Zoological Journal of the Linnean Society, 2019, **XX**, 1–35. With 17 figures.

Palaeobiodiversity of crocodylomorphs from the Lourinhã Formation based on the tooth record: insights into the palaeoecology of the Late Jurassic of Portugal

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Received 7 March 2019; revised 19 August 2019; accepted for publication 28 August 2019

Crocodylomorphs were a diverse clade in the Late Jurassic of Portugal, with six taxa reported to date. Here we describe 126 isolated teeth recovered by screen-washing of sediments from Valmitão (Lourinhã, Portugal, late Kimmeridgian–Tithonian), a vertebrate microfossil assemblage in which at least five distinct crocodylomorph taxa are represented. Ten morphotypes are described and attributed to five clades (*Lusitanisuchus*, Atoposauridae, Goniopholididae, Bernissartiidae and an undetermined mesoeucrocodylian). Four different ecomorphotypes are here proposed according to ecological niches and feeding behaviours: these correspond to a diet based on arthropods and small vertebrates (*Lusitanisuchus* and Atoposauridae), a generalist diet (Goniopholididae), a durophagous diet (Bernissartiidae) and a carnivorous diet. *Lusitanisuchus mitracostatus* material from Guimarota is here redescribed to achieve a better illustration and comparison with the new material.

This assemblage shares similar ecomorphotypes with other Mesozoic west-central European localities, where a diversity of crocodylomorphs lived together, avoiding direct ecological competition through niche partitioning. The absence of large marine crocodylomorphs, present in other contemporaneous assemblages, is here interpreted as evidence that the Valmitão assemblage was deposited in a freshwater environment, although sample bias cannot be completely ruled out. These affinities are further supported by the presence of lanceolate and leaf-shaped teeth associated with continental clades.

ADDITIONAL KEYWORDS: Atoposauridae – Bernissartiidae – Goniopholididae – Kimmeridgian–Tithonian – vertebrate microfossil assemblage.

INTRODUCTION

Isolated crocodylomorph teeth are among the most common elements in Mesozoic vertebrate microfossil assemblages (Thies & Broschinski, 2001; Schwarz-Wings *et al.*, 2009; Lauprasert *et al.*, 2011; Gasca *et al.*, 2012; Ullmann *et al.*, 2012; Kuzmin *et al.*, 2013; Oreska *et al.*, 2013; Vullo *et al.*, 2014; Puértolas-Pascual, Rabal-Garcés & Canudo, 2015b; Carrano *et al.*, 2016; Marmi *et al.*, 2016; Puértolas-Pascual *et al.*, 2016; Blanco *et al.*, 2018, 2019). Although crocodylomorph tooth morphology is strongly correlated with feeding habits and shows a high level of homoplasy, isolated teeth are usually considered elements of low taxonomic and phylogenetic value, being difficult to classify at a generic or specific level (Prasad & de Lapparent de Broin, 2002; Buscalioni *et al.*, 2008; Wings *et al.*, 2010; Puértolas-Pascual *et al.*, 2015b; Young *et al.*, 2016). Nevertheless, studies have identified similar crocodylomorph faunal assemblages across Mesozoic European communities, ranging from the Jurassic to the Late Cretaceous. These comprise mainly durophagous feeders, cursorial hunters, insect feeders and generalist forms, exemplified by taxa such as *Bernissartia*, *Theriosuchus* and *Goniopholis*, in association with other taxa that vary according to the locality (Schwarz-Wings *et al.*, 2009).

The Upper Jurassic of Portugal yields abundant vertebrate remains, notably vertebrate microfossils as illustrated by the Guimarota Mine assemblage (Martin & Krebs, 2000). One of the more diverse clades is the

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*Corresponding author. E-mail: alexandre.guillaume.763@gmail.com archosaurs, with more than 30 species of dinosaurs described to date (Rauhut, 2000; Antunes & Mateus, 2003; Mateus *et al.*, 2009; Escaso *et al.*, 2014; Hendrickx & Mateus, 2014; Tschopp *et al.*, 2015; Malafaia *et al.*, 2018; Mocho *et al.*, 2019). Other archosaurs are less well-studied and, to date, only six crocodylomorph taxa have been described from the Late Jurassic of Portugal, mainly from the Guimarota Mine, located near the town of Leiria (Krebs & Schwarz, 2000).

