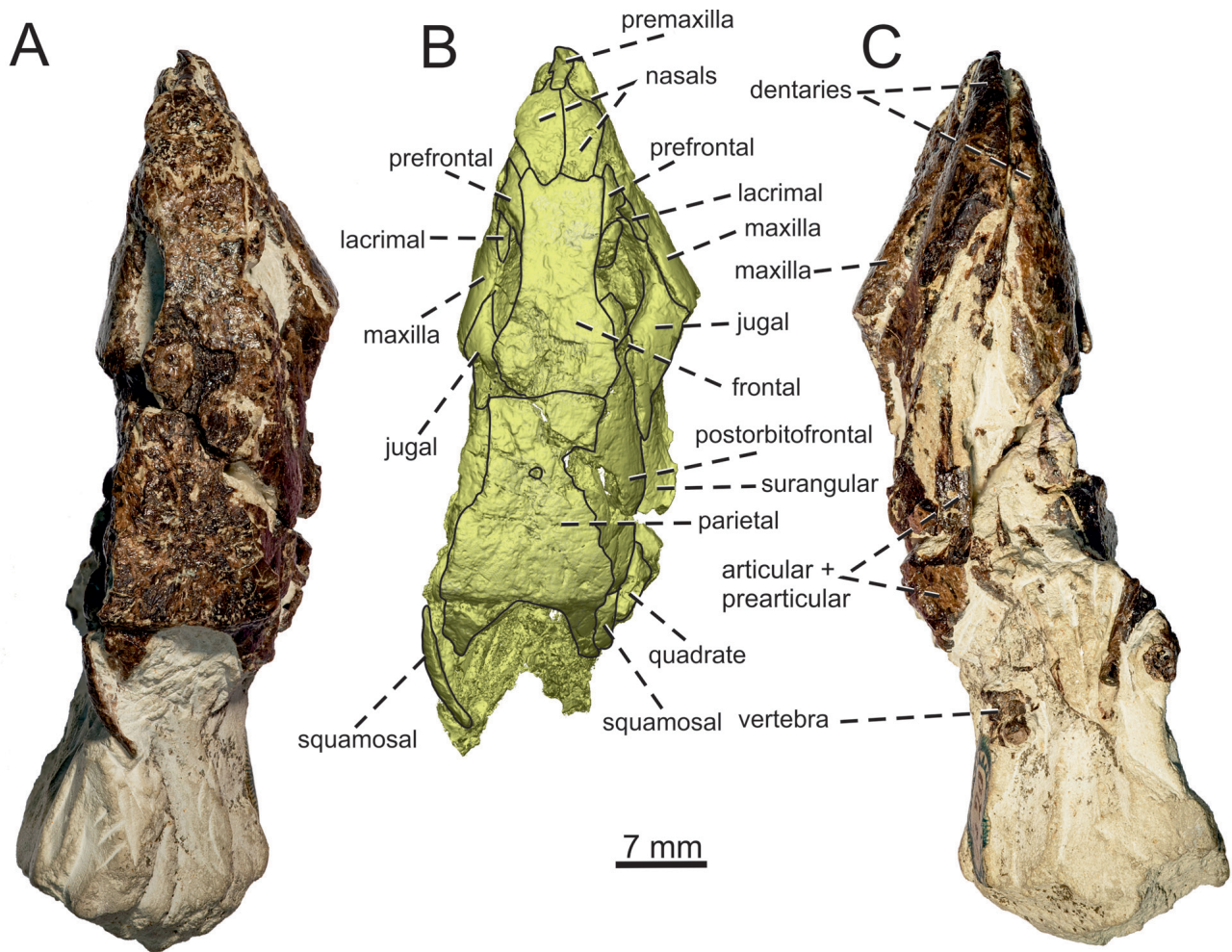


FIGURE 2. *Dracaenosaurus croizeti*, MNHN.F.COR7. A, dorsal view and B, micro-CT visualization. C, ventral view.

DESCRIPTION

Skull

Premaxilla—This bone is poorly preserved (Fig. 3A, B). It is ‘T’-shaped and a very small element compared with the rest of the skull bones. Its posterodorsally elevated nasal process is narrow in anterior view, but oblong posteriorly in cross-section. It bears a facet for the nasal on each side. The maxillary process, preserved on the right side, is short. On the lateral side, the ethmoidal foramen is located close to the base of the nasal process. The supradental shelf (sensu Rage and Augé, 2010) is well expanded posteriorly. No teeth are preserved because this part was probably damaged during excavation and/or preparation.

Although teeth are not preserved in the specimen studied here, Müller (2004) reported that at least six teeth are present on the premaxilla in *Dracaenosaurus*.

Maxilla—The maxilla is a very robust element (Figs. 1, 3D) forming the high lateral wall in the anterior section of the skull. It bears seven teeth. In the right maxilla, an empty space is present between the posterior-most largest tooth and the more anteriorly located tooth (the latter tooth is present on the left maxilla). The anterior tip of the maxilla is divided into a short, more medially oriented internal ramus of the premaxillary process and a slightly broader external ramus (Fig. 3E). In dorsal view, the posterior part of an oval premaxillary fenestra is present between these rami. The posterior process of the maxilla, forming the connection to the jugal on its medial side, is

rectangular, and ends at the level of the posteroventral section of the jugal. It is markedly tall along its entire length and not narrowing posteriorly. The posterior margin of the process is concave, where its ventral posterior-most margin forms a small process. The nasal process of the maxilla is anteroposteriorly short. Due to the presence of a very tall posterior process, the nasal process, markedly less deep than the former at its end, appears relatively low. The nasal process contacts the nasal, and a short posterodorsal tip is attached to the frontal. The external surface of the maxilla is pierced by several labial foramina of various sizes, close to the lower margin of the bone.

In internal view, the supradental shelf is well expanded medially, especially in the region at the level between the first and second posterior teeth (counting from the posterior-most one). A palatine articulation is located here (note, however, that the supradental shelf in this region is poorly preserved). At this level, a large superior alveolar foramen is situated (Fig. 3D).

A markedly tall posterior process of the maxilla, which does not narrow posteriorly, is also present in the German material (see Čerňanský et al., 2016b:fig. 4k, 1). This character state was not shown in Müller’s reconstruction due to poor preservation of this region in the material studied by him (see Müller, 2004: fig. 3). The superior alveolar foramen in the maxilla described here is located in the same place as it is in the specimen from Germany (Čerňanský et al., 2016b:fig. 4k).

Nasals—The nasals are paired and grow wider anteriorly (Fig. 2A). The osteodermal shields, attached to the dorsal surface,

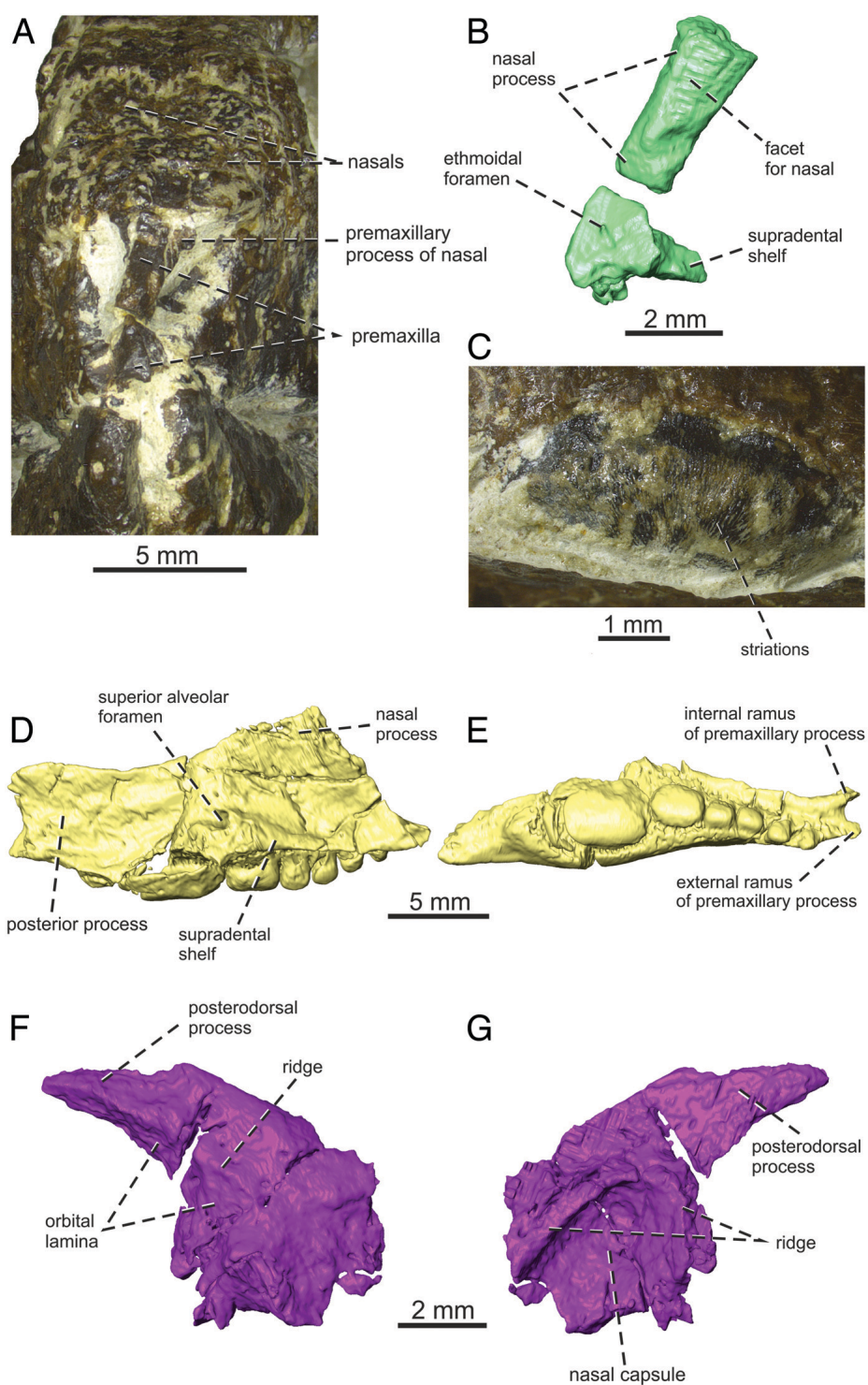


FIGURE 3. *Dracaenosaurus croizeti*, MNHN.F.COR7. Premaxilla in **A**, anterior and **B**, lateral views. **C**, detail of right maxillary largest tooth. Left maxilla in **D**, internal and **E**, ventral views. Right prefrontal in **F**, external and **G**, internal views. **B**, **D**–**G** based on micro-CT visualizations.

are separated along almost their mid-length by a transverse groove. The anterior medial region is well expanded anteroventrally, forming a pointed premaxillary process. This process frames the nasal process of the premaxilla laterally. The lateral region of the anterior-most section of the nasal is blunt and rounded.

Prefrontal—Both prefrontals are preserved, but the right one is more visible (Fig. 3F, G). It is a prominent triangular element, protruding posterodorsally into a posterodorsal process. This process gradually narrows, ending bluntly. The posteroventral surface of the bone forms the wedge-shaped orbital lamina. The

anterodorsal surface of the bone has an attached ornamented osteodermal crust. The ventral base of the prefrontal is slightly expanded posteriorly. The internal surface is excavated for the nasal capsule.

Lacrimal—Both lacrimals are preserved. This element is a thin, anteroposteriorly elongated element lying on the dorsal surface of the maxilla in the anterior part of the orbit (Figs. 1, 2A). The lacrimal gradually widens anteriorly.