Krebs (1967, 1968) reported the marine teleosaurid *Machimosaurus hugii* von Meyer, 1837 in Guimarota, and further isolated teeth have been recovered in the Lourinhã Formation (Young *et al.*, 2014). Buscalioni *et al.* (1996) redescribed *Lisboasaurus estesi* Seiffert, 1973 as a crocodylomorph. Isolated molariform teeth have been attributed to *Bernissartia* sp. (Brinkmann, 1989). Krebs & Schwarz (2000) reported material assigned to goniopholidids, later described as *Goniopholis baryglyphaeus* Schwarz, 2002, as well as material attributed to the atoposaurid *Knoetschkesuchus guimarotae* (Schwarz & Salisbury, 2005) Schwarz *et al.*, 2017 and material attributed to *Lusitanisuchus mitracostatus* (Seiffert, 1973) Schwarz & Fechner, 2004. Despite a lack of detailed study, it is evident that crocodylomorphs were an important component of the Late Jurassic ecosystems of Portugal, occupying specific ecological niches and with different diets, as can be assessed on the basis of differences in their dental morphology (Schwarz *et al.*, 2017).

Here we report a study of a sample of 126 crocodylomorph teeth from the Valmitão vertebrate microfossil assemblage (Valmitão vma). Despite the relatively low productivity of the Lourinhã Formation compared with that of the Guimarota Mine, findings from this formation have provided important insights into crocodylomorph diversity. For example, the taxonomy of *Lusitanisuchus mitracostatus* and *Lisboasaurus estesi* was for a long time problematic. Both species were originally referred to the same genus, *Lisboasaurus* and described as anguimorph lacertilians (Seiffert, 1973), later reinterpreted as maniraptoran theropods (Milner & Evans, 1991) and then as mesoeucrocodylian crocodylomorphs (Buscalioni *et al.*, 1996). New, isolated teeth from the Lourinhã Formation, at Porto Dinheiro, allowed the material from the Guimarota Mine referred to *Lisboasaurus mitracostatus* to be attributed to the new genus *Lusitanisuchus* (Schwarz & Fechner, 2004). However, due to the lack of good-quality illustrations in the literature, specimens attributed to *Lusitanisuchus* and housed in the Museu Geológico de Lisboa are here studied, figured and redescribed. Material attributed to *Lisboasaurus estesi* was not found in the collection in the Museu Geológico de Lisboa.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Valmitão vertebrate microfossil assemblage (vma), found at the top of a cliff above Valmitão Beach, near the town of Ribamar in the municipality of Lourinhã, is located within the Lourinhã Formation in the Lusitanian Basin, the largest sedimentary basin in Portugal (Wilson *et al.*, 1989; Alves *et al.*, 2003). The Lusitanian Basin was formed during the opening of the north Atlantic Ocean, and was filled during four rifting episodes and one major seafloor-spreading episode, from the Late Triassic to the Early Cretaceous (Martinius & Gowland, 2011; Taylor *et al.*, 2014; Gowland *et al.*, 2017; Mateus *et al.*, 2017).

The Lourinhã Formation (Fig. 1) consists of a clastic continental succession of sedimentary deposits throughout the Lusitanian Basin, ranging in thickness from 200 m to 1100 m (Leinfelder & Wilson, 1989; Wilson *et al.*, 1989; Taylor *et al.*, 2014). This variation in thickness according the palaeogeographic position can be explained by the transitional/regressive boundaries between the members of the Lourinhã Formation (Mateus *et al.*, 2017). This formation has usually been considered to be Late Jurassic in age, and recent studies confirm an age ranging from Late Kimmeridgian to Late Tithonian, lying between the Consolação unit and the Porto da Calada Formation (Taylor *et al.*, 2014; Mateus *et al.*, 2017). The base of the laterally extensive Lourinhã Formation is traditionally considered to represent the first significant and sustained development of continental deposits, above either the shallow marine to estuarine sandstones of the Sobral Formation, the oolitic limestones of the Amaral Formation, the shelf-carbonates of the Consolação unit/Alcobaça Formation or the shelf to deep-water clastic deposits of the Abadia Formation (Taylor *et al.*, 2014). The dominant continental deposits of the Lourinhã Formation are sandy channel fills and contemporaneous muddy floodplain deposits (Martinius & Gowland, 2011; Taylor *et al.*, 2014; Gowland *et al.*, 2017). The sedimentology of the Lourinhã Formation suggests a semi-arid climate, with a mean temperature range from 16 °C to 19 °C and seasonal rainfall lower than 500 mm. It was, thus, more humid than the contemporary Morrison Formation of North America (Mateus *et al.*, 2017).