Müller (2004) tentatively identified a long element of MNHN.F.COR5 as the lacrimal. We can confirm from the better-preserved

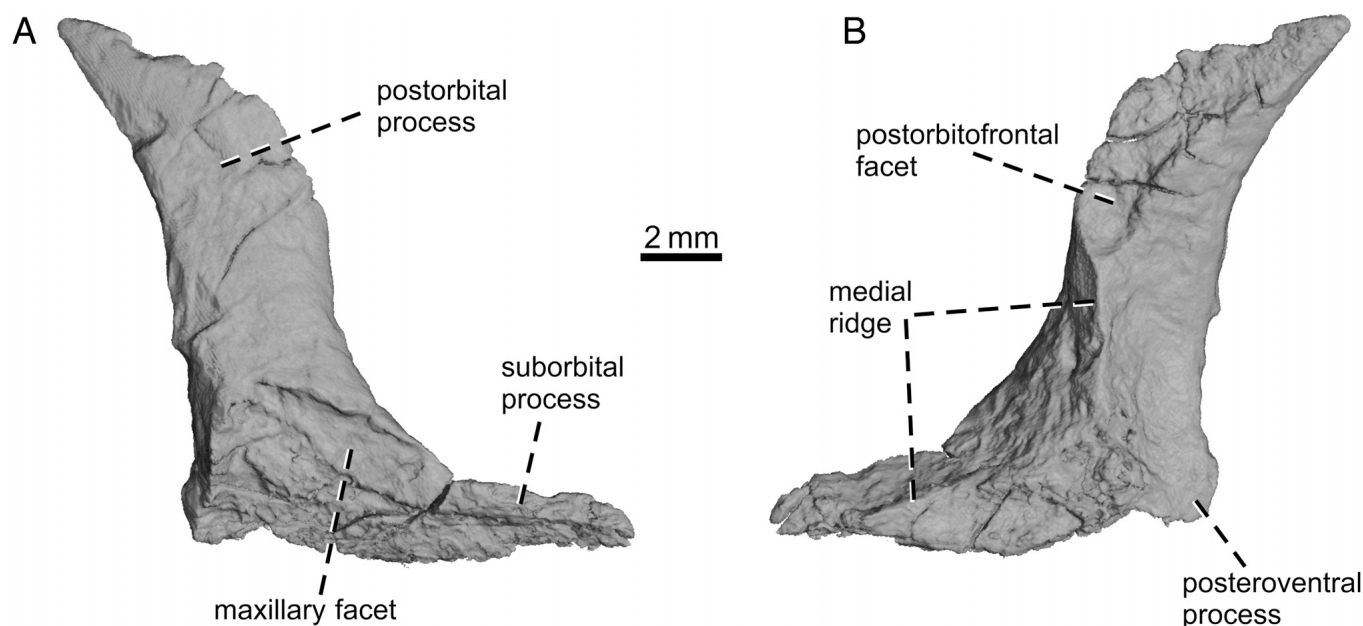


FIGURE 4. *Dracaenosaurus croizeti*, MNHN.F.COR7. Right jugal in **A**, external and **B**, internal views based on micro-CT visualizations.

MNHN.F.COR7 that this element was correctly identified. The identity of the element tentatively identified as the lacrimal in MNHN.F.COR4 is less clear.

Jugal—The jugal is a very robust triradiate element (Fig. 4). The postorbital process is distinctly anteroposteriorly broad. The posteroventral process is weakly developed, forming only a small, bulge-like structure. The suborbital process is thinner than the postorbital one. The lateral surface of the suborbital process bears a well-developed facet for the articulation with the maxilla, which almost completely covers it.

In medial view, the medial ridge is well developed, corresponding to Type 1 in Čerňanský et al. (2014). A large postorbitofrontal facet is developed in the upper portion of the postorbital process.

The posteroventral process of the jugal is reduced in members of Gallotiinae, in contrast to the distinctive posteroventral process of *Lacerta*, *Dalmatolacerta*, or *Anatololacerta* (Arnold, 1989; Barahona, 1996; Čerňanský et al., 2016a). It should be noted that this process is absent in many members of Eremiadini (see, e.g., Khosravani et al., 2011:fig. 2). This character state can be observed especially in the desert forms.

Frontal—These elements are fused, with traces of fusion still clearly visible. They form an anteroposteriorly elongated element, rectangular in shape, with its posterolateral corners slightly extended laterally (Fig. 5A–C). The whole dorsal surface of the frontals is covered by fused osteodermal shields bearing a marked sculpture. The sculpture is formed by small pits and delicate grooves and ridges. One exception is the anterior region, which bears two ovoid facets for the nasals. A small facet for the maxilla is present on each side lateral to the nasals. Small prefrontal shields are located posterolateral to these facets (their borders are indistinguishable). A rectangular frontal shield covers most of the anterior half of the frontal. This osteodermal shield is separated from two posteriorly located large frontoparietal shields by an obtusely ‘V’-shaped groove (sulcus interfacialis). The posterior margin, forming a contact with the parietal, shows interdigitations.

On the lateral side, a wedge-shaped facet for the prefrontal and one for the postorbitofrontal are not in contact, leaving the frontal exposed on the orbital margin. The ventral side bears large, well-developed, and robust subolfactory processes, which are directed anteroventrally.

Parietal—The parietal is a large element consisting of the parietal plate, which is completely covered by ornamented osteodermal shields fused to its dorsal surface, and two posteroventrally diverging supratemporal processes (Fig. 5D–F). The anteroposterior length of the parietal table is markedly higher than its width. The anterior margin possesses two small parietal tabs (only the right one is preserved), which, as in other lacertoids, underlapped the frontal. The centrally located interparietal shield, bearing the parietal foramen, is small and rhomboidal in shape. The posteriorly located occipital shield is very large and distinctly expanded laterally in a posterior direction. The supra-temporal processes are long and ventrally directed at an angle of approximately 45° to the parietal table.

Ventrally, the parietal cranial crests (cristae cranii parietalis) originate from the anterolateral corners of the parietal and converge posteromedially. This state is present in most modern members of Lacertidae (see Peters, 1962). However, here they fuse together posteriorly and form a deep, ventrally sharp crest (or flange). This crest fits into the processus ascendens of the supraoccipital and forms a strong articulation. Among lacertids, the presence of a strong crest appears to be an autapomorphy of *Dracaenosaurus*.

The overall shape of the parietal (being anteroposteriorly elongated) resembles that of large *Gallotia* specimens. A relatively short, narrow interparietal shield and a long, wide occipital shield are found in adults of *Gallotia* (see Čerňanský et al., 2016a).

Postorbitofrontal—The postorbitofrontal comprises the fused postorbital and postfrontal. The element is anteroposteriorly elongated and subrectangular in shape (Fig. 1). It tapers slightly posteriorly and does not fully close the upper supratemporal fossa. In cross-section, its ventral surface is slightly concave. Anteriorly, the postorbitofrontal is forked, thus embracing the frontoparietal suture as well as the anterodorsal margin of the postorbital process of the jugal. The external surface bears a groove that separates the supratemporal and parietal shields.

Squamosal—This bone is hockey-stick-shaped, robustly built, and anteroposteriorly elongated (Fig. 6A–D). The squamosal is better preserved on the right side (Fig. 6D). It extends anteriorly into a flat process bearing a dorsomedial facet for the postorbitofrontal. Its posterior-most region is broad and slightly lateroventrally expanded.

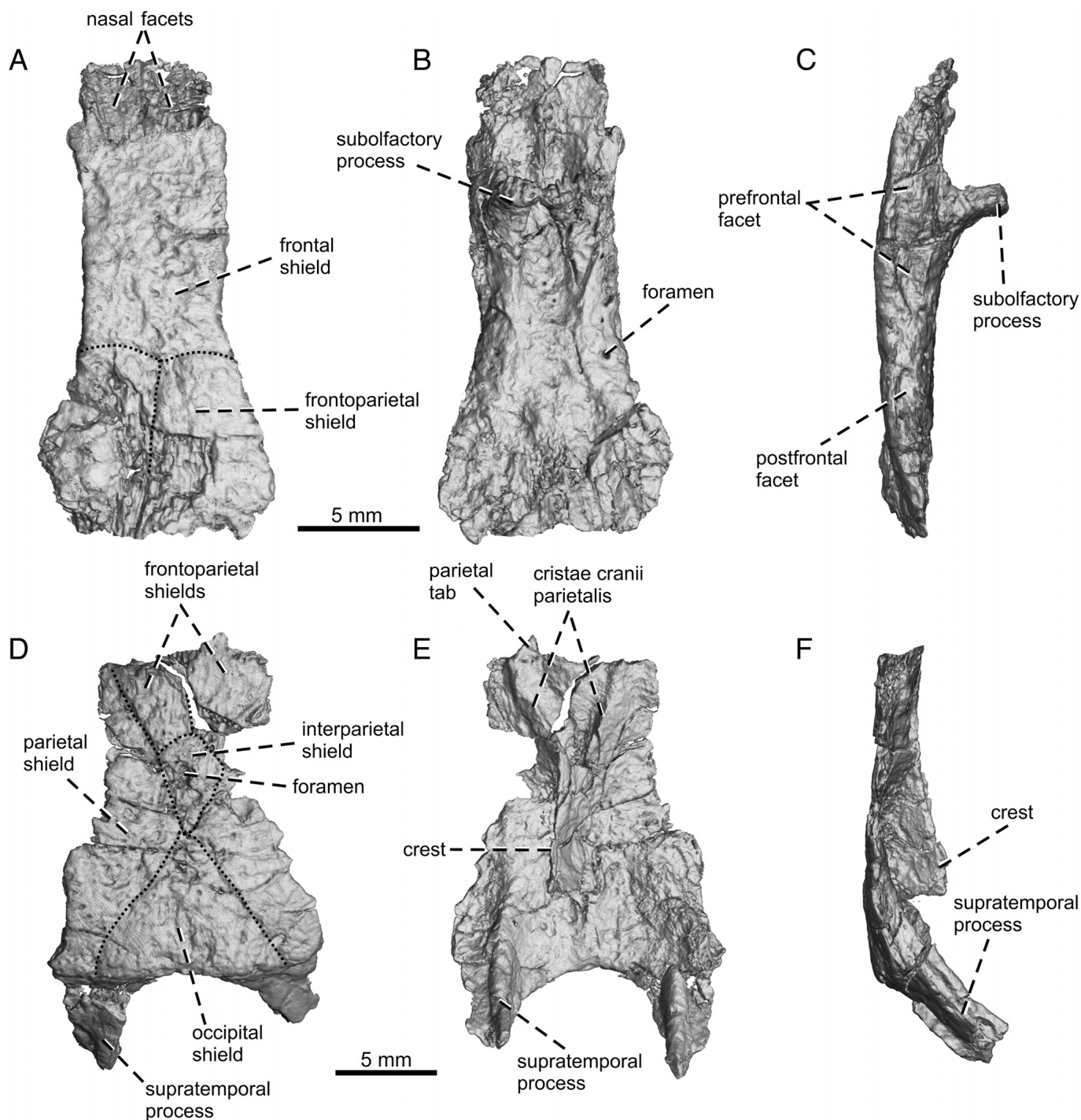


FIGURE 5. *Dracaenosaurus croizeti*, MNHN.F.COR7. Frontals in **A**, external, **B**, internal, and **C**, lateral views. Parietal in **D**, external, **E**, internal, and **F**, lateral views based on micro-CT visualizations. The dotted lines indicate borders of the osteodermal shields.

Supratemporal—Only the right element is preserved, and it is incomplete (Fig. 6D). The supratemporal is a small, lateromedially compressed element. It is wedged between the posterior region of the parietal supratemporal process and the squamosal.

Palpebral—A palpebral could not unequivocally be identified.

Supraoculars—Supraoculars are preserved only on the right side of the skull (Fig. 6E). Only two of them are preserved. They are small. The posterior one is oval, whereas the other is roughly rectangular in shape. They are flat and ornamented like the dermal roofing bones.

The elements interpreted by Müller (2004) as palpebrals are actually supraoculars. According to Borsuk-Bialynicka et al. (1999), the occurrence of four supraocular scales is highly consistent within Lacertidae but not within other scincomorphans.