The Valmitão vma is located in the upper half of the Porto Novo/Praia da Amoreira unit of the Lourinhã Formation, comprising an alternation of metric levels of cross-bedded sandstones and bioturbated mudstones with palaeosols (Fig. 1D). These have been interpreted as fluvial channel sands and calcrete-bearing floodplain muds, deposited within a meandering system where crevasse splays are rare (Taylor *et al.*, 2014). The microfossils are distributed within a 3-m thick mudstone layer with occasional intercalations

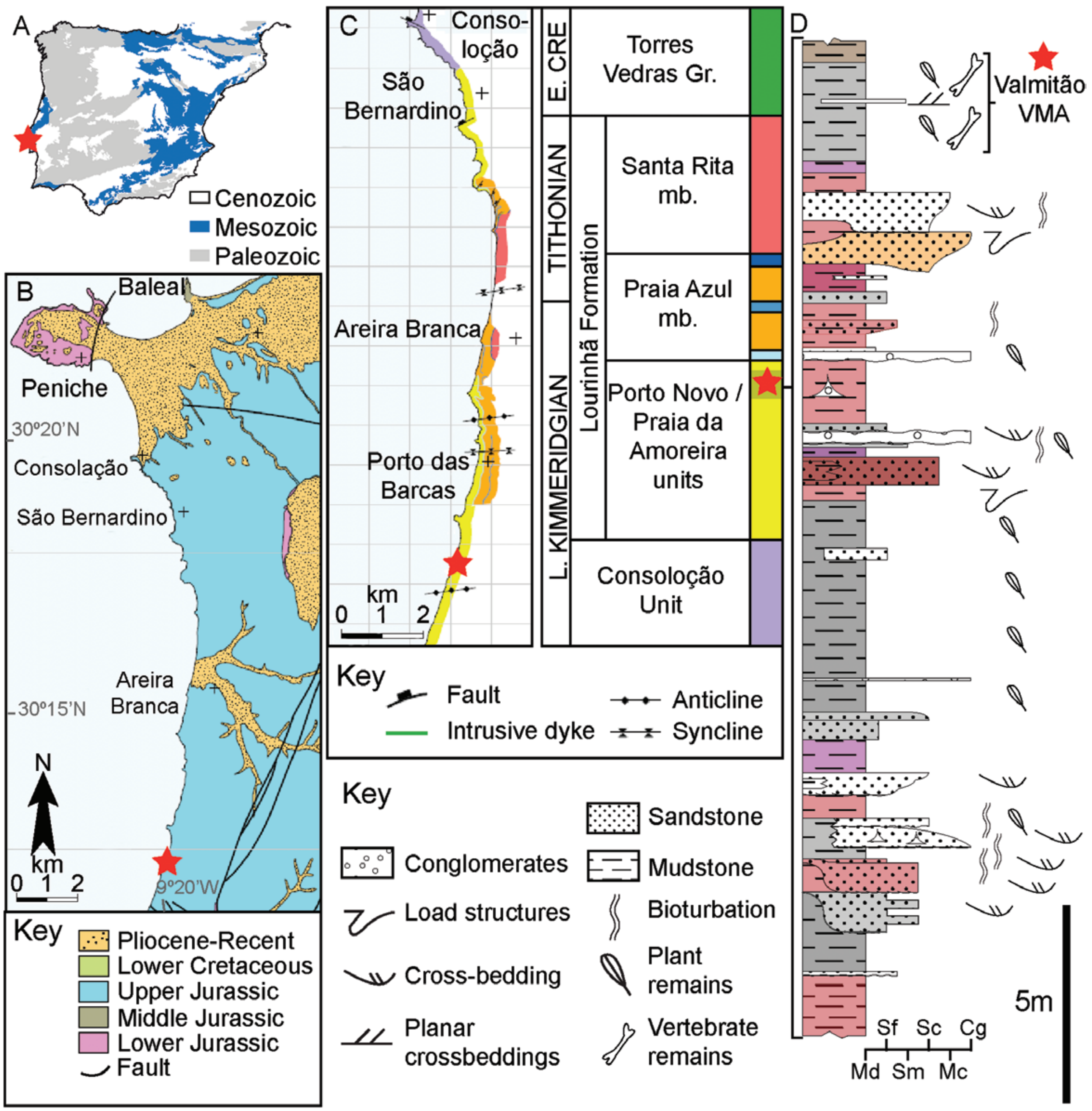

Figure 1. Geological and geographical context of the Valmitão vertebrate microfossil assemblage. A, geological sketch of the Iberian Peninsula, showing the location of the study area. B, map of the onshore part of the Consolação subbasin south of Peniche (modified from Taylor *et al.*, 2014). C, north–south mapping of the main units in the area of study and their corresponding lithostratigraphic framework (modified from Taylor *et al.*, 2014, based on Mateus *et al.*, 2017). D, stratigraphic log of the upper part of the Porto Nova/Praia da Amoreira Member at Valmitão Beach. The red star indicates the location of the Valmitão vma.

of centimetric sandstones. Darker greyish mudstones rich in organic matter, such as those observed in the Valmitão vma, have been interpreted as lacustrine muds (Gowland *et al.*, 2017) probably deposited in an oxbow lake, with a slow rate of sedimentation.