Quadrate—Only the right quadrate is completely preserved (Fig. 7). It is a small (compared with overall skull size), but robust element. Its dorsal region is distinctly anteroposteriorly widened. This dorsal region, forming the large cephalic condyle, is convex and slightly inclined anteriorly. The lateral section of the condyle forms a small, ventrally oriented lateral flange

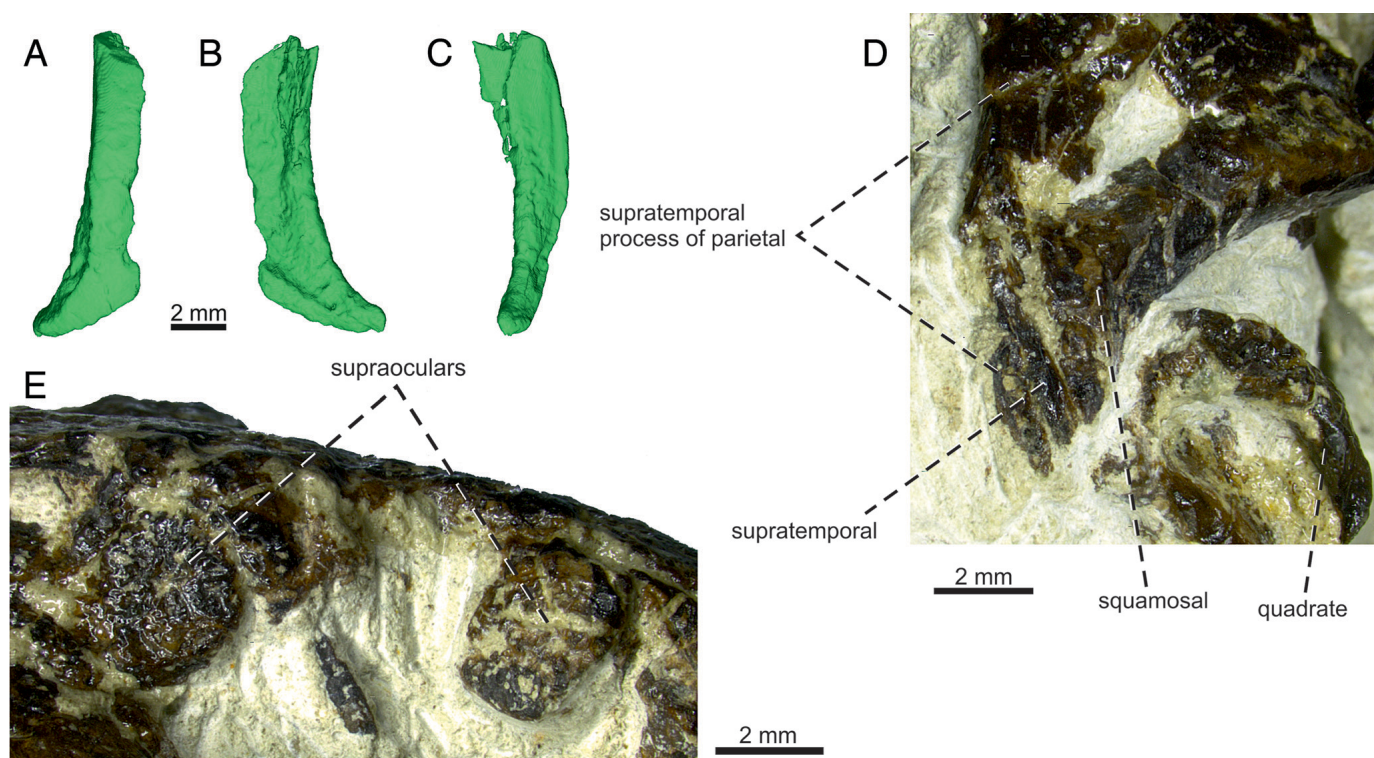


FIGURE 6. *Dracaenosaurus croizeti*, MNHN.F.COR7. Left squamosal in **A**, posterodorsal, **B**, anterodorsal, and **C**, lateral views based on micro-CT visualizations. Right supratemporal **D**, with contact to other bones. **E**, supraoculars in the right orbit.

(Fig. 7A). The anterior end of the condyle does not smoothly continue into the ventrally located portion but presents an angle at that point. For this reason, the whole anterior portion of the condyle, together with the flange, forms a blunt, anteriorly protruding triangle. Ventrally, this portion continues into a sharp ridge, i.e., the tympanic crest. This crest extends from the cephalic to the mandibular condyle. The dorsal surface of the cephalic condyle protrudes more posteriorly than the mandibular condyle. The mid-region of the quadrate is markedly narrow. The mandibular condyle is saddle-shaped and small. It is slightly more expanded anteriorly than posteriorly.

In medial view, the large cephalic condyle is well expanded medially, having an oval depression located ventrally to the condyle. The condyle is rounded, with its posterior region being more ventromedially inclined. The medial ridge (= pterygoid crest) is completely turned anteriorly. This forms the division of the anterior section of the cephalic condyle into two branches in dorsal view. The branches are separated by an anterior groove that runs along the entire middle section of quadrate to the dorsal side of the mandibular condyle. The lateral branch is smaller. The larger medial one, formed by an anteriorly turned medial ridge, bears a deep longitudinal fossa (Fig. 7C, D). On its medial side, a small quadrate foramen is located in the ventral one-third of quadrate height. In posterior view, the mediolateral widths of the cephalic and mandibular condyles are almost equal.

Palatal Bones—Both pterygoids are heavily damaged; only the quadrate processes are in good condition. The pterygoid dentition appears to be absent. Other palatal bones cannot be adequately interpreted.

Epipterygoid—Both elements are preserved. They are dorsoventrally elongated, robust, rod-like elements (Fig. 8), roughly triangular in cross-section. They become narrower dorsally, ending in a sharp tip. The posterior margin has an almost straight course, whereas the anterior one slightly wavy, which is caused by the width of the middle portion, which is slightly expanding

anteriorly. The stem portion, forming the connection between the dorsal section and the base of epipterygoid, is thin. The base, which contacts the pterygoid, forms a broad, node-like structure.

Dentary—The dentary is a robust and anteroposteriorly short element, being equal in length to the postdentary mandibular region (Figs. 9, 10). It is wide (i.e., transversely thick), ventrally expanded, and ‘C’-shaped in cross-section. Its posterior half is slightly taller than the anterior portion. The lateral surfaces of both dentaries are slightly damaged, but four mental foramina can be observed on the anterior half of the right dentary. They pierce the lateral surface of the bone approximately midway along its height. In medial view, the Meckelian canal is completely open, although it narrows anteriorly and is roofed by a robust subdental shelf. The alveolar crest supports seven teeth on the left dentary and six on the right one.

Splenial—The splenial is best preserved in the right mandible (Figs. 9B, 10B). It is an anteroposteriorly elongated, mediolaterally flat element. It gradually tapers anteriorly, reaching the level of the fifth tooth position. In its posterior portion, it bears an elliptical anterior inferior alveolar foramen. The foramen is located at the level of the posterior-most tooth and is fully enclosed in the splenial, not contacting the dentary.

Coronoid—Both coronoids are preserved (Figs. 9, 10). The coronoid is markedly large and triangular. Its ventral portion is wide and anteriorly expanded, forming an anterolateral process. This process covers the posterolateral area of the dentary. The anterior margin of the coronoid bears a robust distinctive ridge on its lateral surface. This ridge slightly widens posterodorsally. Posteriorly to the ridge there is a depression. The angle between the anterior and posterior processes is around 75°. In medial view, the anteromedial process of the coronoid extensively covers the dentary, although it does not reach the level of the tooth row.

Surangular—The surangular is an anteroposteriorly elongated element (Figs. 9, 10). It gradually narrows anteriorly in lateral view. The lateral side of the surangular is slightly concave,

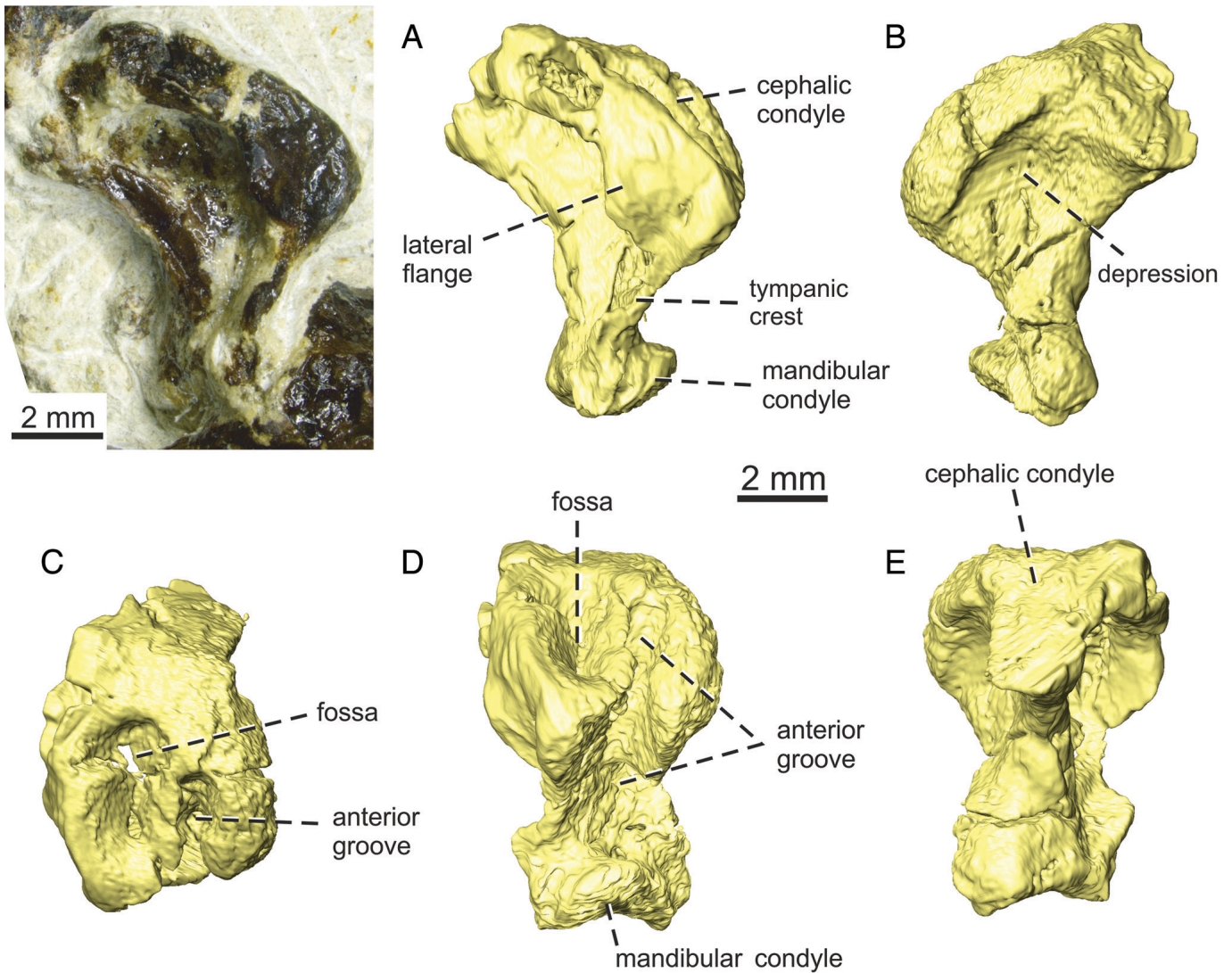


FIGURE 7. *Dracaenosaurus croizei*, MNHN.F.COR7. Right quadrate in **A**, lateral views, with micro-CT visualizations in **B**, medial, **C**, dorsal, **D**, anterior, and **E**, posterior views.

bearing a longitudinal depression (Fig. 9A). The latter continues to the depression located on the coronoid. It is bordered ventrally by a laterally expanded sharp ridge, forming the ventral margin of the surangular in lateral view. The whole depression, extending from the coronoid to the surangular, was interpreted by Müller (2004) as the attachment area for the large musculus adductor mandibulae externus superficialis. At the posterior end, the bone is slightly elevated dorsally and forms the anterior border of the glenoid fossa. In medial aspect, the bone participates in the enlarged mandibular fossa (Figs. 9B, 10B).

Angular—Both angulars are incompletely preserved, the right one mostly as a negative imprint in the surrounding matrix. The angular is an anteroposteriorly elongated element underlying the surangular. It is ventrally convex, forming the ventral margin of the posterior region of the mandible (Figs. 9A, B, 10). In medial view, the posterior mylohyoid foramen can be observed in the anterior region of the left angular.

Prearticular and Articular—These elements are fused (Figs. 9, 10). The prearticular is thin and gradually widens anteriorly, forming an anterior process. The articular is short and robust, bearing a small glenoid fossa for the quadrate on its dorsal surface. The retroarticular process is short, posteroventrally

directed, and with a fossa on its dorsal side. In the anterior region of this fossa, a large foramen for the chorda tympani is located. In lateral view, the process is rectangular in shape and shallow, with its rounded end being slightly bent horizontally.