PRELIMINARY OVERVIEW OF THE PALAEONTOLOGICAL ASSEMBLAGE OF THE VALMITÃO VMA

As part of the larger systematic sampling of the microfauna from the Lourinhã Formation, other vertebrates from the Valmitão vma were collected and studied. In total, 427 vertebrate remains from Valmitão were recovered, among which were 159 teeth from crocodylomorphs, ray-finned fishes, dinosaurs, pterosaurs and undetermined vertebrates, and 210 identified vertebrate remains, including ray-finned fish scales, tetrapod vertebral arches, albanerpetontid vertebrae, dentaries, maxillae and frontal, a putative caudatan vertebra and fragmentary remains from lepidosaurs, an archosaur and an undetermined tetrapod (Supporting Information, Data S1). The preliminary palaeoecological analyses suggest that Valmitão was dominated by a terrestrial fauna (Guillaume *et al.*, 2018). As well as the vertebrate remains, gastropods were found in the sample along with fragmented bivalve shells, the latter possibly suggesting a low marine influence in a continental environment.

MATERIAL AND METHODS

This study is based on a 50-kg sample of sediments collected in Valmitão during a field campaign in June 2016. These were dried for three months, then disaggregated in water with hydrogen peroxide (H_2O_2, final solution at 0.5%). The sediments were screen-washed, using a sieving table comprising three levels of mesh (2 mm, 1 mm and 0.5 mm). The study focuses on 126 isolated crocodylomorph teeth (Table 1) recovered from these fractions. These were divided into morphotypes according to their morphologies, on the basis of their overall shape, cross-section shape and the ornamentation of the enamel and the distal and mesial margins. Since morphological continuity is expected in a heterodont crocodylomorph, because the tooth morphologies are related to their position in the tooth arcade, the tooth count presented in this study includes a degree of uncertainty concerning morphologically close morphotypes.

A subsample of 32 isolated teeth, chosen on the basis of their relatively good preservation and representing the range of morphotype diversity, was used for the measurements and illustration of the different morphologies (Supporting Information, Data S2). The teeth were photographed with a Leica M165C stereomicroscope equipped with a Leica DFC295 camera and using Leica Application Suite software v.4.10.0, developed by Leica Microsystems CMS GmbH.

The tooth measurements were made using ImageJ (Rasband, 2003). Selected teeth were coated in gold and photographed using a JEOL 6400 scanning electron microscope housed at the Universidad de Zaragoza, Spain. Selected measurements include: height (H), the length of the longitudinal axis from the base of the crown to the apex; width (W), measured at the largest width of the crown, from the mesial to the distal margins; labiolingual width (Lb), the distance between the labial and mesial surfaces at the base of the crown in basal view; mesiodistal width (Mb), the distance between the distal and mesial margins at the base of the crown in basal view. The angle of the apex is the angle formed by the longitudinal axis in mesial/distal view. The angle of the axis is the longitudinal axis angle in lingual view.

A direct examination of the specimens of *Lusitanisuchus* housed at the Museu Geológico de Lisboa was undertaken. Specimens, including teeth, were photographed using a Dinolite digital microscope and are here figured, described and compared with the material collected in Valmitão.

In the present work, we follow the traditional phylogenetic framework that includes *Theriosuchus* and *Knoetschkesuchus* as members of the clade Atoposauridae. This topology has been challenged by Tennant *et al.* (2016), who removed *Theriosuchus* from Atoposauridae, whereas both genera were included in this clade for their descriptions by Schwarz *et al.* (2017). For the present work, an open and conservative

Table 1. Tooth counts for the crocodylomorph assemblage from Valmitão

Clades	Ecomorphotype	Morphotype	Number of teeth	Percentage	Number of teeth	Percentage
Lusitanisuchus	Ecomorphotype A	Morphotype 1	1	0.79	51	40.48
Atoposauridae		Morphotype 2	14	11.11		
		Morphotype 3	11	8.73		
		Morphotype 4	10	7.94		
		Morphotype 5	15	11.90		
Goniopholididae	Ecomorphotype B	Morphotype 6	33	26.19	51	40.48
		Morphotype 7	18	14.29		
Bernissartiidae	Ecomorphotype C	Morphotype 8	1	0.79	19	15.08
		Morphotype 9	18	14.29		
Mesoeucrocodylia	Ecomorphotype D	Morphotype 10	5	3.97	5	3.97
Total			126	100.00	126	100

nomenclature is favoured for the taxonomic identification of each morphotype.

As the Valmitão vma was not part of the stratigraphic study of Gowland *et al.* (2017), a stratigraphic log of the upper layers of this locality was produced by the authors (Fig. 1D) to situate the assemblage geologically and shed light on its palaeoenvironment.

Institutional abbreviations

FCT-UNL, Faculdade de Ciências e Tecnologia – Universidade Nova de Lisboa; IPFUB, Institut für Paläontologie der Freien Universität Berlin; ML, Museu da Lourinhã; MG, Museu Geológico de Lisboa

Description of tooth morphotypes

Crocodylomorpha Hay, 1930 (*sensu* Clark, 1986)

Mesoeucrocodylia Whetstone & Whybrow, 1983 (*sensu* Benton & Clark, 1988)

Family *incertae sedis*

Lusitanisuchus mitracostatus (Seiffert, 1970)

(Fig. 2A)

Referred material: ML2586, one isolated spatulate tooth.

Locality, horizon and age: Valmitão vertebrate microfossil assemblage; Lourinhã Formation, Porto Novo/Praia da Amoreira unit, late Kimmeridgian (Upper Jurassic).

Description

Morphotype 1, spatulate : The [TS - for some reason parts of D-headings, which I made italic, have reverted to non-italic - I have changed them back but in case they revert again, follow journal style - thay are correctly tagged]tooth is spatulate, with an apiculate (tapering and ending in a short, slender point), sharp apex, similar to a human incisor. The edge of the apex exhibits wear facets and a small denticle pointing outwards from the centre. The crown has a faint constriction at the base. It is 0.73 mm high and 0.83 mm wide, resulting in a height/width (H/W) ratio of 0.88. Its cross-section is labiolingually compressed, with a labiolingual/mesiodistal (Lb/Mb) ratio of 0.5, producing a stadium-shaped base of the crown. Both labial and lingual surfaces are planar, and both mesial and distal margins bear a carina without denticles. The enamel on both lingual and labial surfaces is covered by ridges forming basiapical striations, extending toward the apex. There are ten striations on the labial surface, although part of the enamel is not preserved, and 14 on the lingual surface. The central striations converge toward the small denticle of the apex, whereas the lateralmost striations have a flabelliform (fan-shaped) distribution, extending toward the margins and the edge of the apex.

Remarks: This tooth morphology differs from all other morphotypes observed in the sample, which is why, even though it includes only one tooth so far, morphotype 1 can be considered a morphotype in its own. The tooth is not conical, which excludes it from other, conical morphotypes observed in homodont and heterodont taxa. Morphotype 1 differs as well from morphotype 4 and the molariform teeth typical of Bernissartiidae, by having a sharp apex with denticles and different enamel ornamentation (Buffetaut & Ford, 1979; Schwarz & Fechner, 2004). Not being multicuspid, the tooth differs from other spatulate teeth observed in *Simosuchus* and *Uruguaysuchus* (Buckley *et al.*, 2000), and it differs from those observed in *Acynodon* by being less broad and more labiolingually compressed (Buscalioni *et al.*, 1997; Martin, 2007; Delfino *et al.*, 2008; Blanco *et al.*, 2019). The tooth shares the flabelliform enamel ornamentation observed in atoposaurids (Brinkmann, 1992; Schwarz-Wings *et al.*, 2009; Salisbury & Naish, 2011; Tennant *et al.*, 2016; Young *et al.*, 2016; Schwarz *et al.*, 2017), but differs from these by being spatulate instead of lanceolate to leaf-shaped and by having a truncate, sharp apex with denticles. The tooth has the same spatulate morphology, enamel ornamentation and the typical tip of the apex observed in *Lusitanisuchus mitracostatus* (Seiffert, 1973; Schwarz & Fechner, 2004), particularly in the posterior part of the dentary of the specimens from Guimarota redescribed below, which allows morphotype 1 to be attributed with confidence to this species.

Neosuchia Benton & Clark, 1988

Atoposauridae? Gervais, 1871

Atoposauridae indet.

(Figs 2B, C, 3–5)

Referred material: ML2511 to ML2521, 11 isolated conical teeth with parallel striations; ML2497 to ML2510, 14 isolated conical teeth with flabelliform striations; ML2522 to ML2546, ten isolated lanceolate teeth and 15 leaf-shaped teeth.