Due to the poor preservation of the specimens described by Müller (2004), it was unclear if the articular and prearticular were fused or not. The skull described here demonstrates the presence of this fusion, as in modern lacertids.

Braincase—The braincase is poorly preserved and laterally strongly compressed (Fig. 11). The supraoccipital has a high and bifurcate ascending process, with which the ventral crest of the parietal articulates. The prootic bears an anteriorly strongly expanded alar process. It is oval, with its anterior end being blunt. The unpaired basioccipital and paired otooccipitals (the units formed by co-ossification of the opisthotics and the exoccipitals), are well preserved. The basioccipital is broad and rhomboidal in outline, its posterior part forming the central region of the occipital condyle. The occipital condyle is markedly depressed and slightly concave ventrally. The paroccipital processes are robust. Anterior to the basioccipital, the sphenoid is present and the suture between these two bones is still visible. A ventrally oriented process is interpreted here as the



FIGURE 8. *Dracaenosaurus croizeti*, MNHN.F.COR7. Left epipterygoid in **A**, lateral view, with micro-CT visualizations in **B**, lateral and **C**, medial views.

basipterygoid process. However, because of poor preservation, this needs to be interpreted with caution. The parasphenoid forms a thin, anteriorly directed process.

Dentition—The dentition is pleurodont and strongly heterodont. The teeth form blunt cylinders (amblyodont dentition sensu Hoffstetter, 1944). Their size increases posteriorly, the posterior-most one being the largest and most blunt. This tooth is mediolaterally compressed in cross-section, and it slightly narrows posteriorly. The tooth apices bear delicate striations on both maxillary (Fig. 3C) and dentary teeth. The tooth bases are frequently covered by cement.

Postcranial Skeleton

Humerus—The left element is elongate and slender, with the proximal and distal epiphyses appearing to be fused to the diaphysis (Fig. 12). The proximal portion is moderately broad. The diaphysis is slim and oval in cross-section. The large entepicondylar foramen, forming the orifice for the brachial nerve, is located in the ventral section of the distal epiphysis, close to the slightly expanded entepicondyle. The radial and ulnar condyles are poorly preserved.

Radius and Ulna—The ulna and the radius are slightly shorter than the humerus (Fig. 12). The ulna is markedly robust compared with the radius. Its proximal end is slightly more expanded than the distal end.

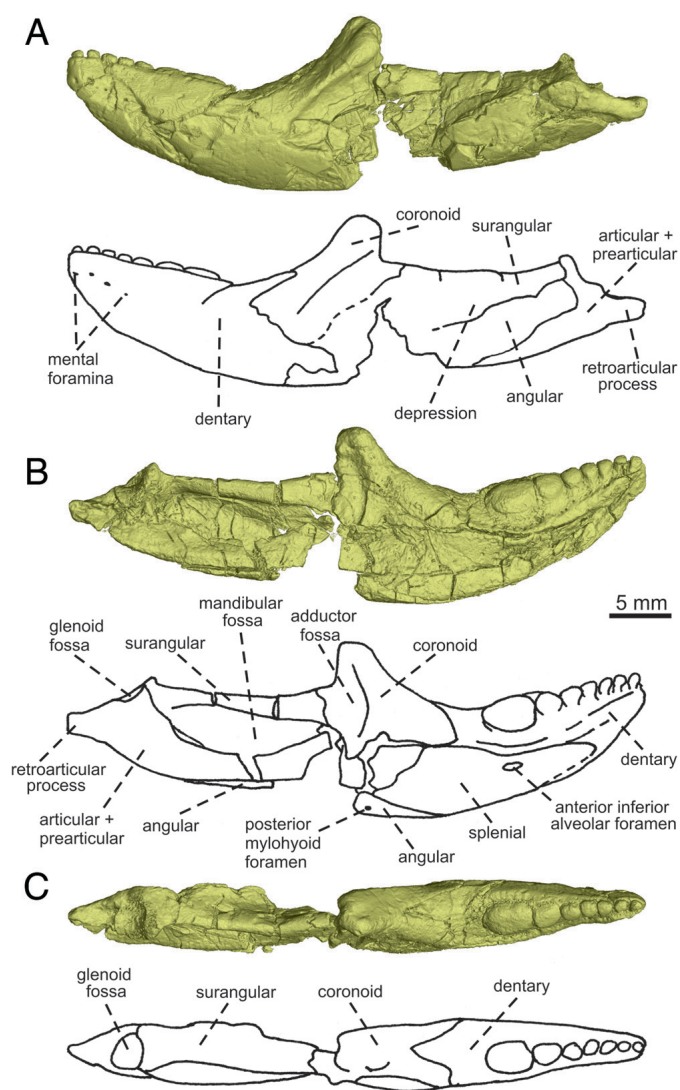


FIGURE 9. *Dracaenosaurus croizeti*, MNHN.F.COR7. Left mandibular ramus in **A**, external, **B**, internal, and **C**, dorsal views based on micro-CT visualizations.

Cervical Vertebra—The cervical vertebra is poorly preserved (Fig. 13). The neural spine is tall. It rises dorsally at the anterior one-third of the neural arch. The neural canal is large. Prezygapophyses are oval, more anteriorly oriented, and not markedly expanded laterally. They are inclined from the horizontal plane at an angle of ca. 29°. The interzygapophyseal constriction is shallow. The postzygapophyses are roughly triangular in shape. The cotyle is rounded, whereas the condyle is badly preserved. The ventral region is slightly concave in lateral view. In ventral view, the centrum bears a longitudinal ridge in its central region extending through its entire length, from cotyle to condyle. No evidence for a zygosphenes is observed.

PHYLOGENETIC ANALYSIS

A recent analysis (Čerňanský et al., 2016a) recovered two fossil lacertids, *Pseudeumeces cadurcensis* and *Janosikia ulmensis*, as members of Gallotiinae. As stated in the same paper, *Dracaenosaurus croizeti* had been also reported as a relative of *Gallotia* (see Müller et al., 2011), but the exclusion of *Psammadromus*

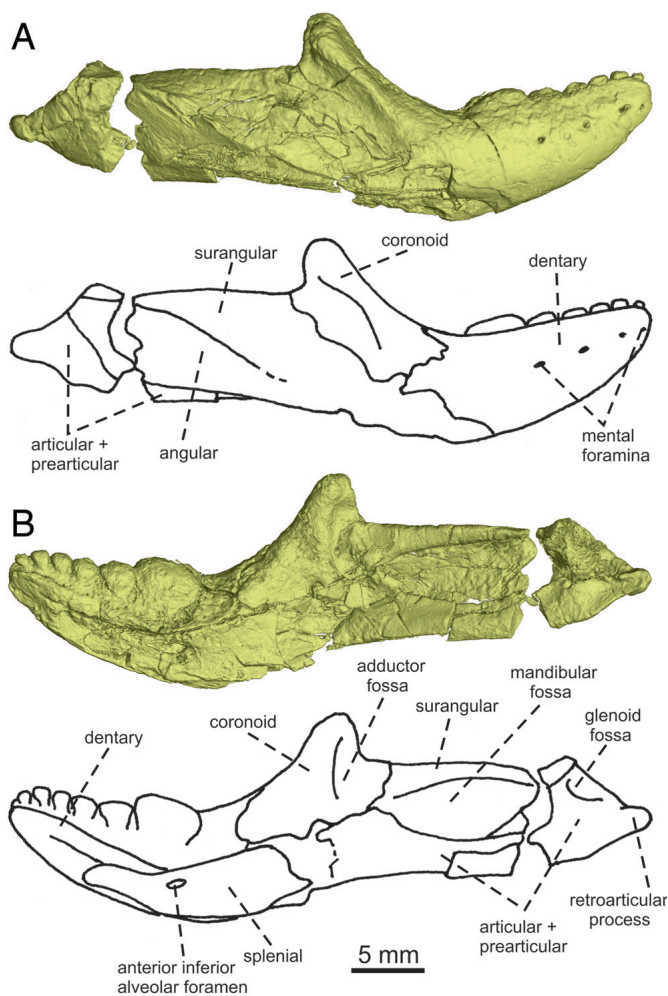


FIGURE 10. *Dracaenosaurus croizeti*, MNHN.F.COR7. Right mandibular ramus in **A**, external and **B**, internal views based on micro-CT visualizations.

from the analysis precluded an evaluation of its position in the stem of *Gallotia* or of Gallotiinae. We have added the codings of *Dracaenosaurus* based on the model resulting from the CT scan (as well as available information on the external morphology of the two skulls described by Müller [2004]) to the matrix of Čerňanský et al. (2016a) in order to infer the phylogenetic position of the genus. *Smaug giganteus* was set as the outgroup in all analyses. We used two versions of the matrix: (1) the original matrix of Čerňanský et al. (2016a) with the addition of *Dracaenosaurus* (see Appendix S1 for codings of this taxon) and changes to a few codings of some taxa (see Appendix S2); and (2) the same matrix plus the addition of a few selected extant lacertids: *Timon lepidus*, *Acanthodactylus erythrurus*, *Podarcis hispanica*, and *Psammodromus hispanicus* (see Appendix S1, and Nexus file). A complete list of characters is provided as Appendix S3. *Acanthodactylus erythrurus* was added in order to test if the inclusion of a member of Eremiadini (a non-Lacertini lacertine) had some effect on the composition of Gallotiinae, mainly regarding the fossil taxa. The inclusion of the other three lacertids (*Timon lepidus* and *Podarcis hispanica* as members of Lacertinae, and *Psammodromus hispanicus* as a member of Gallotiinae) had the objective of testing if increasing the sample size had any effect on the results and, at the same time, to test the resolution of the analysis for recovering as sister taxa species of the same genus (*Gallotia*, *Psammodromus*, *Podarcis*, *Lacerta*,

and *Timon*). For each version of the matrix, we performed the analysis twice, one in which additive characters were ordered under the option between character weighting (Wiens, 2001) and another with all characters unordered and equally weighted. We also excluded character 5 from the analysis because we interpreted that the way it should be measured remains equivocal and it is currently difficult to provide unambiguous scores for some taxa. Multistate characters were treated as polymorphisms. Analysis 1 with characters ordered and weighted recovered three trees (tree length [TL] = 75.20, consistency index [CI] = 0.70, retention index [RI] = 0.74, and rescaled CI [RC] = 0.52) in which Gallotiinae is monophyletic and includes *Psammodromus*, *Pseudeumeces*, *Dracaenosaurus*, *Janosikia*, and *Gallotia*. Support for inclusion of *Pseudeumeces*, *Dracaenosaurus*, and *Janosikia* as members of Gallotiinae is very high (bootstrap support = 0.95; Fig. 14A), and this clade is supported by 15 unambiguous synapomorphies (see Appendix S4 for a complete list of synapomorphies in this tree): 4(0→1), 13(0→1), 14(1→0), 16(0→1), 21(0→1), 25(0→1), 37(1→0), 38(0→1), 40(1→0), 41(1→4), 43(1→2), 54(0→1), 55(2→4), 63(0→1), and 64(0→1). Of these, characters 54 (tongue), 63 (voice), and 64 (copulatory position) cannot be scored in fossils because they are related to soft tissues or behavior, and characters 16 (septomaxilla), 43 (clavicle), and 55 (nasal vestibule) are related to elements not preserved (or poorly preserved) in the available fossil specimens. The remaining characters have the potential to provide information on the composition and interrelationships of fossils on the stem of *Gallotia*. All three trees recover the same relationships within Gallotiinae as reported by Čerňanský et al. (2016a), with the fossil taxa (this time including *Dracaenosaurus*) on the stem of *Gallotia* (the topology is the same as in Fig. 14B, which, however, corresponds to the consensus tree of the bootstrap analysis with characters unordered and equally weighted; see below). Of the three trees, two fail in recovering a monophyletic Lacertinae as currently understood because *Podarcis muralis* appears as sister to Gallotiinae or sister to the remaining lacertids, but this position is poorly supported (see the position of *Podarcis muralis* collapsed at the base of Lacertidae in the bootstrap consensus tree; Fig. 14A). The grouping of the remaining Lacertinae has, however, high support (bootstrap value = 0.86). Character 4 (width of the nasal process of the premaxilla) distribution is as follows: the outgroup is scored with the plesiomorphic state of a broad process (0), and taxa on the stem of *Gallotia* are scored as intermediate (1), whereas *Gallotia* is scored with the more derived state: slender (2). Note, however, that although the included species of *Psammodromus* is scored as intermediate (1), the second species of *Psammodromus* included in the second analysis (see below) is scored as '2' and thus can be interpreted as convergent with *Gallotia* in this topology. Regarding characters 13 (size and height of the maxillary teeth) and 21 (posteroventral process of the jugal), all taxa interpreted here as members of Gallotiinae share the derived condition (1). Character 14 is more difficult to interpret, because the amblyodont taxa (*Pseudeumeces*, *Dracaenosaurus*, and *Janosikia*) are scored as having a low number of maxillary teeth (0), whereas *Psammodromus* and *Gallotia* would be convergent in having state 2 (20–25 maxillary teeth). Regarding character 25 (fusion of frontals), *Gallotia* and *Psammodromus* include members scored as '0,' corresponding to paired frontals, and (1) partial fusion in adults, whereas the fossil species are all scored '1.' A relatively short dentary (equal in length to the rest of the jaw; see character 37; scored '0') and a weak curvature of the subdental shelf in the symphyseal region (character 38; scored '1') unite all members of Gallotiinae. Regarding dentary tooth number (character 40) and shape (character 41), all taxa have a low or intermediate number of teeth, and shapes include bicuspid (*Psammodromus*), tricuspid and polycuspid (*Gallotia*), and amblyodont (*Pseudeumeces*, *Dracaenosaurus*, *Janosikia*) teeth, scored as '1,' '2,' and '3,' and '4,' respectively.