Description

Morphotype 2, conical with parallel striations (Fig. 2B, C): The teeth are conical to sublanceolate, with

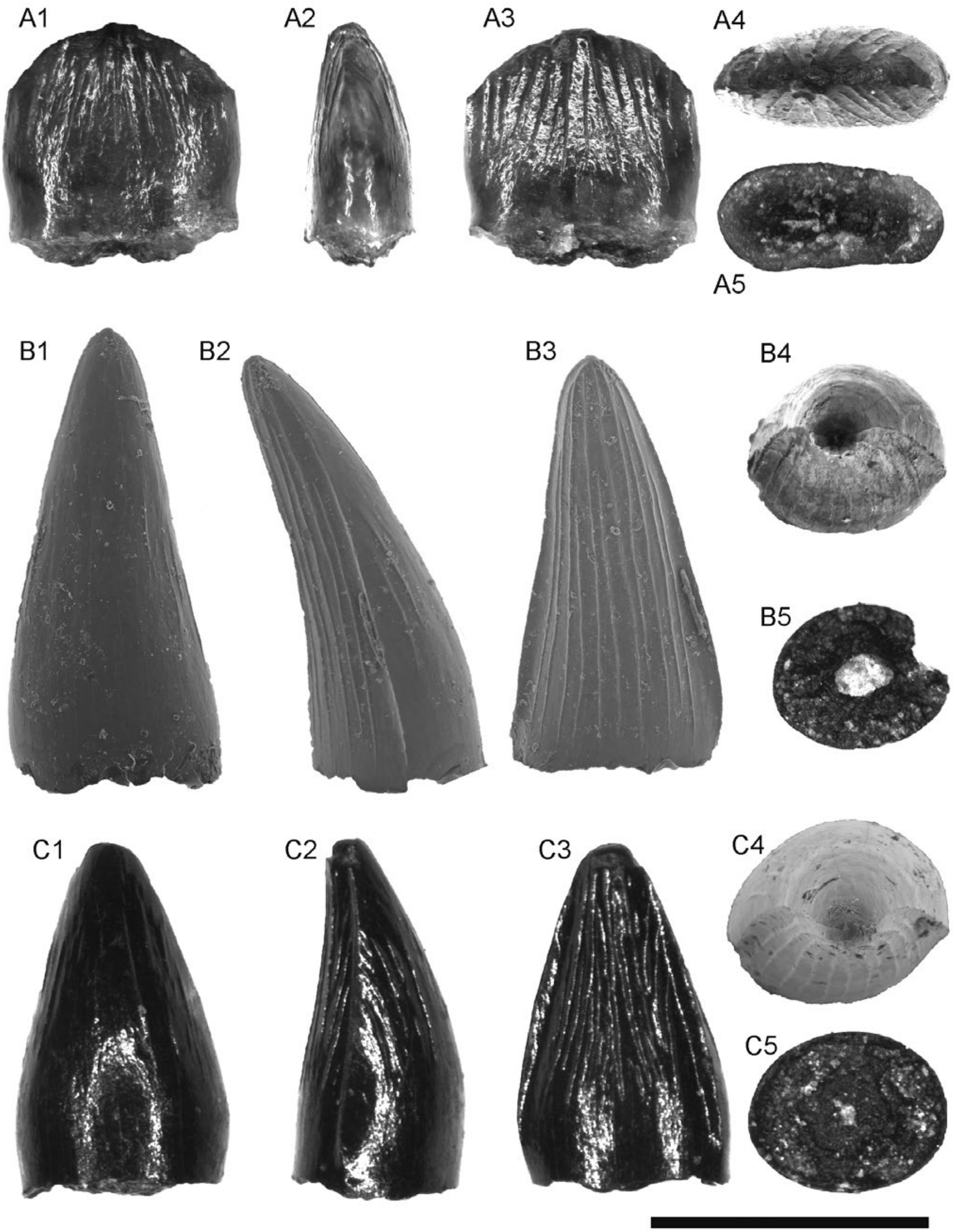

Figure 2. Morphotype 1 (A) and 2 (B and C) teeth; ML2586 (A), ML2497 (B) and ML2498 (C) in labial (1), lateral (2), lingual (3), apical (4) and basal (5) views. Scale bar is 1mm. All images are normal-light photomicrographs except for A1–A3 and B4, which are SEM photomicrographs.

lingually curved, acute apices (16° to 20°). Their height ranges from 1.22 mm to 1.35 mm and their width from 0.67 mm to 0.77 mm, with an H/W ratio that ranges from 1.58 to 2.02. Their cross-sections are labiolingually compressed with an Lb/Mb ratio of 0.80 to 0.81, resulting in a subcircular base of the crown. Both distal and mesial margins exhibit a carina without denticles. The labial surface is convex in lateral view, the lingual surface less so. In some teeth, the enamel on the labial surface is smooth, whereas it is covered by ten ridges in others, forming parallel basiapical striae. On the lingual surface, the enamel is covered by 11 to 14 parallel basiapical ridges.