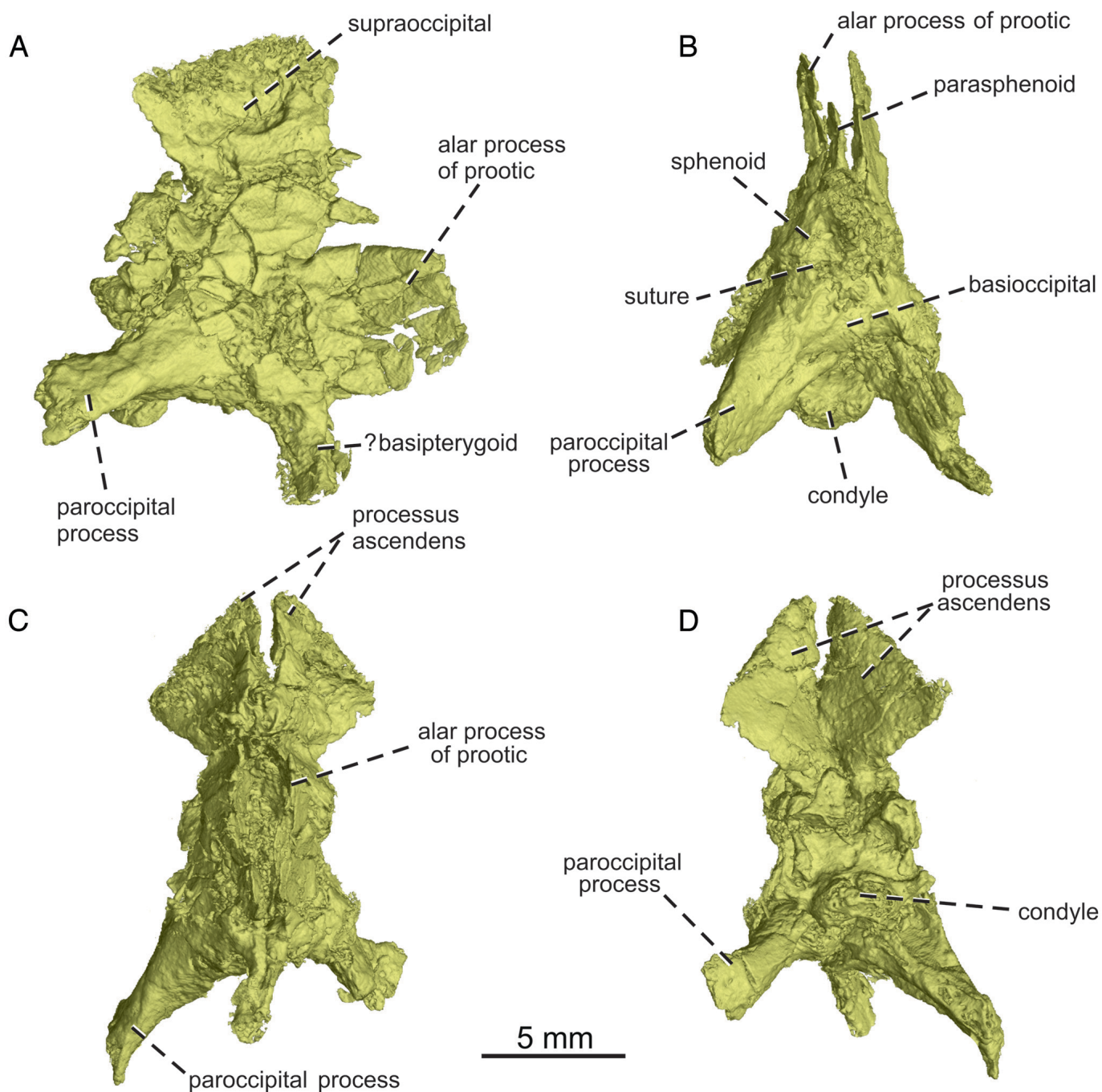


FIGURE 11. *Dracaenosaurus croizeti*, MNHN.F.COR7. Braincase in **A**, lateral, **B**, ventral, **C**, anterior, and **D**, posterior views based on micro-CT visualizations.

The analysis of this same matrix with all characters unordered and equally weighted yielded a single most parsimonious tree (TL = 107, CI = 0.71, RI = 0.72, and RC = 0.51; Fig. 14B) with a preferred topology where *Podarcis* is sister to the remaining Lacertinae, albeit with low bootstrap support (0.52), and Gallotiinae is monophyletic and includes, apart from *Gallotia* and *Psammodromus*, the genera *Pseudeumeces*, *Dracaenosaurus*, and *Janosikia* (bootstrap support = 0.97).

For analysis 2, the matrix included four additional lacertids (see Appendix S2 for codings). Performing the analysis with characters ordered and weighted, following Čerňanský et al. (2016a), resulted in a single most parsimonious tree (TL =

104, CI = 0.56, RI = 0.69, and RC = 0.39; Fig. 14C). In this tree, Gallotiinae is monophyletic and composed of the same taxa as in analysis 1 (with the addition of *Psammodromus hispanicus*, which was not included in the former analysis) and with an equivalent topology. *Dracaenosaurus* is, as in our analysis 1 (unordered and equally weighted; Fig. 14B), the sister taxon of *Janosikia* + *Gallotia*. *Acanthodactylus* is recovered as the sister taxon of the remaining lacertids instead of in the expected position as sister to the remaining Lacertinae (Fig. 14C). *Podarcis* (here, *Podarcis muralis* + *Podarcis hispanica*, bootstrap support = 0.9) is recovered as the sister taxon of Gallotiinae with very low support (0.53).

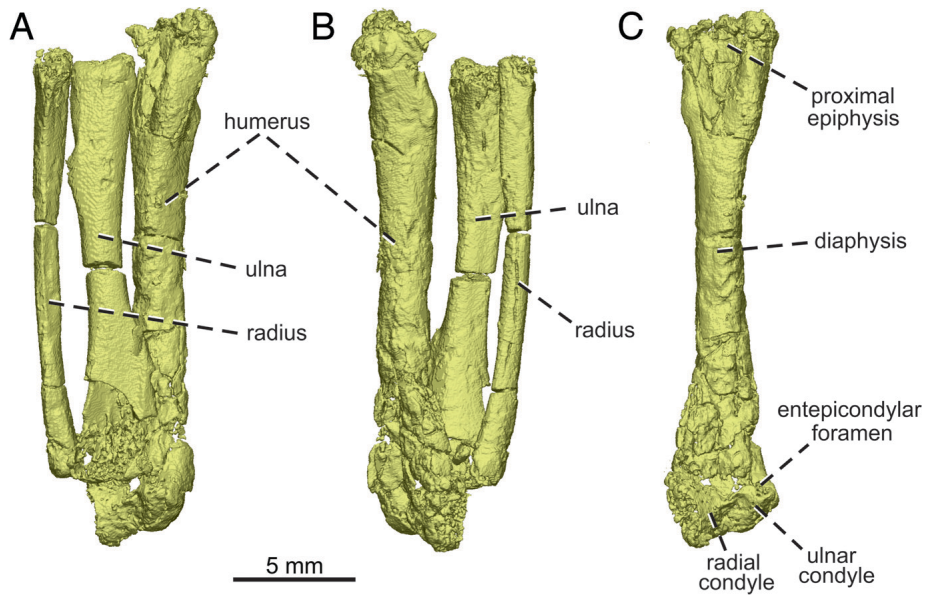


FIGURE 12. *Dracaenosaurus croizeti*, MNHN.F.COR7. Left stylopodium (humerus) and zeugopodium (radius + ulna) in **A**, lateral and **B**, medial views. **C**, humerus in anterior view. All based on micro-CT visualizations.

The bootstrap value for the inclusion of *Dracaenosaurus*, *Pseudeumeces*, and *Janosikia* in Gallotiinae remains high (0.92). An analysis of the same matrix performed with all characters unordered and equally weighted yielded a single most parsimonious tree (TL = 164, CI = 0.58, RC = 0.44,

and RI = 0.65; Fig. 14D) where, again, Gallotiinae is strongly supported (bootstrap value = 0.97), but relationships among Lacertinae are poorly resolved. In this tree, *Podarcis* forms a monophyletic group (bootstrap value = 0.85) and a monophyletic *Timon* plus a paraphyletic *Lacerta* form another

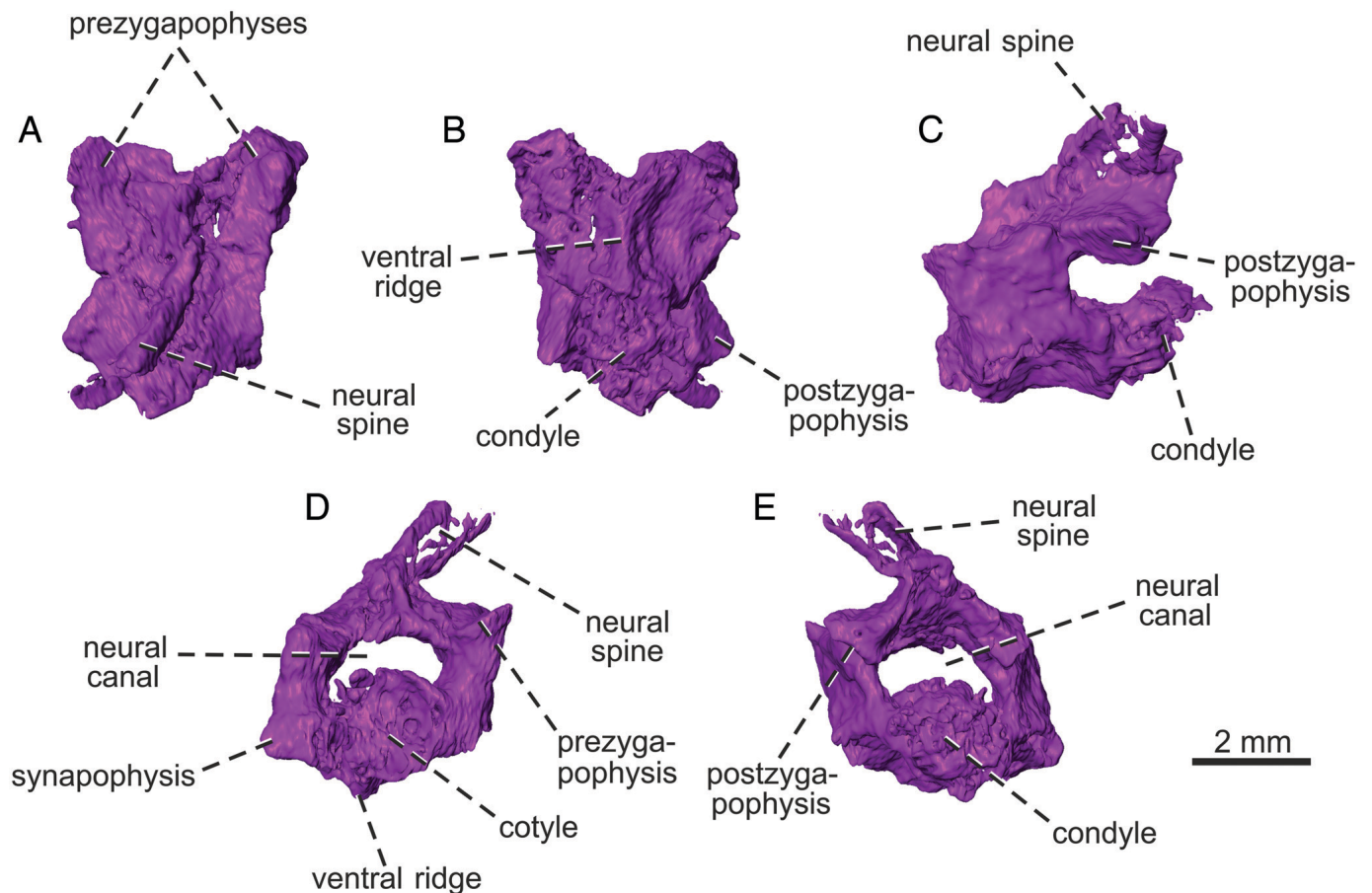


FIGURE 13. *Dracaenosaurus croizeti*, MNHN.F.COR7. Cervical vertebra in **A**, dorsal, **B**, ventral, **C**, lateral, **D**, anterior, and **E**, posterior views based on micro-CT visualizations.