Remarks: Conical teeth with parallel basiapical striations on the enamel of the lingual surface, and smooth or ornamented enamel on the labial surface, differ from goniopholidid-like conical teeth, which have basiapical striations on both lingual and labial surfaces, or are smooth on both surfaces. In addition, teeth belonging to Goniopholididae present more conical morphologies and a weak to almost absent constriction at the base of the crown. In contrast, the conical or pseudocaniniform teeth assigned to an atoposaurid-like morphotype are slightly more flattened labiolingually and have a stronger constriction at the base of the crown that gives them a more lanceolate appearance. This morphotype has been described in pseudocaniniform teeth from the premaxilla, and the anteriormost maxilla and dentary, in *Knoetschkesuchus*, *Theriosuchus* and *Sabresuchus* (Schwarz & Salisbury, 2005; Tennant *et al.*, 2016; Schwarz *et al.*, 2017).

Morphotype 3, conical with flabelliform striations (Fig. 3): The teeth are conical to sublanceolate, with a sharp, lingually curved apex (29° to 43°). The smallest teeth are more strongly curved, making them almost hook-shaped (Fig. 3 A2, C2). Their height ranges from 1.49 mm to 1.95 mm and their width from 0.76 mm to 0.95 mm, with an H/W ratio from 1.94 to 2.46. Their cross-sections are labiolingually compressed with an Lb/Mb ratio from 0.41 to 0.82, resulting in a subcircular to elliptical base of the crown. Both distal and mesial margins exhibit a carina lacking denticles. The enamel is smoother on the labial surface, whereas it exhibits twelve to thirteen ridges forming striations on the lingual surface. These striations are flabelliform: the centremost striations are basiapically directed, whereas the lateral striations extend from the base of the crown and diverge to the carinae.

Remarks: Conical teeth with flabelliform basiapical striations on the enamel of the lingual surface and smoother enamel on the labial face, differ from goniopholidid conical teeth, which have parallel basiapical striations on both labial and lingual surfaces. This ornamentation pattern is characteristic of atoposaurids and has been described in teeth from the anterior regions of the dentition in *Theriosuchus*, *Sabresuchus* and *Knoetschkesuchus* (e.g. Brinkmann, 1992; Schwarz-Wings *et al.*, 2009; Salisbury & Naish, 2011; Tennant *et al.*, 2016; Young *et al.*, 2016; Schwarz *et al.*, 2017).

Morphotype 4, lanceolate (Fig. 4): These teeth are lanceolate, with a pointed apex and a weak mesiodistal constriction at the base of the crown. Their height ranges from 1.04 mm to 2.58 mm and their width from 0.76 mm to 1.68 mm, with an H/W ratio from 1.36 to 1.53. Their cross-sections are labiolingually compressed, with an Lb/Mb ratio from 0.65 to 0.74, resulting in an elliptical base of the crown. Mesial and distal carinae are present. The labial surface is more convex than the lingual in lateral view. The enamel on the labial surface is smooth at the base and in the centre of the crown, but exhibits parallel, longitudinal ridges, forming basiapical striations extending towards the distal and mesial margins of the carinae apically. On the lingual surface, the ridges cover almost all the upper part, leaving only the base and a small portion of the centre smooth. The ornamentation consists of striations with a flabelliform distribution. The centremost ridges form striations extending up to the apex, whereas the lateralmost striations extend to the mesial and distal carinae. In some cases, these ridges may give the appearance of denticles on the carinae, which they are not (false-ziphodont dentition; Fig. 4A6).

Morphotype 5, leaf-shaped (Fig. 5): These teeth are mesiodistally broad and leaf-shaped, with an almost horizontal blunt apex and a weak mesiodistal constriction at the base of the crown. Their height ranges from 1.16 mm to 1.49 mm, with a width from 1.04 mm to 1.47 mm and an H/W ratio from 0.89 to 1.11. Their cross-sections are strongly labiolingually compressed with an Lb/Mb ratio from 0.53 to 0.63, resulting in an elliptical crown base. A faint carina is present on both mesial and distal margins, adjacent to a faint basiapical lingual groove. The labial surface is strongly convex in the lower part, whereas the lingual surface is less so. The enamel is covered by more than 15 ridges on both labial and lingual surfaces, forming vertical striations extending over the upper two-thirds of the crown. On the labial surface, the striae are basiapical, whereas their distribution on the lingual surface gives the enamel a flabelliform ornamentation. In some cases, the contact of the ridges or striae with the carinae may form false-ziphodont serrations.