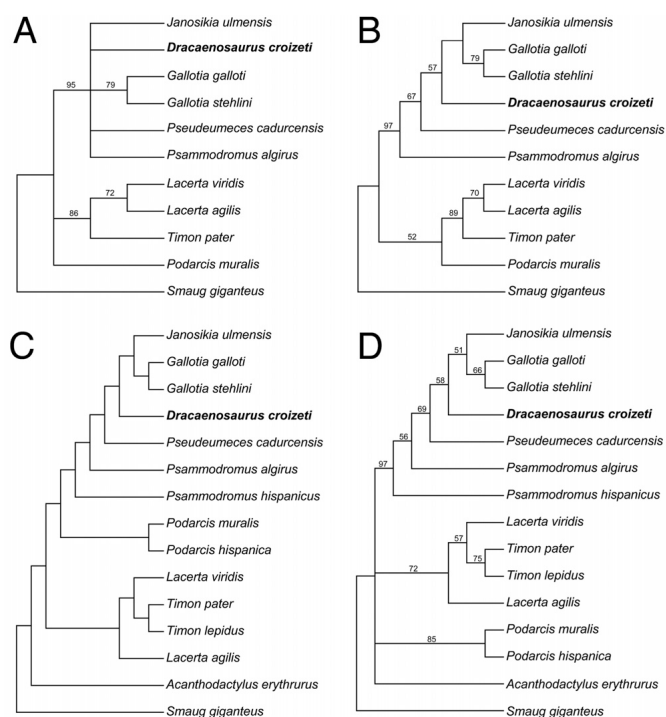


FIGURE 14. Phylogenetic position of *Dracaenosaurus croizeti*. Bootstrap majority-rule consensus tree recovered in **A**, the ordered and weighted version and **B**, the unordered and equally weighted version of analysis 1. **C**, single most parsimonious tree recovered in the ordered and weighted version of analysis 2. **D**, bootstrap majority-rule consensus tree recovered in the unordered and equally weighted version of analysis 2. Numbers correspond to bootstrap frequencies. See text for explanation.

group (bootstrap value = 0.72). Both form a polytomy together with *Acanthodactylus* and Gallotiinae.

In summary, the analyses performed here demonstrate that the inclusion of *Dracaenosaurus*, as well as a few changes in the original codings of other taxa, have little effect on the relative position of the remaining taxa as reported in Čerňanský et al. (2016a). The monophyly of Gallotiinae, and its composition including the fossil genera *Pseudeumeces*, *Dracaenosaurus*, and *Janosikia*, is strongly supported, even when increasing the number of extant taxa sampled.

DISCUSSION

Dracaenosaurus croizeti represents a large lacertid lizard with a total skull length of 46 mm. The skull of this taxon is narrow relative to its length due to the presence of a relatively long frontal and parietal. In lateral view, the preorbital region is rounded and short relative to, e.g., *Lacerta viridis* (see Digimorph.org, 2002–2012). The presence of an anterior overlapping snout mentioned by Müller (2004) is not supported by the skull studied here and that erroneous interpretation is probably related to poor preservation and deformation of the region of the snout of the two specimens studied by Müller (2004), as well as a slight backwards movement of the lower jaws (as observed in MNHN.F.COR4 in comparison with the specimen studied here). The maxilla and the dentary are exceptionally robust in this taxon. A very unique character among the lacertid clade is a strong connection of the parietal and the braincase: the deep ventral crest in the posterior section of the parietal fits into the divided processus ascendens of the supraoccipital. In fact, such a connection represents a different way of connection relative to the modern members of Lacertidae in which this character has been studied,

and where the ascending process of the supraoccipital fits into a groove (parietal fossa) in the posterior ventral section of the parietal (see, e.g., Klemmer, 1957). In some taxa, the posterior margin of the parietal does not reach the anterior edge of the supraoccipital (see Barahona and Barbadillo, 1998), leading to the absence of a connection, which also occurs frequently in eremiadine lacertids (J.M., pers. observ.). It also has to be acknowledged that the cranial morphology of many modern lacertids is still poorly known, with only a few taxa having been studied in sufficient detail.

The phylogenetic analysis strongly supports the inclusion of all three fossil amblyodont lacertids (*Pseudeumeces*, *Dracaenosaurus*, and *Janosikia*) in Gallotiinae. Moreover, the extant *Psammotromus* is recovered as the sister taxon of the remaining Gallotiinae. Because *Pseudeumeces*, *Dracaenosaurus*, and *Janosikia* all have large body sizes, this seems to indicate that large body size in *Gallotia* might not have been the result of insular evolution but would have already been achieved earlier by more basal members of Gallotiinae on the European mainland. Body size change in *Gallotia* was more complex, which was already suggested by Čerňanský et al. (2016a), but it is here further supported by the phylogenetic position recovered for *Dracaenosaurus*. In any case, this hypothesis should be tested by future studies and new, more complete fossils of lacertid lineage members.

Comparisons

The morphological analysis shows that *Dracaenosaurus* shares many character states with the early Miocene lacertid *Janosikia* from Germany (for character states in *Janosikia*, see Čerňanský et al., 2016a) and with the extant genus *Gallotia* from the Canary Islands.

Overall, the skull of *Dracaenosaurus* resembles the extant South American teiid *Dracaena*, but also the extinct *Paradracaena* from the Miocene of South America (see Pomel, 1846; Sullivan and Estes, 1997; Müller, 2004; Nydam et al., 2007; Pujos et al., 2009). *Dracaena* belongs to Tupinambinae and is a truly durophagous form (Vanzolini and Valencia, 1965), whereas other teiids with less amblyodont teeth (e.g., *Tupinambis*) are omnivorous (Mercolli and Yanosky, 1994; Kiefer and Sazima, 2002). The similarities with *Dracaena* are as follows: (1) amblyodont dentition developed to a large extent; (2) pterygoid dentition in *Dracaena* is absent (see Dalrymple, 1979:fig. 1, p. 304). Although the CT scan reveals that both pterygoids in our *Dracaenosaurus* specimen are heavily damaged, the dentition appears to be absent as well; (3) the lateral sulcus of the quadrate forms a deep recess. It is framed by an increased lateral flange in the anterior region of the quadrate, where the M. adductor mandibulae pars superficialis originates (see Haas, 1973); and (4) the presence of a robust jugal. It is clear that not all of these characters are strictly related to durophagy, e.g., the absence of pterygoid teeth is observed in many other lizards.

The characters listed above are clearly related to the convergence between the two forms and highlight the constraints imposed by a similar diet driving cranial similarities in these distantly related taxa. However, several significant morphological differences (besides those between lacertids and teiids in general) between the extinct lacertid *Dracaenosaurus* and *Dracaena* exist. This shows, that although several states are convergently present, the biting mechanism of these two taxa is likely not the same (for *Dracaena*, see Dalrymple, 1979). In *Dracaenosaurus*: (1) the posterior blunt crushing tooth is large relative to mandible size; (2) there is a lower tooth number (seven or eight teeth) of teeth that are arranged in a single line along the tooth row rather than a high tooth number (12–14) of asymmetrically distributed teeth; (3) the dentary is shorter relative to the entire length of the mandible rather than longer than the postdentary

mandibular region. The ratio of the distance of the jaw articulation to the posterior end of the tooth row and the distance of the jaw articulation to the anterior end of the mandible is ca. 3:4 in *Dracaenosaurus* and ca. 1:2 in *Dracaena*; (4) the anterior process of the coronoid is longer, having a straight anterodorsal margin rather than a rounded, convex margin; (5) the coronoid apex is slightly posterodorsally inclined, following the course of the posterodorsal margin of the coronoid anterior process, rather than being simply dorsally directed; (6) the depression on the surangular of *Dracaenosaurus*, ventrally bordered by a laterally expanded distinct sharp ridge, is absent in *Dracaena*; (7) the posterior process of the maxilla is robust and dorsally tall, rectangular in shape, rather than narrowing posteriorly; (8) the suborbital process of the jugal is mostly covered by the maxilla, rather than the lateral surface of the suborbital process being exposed; (9) the preorbital region is short and the postorbital one is much longer, whereas the orbital region of the skull of *Dracaena* is located at half the length of the skull, so pre- and postorbital regions are equally long (or the preorbital region even being slightly longer); (10) the quadrate of *Dracaena* is markedly larger relative to skull size than it is in *Dracaenosaurus*, where the quadrate is small; and (11) in anterior view, the cephalic and mandibular condyles of the quadrate in *Dracaenosaurus* are equally wide, whereas in *Dracaena* the mandibular condyle is distinctly wider than the cephalic one.

In some cases, these morphological differences might be related to either (1) different solutions to the same problem, posed by an extreme dietary adaptation; or (2) an adaptation to slightly different dietary constraints (resulting in different loads upon key regions of the cranium and lower jaw); or (3) the result of differences in the primitive skull architecture (in this case, morphological differences between teiids and lacertids).

The quadrate as described here has a very distinctive morphology. Its medial ridge is completely turned anteriorly, enlarging the dorsal surface of the cephalic condyle. In comparison with, e.g., *Lacerta viridis*, the quadrate has several differences: (1) it is small relative to the size of the skull; (2) it is robust, its maximum anteroposterior length forms 88% of its maximum dorsoventral height, whereas in *L. viridis* the quadrate is slender and high. Its maximum anteroposterior length forms 67% of the maximum dorsoventral height. The ratio of the maximum anteroposterior length to the maximum dorsoventral height of the quadrate is identical in *Dracaena* and *Dracaenosaurus*; (3) the contact of the anterior and dorsal margin is angled, rather than being completely rounded and smooth; and (4) the lateral sulcus of the *Lacerta* quadrate is shallow in comparison with that of *Dracaenosaurus*, and its anterior section does not show the increased size of the lateral septum.

Durophagy and Paleocology

Nowadays, true feeding specialists among lizards are rare. Although amblyodont teeth occur repeatedly among lacertid members during different periods of the European Cenozoic (Augé, 2005), no other known extinct or extant lacertid has such a greatly developed amblyodont dentition as *Dracaenosaurus*. Amblyodont dentition is not restricted to members of Lacertidae but is present in Iguanidae, Teiidae, Scincidae, Xantusiidae, Anguillidae, Varanidae, Mosasauridae, and Amphisbaenia (Estes and Williams, 1984). In many taxa where amblyodonty is developed (*Quercycerta*, *Escampcerta*, *Mediolacerta*, *Pseudeumeces*, *Janosikia*, *Amblyolacerta*, *Ligerosaurus*, and *Maioricalacerta*; see, e.g., Roček, 1984; Augé et al., 2003; Augé, 2005; Bailon et al., 2014; Čerňanský et al., 2016a, 2016b), this type of dentition does not mean that the diet was restricted to hard-shelled prey. Most were probably faunivorous (or even more likely omnivorous, as it is seen in the extant scincid *Tiliqua*; see, e.g., Christian et al., 2003; Shea, 2006). In other cases, taxa have been

reported as durophagous despite a lack of amblyodont teeth (see Savitzky, 1983, in the case of some snakes).

The morphology of *Dracaenosaurus*, however, suggests an extremely durophagous specialization. Lizards that eat hard-shelled prey should, in addition to a strongly amblyodont dentition, display a specialized cranial morphology with more massive cranial muscles (Dalrymple, 1979; Rieppel and Labhardt, 1979) and greater bite forces (e.g., Schaerlaeken et al., 2012). This is most likely reflected in a strong connection between parietal and braincase (see above), which reduces the possibility of metakinesis. Other skull adaptations are, e.g., a robust jugal together with a large and firm maxillary-jugal contact, a quadrate lateral septum for muscle origin (see below), and an enlargement of the mandibular fossa for jaw muscle attachment (see also Müller, 2004).




It should be noted that feeding on hard-shelled prey by *Dracaena* is suggested to be associated with its semiaquatic lifestyle (Vanzolini, 1961; Duellman, 2005). The data of Bochaton et al. (2015) show the occurrence of a durophagous feeding habit and a possible tendency to association with freshwater environments also in the anigid lizard *Diploglossus montisserrati*. The skull of *Dracaenosaurus* described here is embedded in limnic calcareous marls, and such a lifestyle cannot therefore be excluded and is very plausible. Gastropods are frequent in the Oligocene lacustrine beds of the Cournon area. *Caseolus ramondi* (often reported as *Helix ramondi*) appears to be the most frequent species; although regarded as a terrestrial species by Rey (1974), it is very frequent in lacustrine sediments. True freshwater gastropods (*Lymnaea*) were reported from Cournon by Giraud (1902), which may confirm this presumed mode of life. Amblyodonty is certainly adaptive and can respond to several environmental cues. Semiaquatic lifestyle could be one of them, and climate change may be another. Temperature, humidity, and calcium availability can modify the thickness of gastropod shells. For example, snails living on a more humid stretch of a dune area show a reduction in shell thickness, whereas populations living in arid areas have relatively thick shell (De Smet and Van Rompu, 1984). The Oligocene epoch is often qualified as a cool and dry episode in western Europe and other areas (Rage and Szyndlar, 2005; Rage, 2013). These paleoenvironmental inferences come from different types of data: reptiles (Europe: Rage, 2013; U.S.A.: Hutchison, 1982), mammals (Europe: Huguency, 1969; Vianey-Liaud, 1976, 1991; Cabrera et al., 2002; Alvarez Sierra et al., 1990; U.S.A.: Prothero, 1994; Van Valkenburgh, 1994), paleoflora (Europe: Gorin, 1974; Châteauneuf, 1980a, 1980b; Ollivier-Pierre et al., 1987; U.S.A.: Wing, 1998), paleosols (Europe: Hamer et al., 2007; U.S.A.: Retallack, 1992, 2004), and sediments (Asia: Dong et al., 2013). However, some results demonstrate that a warm period begins in the final part of the late Oligocene (MP 30; Böhme, 2008), at least in central Europe. Several empirical studies point out that xeric terrestrial (and fresh water) molluscs have a thick shell (Sacchi, 1961; Sacchi and Testard, 1971), and shell thickness depends on the exchangeable pools of calcium present in the environment (Goodfriend, 1986; Charrier et al., 2013). How may these pools be related to dry conditions? Studies of the calcium budget of some terrestrial environments may provide an answer. For example, inputs and outputs of calcium have been measured in a forested area in North America (Likens et al., 1996, 1998; Weathers et al., 2013): stream export of calcium represents the primary loss of calcium, and it may even exceed the storage of calcium in the soil. Hence, during dry episodes, it may be expected that less calcium exits the ecosystem in stream water, making it available to organisms.

It also seems straightforward that an increase in shell thickness might help in keeping the appropriate conditions of temperature and/or humidity inside the shell, mainly in adverse conditions such as the increased aridity found in the Oligocene. As in many other phenomena, it is possible that multiple reasons might be involved (see Lawton, 2000).

ACKNOWLEDGMENTS

For CT scanning and photographs of the fossil material, we are indebted to J. Šurka (Slovak Academy of Sciences) and K. Mahlow (Museum für Naturkunde, Berlin). We thank B.-A. S. Bhullar (Yale University) and S. Bailon (Muséum national d'Histoire naturelle Paris) for their critical reading of the manuscript, as well as J. Head (Cambridge University) for editing. A.B. received support from the SYNTHESYS Project <http://www.synthesys.info/>, which is financed by European Community Research Infrastructure Action under the FP7 'Capacities Program,' from CERCA Programme (C0175-20161124) and project (2014/100604) of Generalitat de Catalunya, and from project CGL2014-54373-P of Ministerio de Economía y Competitividad (MINECO), Spanish Government. This project was also supported by the Deutsche Forschungsgemeinschaft (MU 1760/7-1).

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LITERATURE CITED

- Álvarez Sierra, M. A., R. Daams, J. I. Lacomba, N. López Martínez, A. J. van der Meulen, C. Sesé, and J. de Viser. 1990. Paleontology and biostratigraphy (micromammals) of the continental Oligocene–Miocene deposits of the north-central Ebro Basin (Huesca, Spain). *Scripta Geologica* 94:1–77.
- Arnold, E. N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an old-world family of lizards derived from morphology. *Bulletin of the British Museum (Natural History, Zoology)* 55:209–257.
- Arnold, E. N., O. Arribas, and S. Carranza. 2007. Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa* 1430:1–86.
- Augé, M. 2005. Évolution des lézards du Paléogène en Europe. *Mémoires du Muséum national d'Histoire naturelle, Paris* 192:1–369.
- Augé, M., S. Bailon, and J. P. Malfay. 2003. Un nouveau genre de Lacertidae (Reptilia, Lacertilia) dans les faluns miocènes de l'Anjou-Touraine (Maine-et-Loire, France). *Geodiversitas* 25:289–295.
- Bailon, S., R. Boistel, P. Bover, and J. A. Alcover. 2014. *Maiorialacerta rafelinensis*, gen. et sp. nov. (Squamata, Lacertidae), from the early Pliocene of Mallorca (Balearic Islands, western Mediterranean Sea). *Journal of Vertebrate Paleontology* 34:318–326.
- Barahona, F. 1996. Osteología craneal de lacértidos de la Península Ibérica e Islas Canarias: análisis sistemático filogenético. Ph.D. dissertation, Universidad Autónoma de Madrid, Madrid, Spain, 514 pp.
- Barahona, F., and L. J. Barbadillo. 1998. Inter- and intraspecific variation in the post-natal skull of some lacertid lizards. *Journal of Zoology* 245:393–405.
- Bochaton, C., R. Boistel, and L. Charles. 2015. X-ray microtomography provides first data about the feeding behaviour of an endangered lizard, the Montserrat galliwasp (*Diploglossus montiserrati*). *Royal Society Open Science* 2:150461.
- Böhme, M. 2008. Ectothermic vertebrates (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) from the upper Oligocene of Oberleichtersbach (Northern Bavaria, Germany). *Courier Forschungs-Institut Senckenberg* 260:161–183.
- Bolet, A., J.-C. Rage, and J. L. Conrad. 2017. Rediscovery of the long-lost holotype of the lacertid lizard *Pseudeumeces cadurcensis* (Filhol, 1877). *Journal of Vertebrate Paleontology* 37:e1315669. doi: 10.1080/02724634.2017.1315669.
- Borsuk-Białynicka, M., M. Lubka, and W. Böhme. 1999. A lizard from Baltic amber (Eocene) and the ancestry of the crown group lacertids. *Acta Palaeontologica Polonica* 44:349–382.
- Brunet, J., M. Hugué, and Y. Jehenne. 1981. Cournon-Les-Soumèroux: un nouveau site à vertébrés d'Auvergne; sa place parmi les faunes de l'Oligocène supérieur d'Europe. *Geobios* 14:323–359.
- Cabrera, L., M. Cabrera, R. Gorchs, and F. X. C. de las Heras. 2002. Lacustrine basin dynamics and organosulphur compound origin in a carbonate-rich lacustrine system (Late Oligocene Mequinenza Formation, SE Ebro Basin, NE Spain). *Sedimentary Geology* 148:289–317.
- Cano, J., M. Baez, L. F. López-Jurado, and G. Ortega. 1984. Karyotype and chromosome structure in the lizard, *Gallotia galloti* in the Canary Islands. *Journal of Herpetology* 18:344–349.
- Čerňanský, A. 2010. Earliest world record of green lizards (Lacertilia, Lacertidae) from the Lower Miocene of central Europe. *Biologia* 65:737–741.
- Čerňanský, A., and M. Augé. 2013. New species of the genus *Plesiolacerta* (Squamata: Lacertidae) from the upper Oligocene (MP 28) of southern Germany and a revision of the type species *Plesiolacerta lydekkeri*. *Palaeontology* 56:79–94.
- Čerňanský, A., and K. T. Smith. 2017. Eolacertidae: a new extinct clade of lizards from the Palaeogene; with comments on the origin of the dominant European reptile group—Lacertidae. *Historical Biology*. doi: 10.1080/08912963.2017.1327530.
- Čerňanský, A., J. Klembara, and K. T. Smith. 2016a. Fossil lizard from central Europe resolves the origin of large body size and herbivory in giant Canary Island lacertids. *Zoological Journal of the Linnean Society* 176:861–877.
- Čerňanský, A., J. Klembara, and J. Müller. 2016b. The new rare record of the late Oligocene lizards and amphisbaenians from Germany and its impact on our knowledge of the European terminal Palaeogene. *Palaeobiodiversity and Palaeoenvironments* 96:559–587.
- Čerňanský, A., J.-C. Rage, and J. Klembara. 2015. The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. *Journal of Systematic Palaeontology* 13:97–128.
- Čerňanský, A., K. T. Smith, and J. Klembara. 2014. Variation in the position of the jugal medial ridge among lizards (Reptilia: Squamata): its functional and taxonomic significance. *The Anatomical Record* 297:2262–2272.
- Charrier, M., A. Marie, D. Guillaume, L. Bédouet, J. Le Lannic, C. Roiland, S. Berland, J.-S. Pierre, M. Le Floch, Y. Frenot, and M. Lebouvier. 2013. Soil calcium availability influences shell ecophenotype formation in the sub-Antarctic land snail, *Notodiscus hookeri*. *PLoS ONE* 8:e84527.
- Châteauneuf, J. J. 1980a. Palynostratigraphie et paléoclimatologie de l'Éocène supérieur et de l'Oligocène du Bassin de Paris. *Mémoire du Bureau de recherches géologiques et minières* 116:357 pp.
- Châteauneuf, J. J. 1980b. Evolution de la flore et variations climatiques dans les bassins d'Europe occidentale au Paléogène. *Mémoires du Muséum national d'Histoire naturelle, Paris, B* 27:219–231.
- Christian, K. A., J. K. Webb, and T. J. Schultz. 2003. Energetics of blue-tongue lizards (*Tiliqua scincoides*) in a seasonal tropical environment. *Oecologia* 136:515–523.
- Dalrymple, G. H. 1979. On the jaw mechanism of the snail-crushing lizards, *Dracaena* Daudin 1802 (Reptilia, Lacertilia, Teiidae). *Journal of Herpetology* 13:303–311.
- De Smet, W. H., and E. A. van Rompu. 1984. Shell size and thickness in adult *Cepaeaneomoralis* (L.) (Gastropoda) from the Belgian dunes. *Biologisches Jahrbuch Dodonaea* 52:26–34.
- Digimorph.org. 2002–2012. Digital morphology: a National Science Foundation digital library at the University of Texas at Austin. The High Resolution X-ray Computed Tomography Facility at the University of Texas at Austin, Austin, Texas. Available at <http://www.digimorph.org/>. Accessed July 1, 2016.
- Dong, X., Z. Ding, S. Yang, P. Luo, X. Wang, and J. Ji. 2013. Synchronous drying and cooling in central Asia during late Oligocene. *Chinese Science Bulletin* 58:3119–3124.
- Duellman, W. E. 2005. *Cusco Amazonico: The Lives of Amphibians and Reptiles in an Amazonian Rainforest*. Cornell University Press, Ithaca, New York, 433 pp.
- Estes, R. 1983. Sauria terrestria, Amphisbaenia. *Handbuch der Paläoherpetologie, Part 10A*. Gustav Fischer Verlag, Stuttgart, Germany, 249 pp.
- Estes, R., and E. E. Williams. 1984. Ontogenetic variation in the molariform teeth of lizards. *Journal of Vertebrate Paleontology* 4:96–107.
- Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata; pp. 119–281 in R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford University Press, Stanford, California.

- Gervais, P. 1848–1852. Zoologie et Paléontologie françaises (Animaux vertébrés), 3 volumes. A. Bertrand, Paris, 271 pp.
- Giraud, J. 1902. Etudes Géologiques sur la Limagne (Auvergne). Ch. Béranger, Librairie polytechnique, Paris.
- Goodfriend, G. A. 1986. Variation in land-snail shell form and size and its cause: a review. *Systematic Zoology* 35:214–223.
- Gorin, G. 1974. Etude palynostratigraphique des sédiments paléogènes de la Grande Limagne (Massif Central) avec applications de la statistique et de l'informatique. Ph.D. dissertation, Faculté des Sciences, Université de Genève, Geneva, Switzerland, 314 pp.
- Haas, G. 1973. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata; pp. 285–490 in C. Gans and T. Parsons (eds.), *Biology of the Reptilia*, Volume 4. Academic Press, London.
- Hamer, J. M. M., N. D. Sheldon, G. J. Nichols, and M. E. Collinson. 2007. Late Oligocene–Early Miocene paleosols of distal fluvial systems, Ebro Basin, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 247:220–235.
- Hipsley, C. A., D. B. Miles, and J. Müller. 2014. Morphological disparity opposes latitudinal diversity gradient in lacertid lizards. *Biology Letters* 10:20140101.
- Hipsley, C. A., L. Himmelmann, D. Metzler, J. Müller. 2009. Integration of Bayesian molecular clock methods and fossil-based soft bounds reveals early Cenozoic colonization of African lacertid lizards. *BMC Evolutionary Biology* 9:151.
- Hoffstetter, R. 1944. Sur les Scincidae fossiles. I. Formes européennes et nord-américaines. *Bulletin du Muséum national d'Histoire naturelle*, Paris 16:547–553.
- Hugueney, M. 1969. Les rongeurs (Mammalia) de l'Oligocène supérieur de Coderet-Bransat (Allier). Ph.D. dissertation no. 596, Université de Lyon, Lyon, France, 227 pp.
- Hutchison, J. H. 1982. Turtle, crocodylian and champsosaur diversity changes in the Cenozoic of the north-central region of the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37:149–164.
- Khosravani, A., N. Rastegar-Pouyani, and H. Oraie. 2011. Comparative skull osteology of the lacertid lizards *Eremias persica* and *Mesalina watsonana* (Sauria: Lacertidae). *Iranian Journal of Animal Biosystematics* 7:99–117.
- Kiefer, M. C., and I. Sazima. 2002. Diet of juvenile *Tupinambis merianae* (Teiidae) in southeastern Brazil. *Amphibia-Reptilia* 23:105–108.
- Klemmer, K. 1957. Untersuchungen zur Osteologie und Taxonomie der europäischen Mauereidechsen. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft Frankfurt* 496:1–56.
- Lavocat, R. 1951. Révision de la Faune de Mammifères Oligocènes d'Auvergne et du Velay. *Sciences et Avenir*, Paris.
- Lawton, J. H. 2000. Concluding remarks: a review of some open questions; pp. 401–424 in M. Hutchings, E. John, and A. Stewart (eds.), *The Ecological Consequences of Environmental Heterogeneity*. 40th Symposium of the British Ecological Society. Blackwell Science, Oxford, U.K.
- Likens, G. E., C. T. Driscoll, and D. C. Buso. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* 272:244–246.
- Likens, G. E., C. T. Driscoll, D. C. Buso, T. G. Siccama, C. E. Johnson, G. M. Lovett, T. J. Fahey, W. A. Reiners, D. F. Ryan, C. W. Martin, and S. W. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. *Biogeochemistry* 41:89–173.
- Mayer, W., and G. Benyr. 1994. Albumin-evolution und phylogenese in der Familie Lacertidae (Reptilia: Sauria). *Annalen des Naturhistorischen Museums in Wien* 96B:621–648.
- Mercolli, C., and A. A. Yanosky. 1994. The diet of adult *Tupinambis teguixin* (Sauria, Teiidae) in the eastern chaco of Argentina. *Herpetological Journal* 4:15–19.
- Mertz, D. F., P. R. Renne, M. Wuttke, and C. Mödden. 2007. A numerically calibrated reference level (MP28) for the terrestrial mammal-based biozonation of the European Upper Oligocene. *International Journal of Earth Sciences* 96:353–361.
- Müller, J. 2004. Cranial osteology of *Dracaenosaurus crozeti*, a lacertid lizard from the Oligocene of France (Reptilia, Squamata). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 232:101–114.
- Müller, J., C. A. Hipsley, J. J. Head, N. Kardjilov, A. Hilger, M. Wuttke, and R. R. Reisz. 2011. Eocene lizard from Germany reveals amphisbaenian origins. *Nature* 473:364–367.
- Nydam, R. L., J. G. Eaton, and J. Sankey. 2007. New taxa of transversely-toothed lizards (Squamata: Scincomorpha) and new information on the evolutionary history of “teiids”. *Journal of Paleontology* 81:538–549.
- Ollivier-Pierre, M. F., C. Gruas-Cavagnetto, E. Roche, and M. Schuler. 1987. Eléments de flore de type tropical et variations climatiques au Paléogène dans quelques bassins d'Europe nord-occidentale. *Mémoires Travaux de l'E.P.H.E., Institut de Montpellier* 17:173–205.
- Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als prodrom einer naturgeschichte derselben. Joseph Lindauer Verlag, Munich, 85 pp.
- Peters, G. 1962. Die Zwergidechse (*Lacerta parva* Boulenger) und ihre Verwandtschaftsbeziehungen zu anderen Lacertiden, insbesondere zur Libanon-Eidechse (*L. fraasii* Lehrs). *Zoologische Jahrbücher der Systematik* 89:407–478.
- Pomel, A. 1846. Mémoire pour servir à la géologie paléontologique des terrains tertiaires du département de l'Allier. *Bulletin de la Société géologique de France* 3:353–373.
- Pomel, A. 1853. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire. J.B. Baillières, Paris.
- Prothero, D. R. 1994. The Eocene-Oligocene Transition. Columbia University Press, New York, 291 pp.
- Pujos, F., A. M. Albino, P. Baby, and J. L. Guyot. 2009. Presence of the extinct lizard *Paradracaena* (Teiidae) in the middle Miocene of the Peruvian Amazon. *Journal of Vertebrate Paleontology* 29:594–598.
- Rage, J.-C. 2013. Mesozoic and Cenozoic squamates of Europe. *Palaeobiodiversity and Palaeoenvironments* 93:517–534.
- Rage, J.-C., and M. L. Augé. 2010. Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. *Geobios* 43:253–268.
- Rage, J.-C., and Z. Szyndlar. 2005. Latest Oligocene–early Miocene in Europe: dark period for booid snakes. *Comptes Rendus Palevol* 4:428–435.
- Retallack, G. J. 1992. Paleosols and changes in climate and vegetation across the Eocene/Oligocene Boundary; pp. 382–398 in D. Prothero and W. Berggren (eds.), *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton University Press, Princeton, New Jersey.
- Retallack, G. J. 2004. Late Oligocene bunch grassland and early Miocene sod grassland paleosols from central Oregon, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207:203–237.
- Rey, R. 1974. Gastéropodes continentaux et hypohalins de l'Oligocène et du Miocène inférieur. *Revue scientifique du Bourbonnais* 1974:69–124.
- Rieppel, O., and L. Labhardt. 1979. Mandibular mechanisms in *Varanus niloticus*. *Herpetologica* 35:158–163.
- Roček, Z. 1984. Lizards (Reptilia: Sauria) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *Rozpravy Československé Akademie Věd, Rada Matematických a Přírodních Věd* 94:1–69.
- Sacchi, C. F. 1961. Considérations sur les phénomènes microévolutifs animaux des petites îles méditerranéennes. *Colloques internationaux du C.N.R.S.* 94:321–337.
- Sacchi, C. F., and P. Testard. 1971. *Ecologie Animale*. Doin, Paris, 480 pp.
- Savitzky, A. H. 1983. Coadapted character complexes among snakes: fossoriality, piscivory, and durophagy. *American Zoologist* 23:397–409.
- Schaerlaeken, V., V. Holanova, R. Boistel, P. Aerts, P. Velensky, I. Rehak, D. V. Andrade, and A. Herrel. 2012. Built to bite: feeding kinematics, bite forces, and head shape of a specialized durophagous lizard, *Dracaena guianensis* (Teiidae). *Journal of Experimental Zoology* 317A:371–381.
- Schmidt-Kittler, N. (ed.). 1987. *International Symposium on Mammalian Biostratigraphy and Paleogeology of the European Paleogene*, Mainz, February 18–21, 1987. *Münchener Geowissenschaftliche Abhandlungen A*, 10:1–312 pp.
- Shea, G. M. 2006. Diet of two species of bluetongue skink, *Tiliqua multifasciata* and *Tiliqua occipitalis* (Squamata: Scincidae). *Australian Zoologist* 33:359–368.
- Sullivan, R. M., and R. Estes. 1997. A reassessment of the fossil Tupinambinae; pp. 100–112 in R. F. Kay, R. H., Madden, R. L. Cifelli, and J. J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, D.C.

- Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*And Other Methods). Sinauer Associates, Sunderland, Massachusetts.
- Thaler, L. 1965. Une échelle de zones biochronologiques pour les Mammifères du Tertiaire d'Europe. *Compte Rendu sommaire des séances de la Société géologique de France* 4:118.
- Thaler, L. 1972. Datation, zonation et Mammifères. *Mémoire du Bureau de recherches géologiques et minières* 77:411–424.
- Uetz, P., J. Goll, and J. Hallermann. 2007. Die TIGR-Reptiliendatenbank. *Elaphe* 15:22–25.
- Van Valkenburgh, B. 1994. Extinction and replacement among predatory mammals in the North American late Eocene and Oligocene: tracking a paleoguild over twelve million years. *Historical Biology* 8:129–150.
- Vanzolini, P. E. 1961. Notas bionómicas sobre *Dracaena guianensis* no Para (Sauria, Teiidae). *Papéis Avulsos do Departamento de Zoologia da Secretaria de Agricultura de Sao Paulo* 14:237–241.
- Vanzolini, P. E., and J. Valencia. 1965. The genus *Dracaena*, with a brief consideration of macroteiid relationships (Sauria, Teiidae). *Archivos de Zoologia do Estado de Sao Paulo* 13:7–45.
- Vianey-Liaud, M. 1976. Les Issidoromyinae (Rodentia, Theridomyidae) de l'Eocène supérieur à l'Oligocène supérieur en Europe occidentale. *Palaeovertebrata* 7:1–115.
- Vianey-Liaud, M. 1991. Les rongeurs de l'Eocène terminal et de l'Oligocène d'Europe comme indicateurs de leur environnement. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85:15–28.
- Vidal, N., and S. B. Hedges. 2009. The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *Comptes Rendus Biologies* 332:129–139.
- Weathers, K. C., D. L. Strayer, and G. E. Likens. 2013. *Fundamentals of Ecosystem Science*. Academic Press, London, 312 pp.
- Wiens, J. J. 2001. Character analysis in morphological phylogenetics: problems and solutions. *Systematic Biology* 50:689–699.
- Wing, S. L. 1998. Tertiary vegetation of North America as a context for mammalian evolution; pp. 37–60 in C. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America. Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals, Volume 1*. Cambridge University Press, Cambridge, U.K.

Submitted March 22, 2017; revisions received July 11, 2017; accepted September 4, 2017.
Handling editor: Jason Head.