Remarks: Teeth attributed to atoposaurids show the largest morphological variability observed in the sample, with three clearly different morphologies: conical, lanceolate, and broad leaf-shaped (Schwarz & Salisbury, 2005; Schwarz-Wings *et al.*, 2009; Lauprasert *et al.*, 2011; Puértolas-Pascual *et al.*, 2015b; Schwarz *et al.*, 2017). As has already been noted, this dental variability is related to the position in the dental arcade (Schwarz-Wings *et al.*, 2009; Tennant *et al.*, 2016). Among crocodylomorphs, the striation patterns observed in these teeth are typical of atoposaurids such

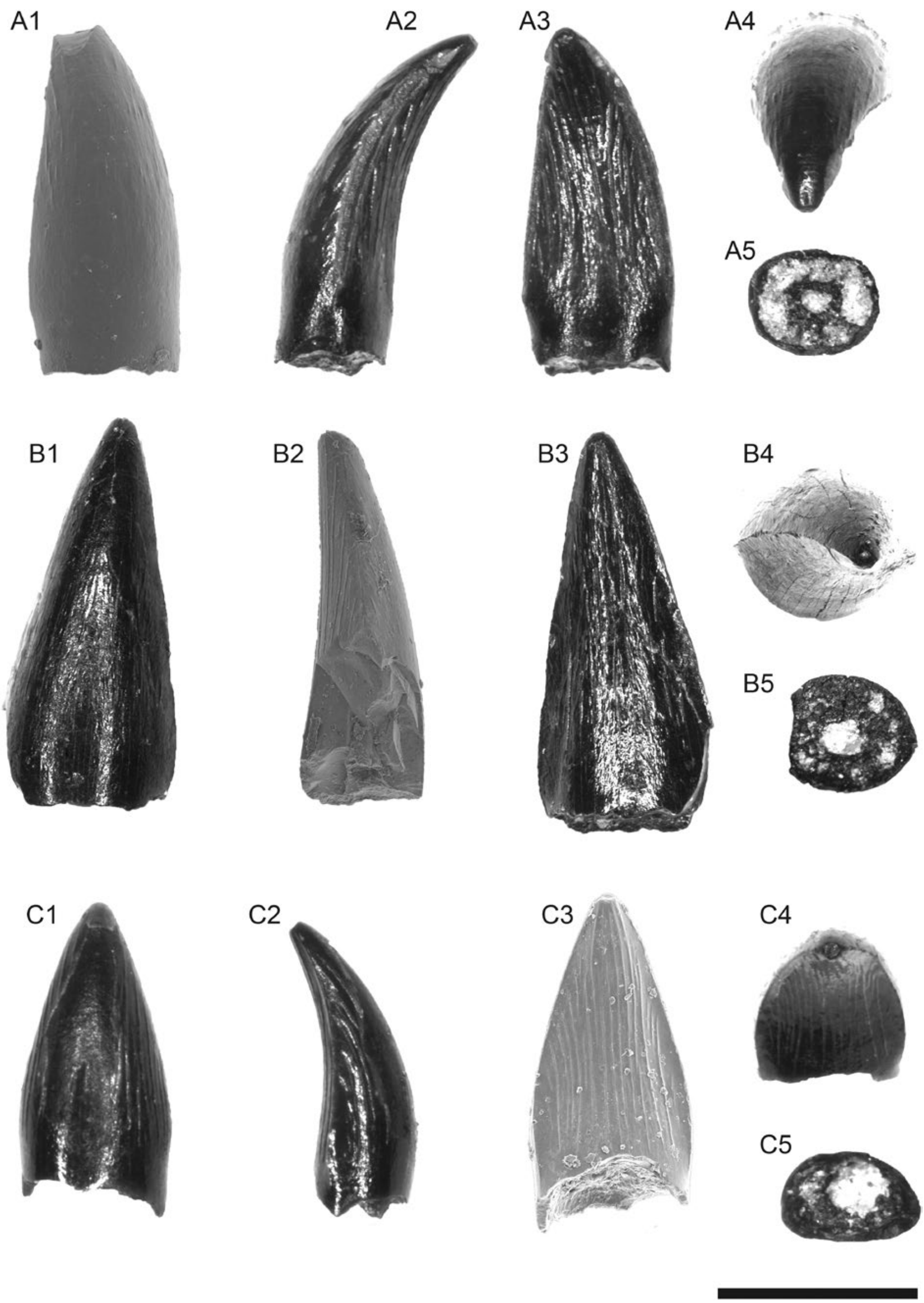

Figure 3. Morphotype 3 teeth ML2508 (A), ML2509 (B) and ML2510 (C) in labial (1), lateral (2), lingual (3), apical (4) and basal (5) views. Scale bar is 1 mm. All images are normal-light photomicrographs except for A1, B2 and C3, which are SEM photomicrographs.

as *Theriosuchus*, *Sabresuchus* and *Knoetschkesuchus*, and allow them to be assigned to Atoposauridae (Schwarz *et al.*, 2017). The degree of development of the striae may be related to ontogeny, as they are more strongly developed in larger teeth than in smaller ones (Schwarz-Wings *et al.*, 2009). In some specimens the

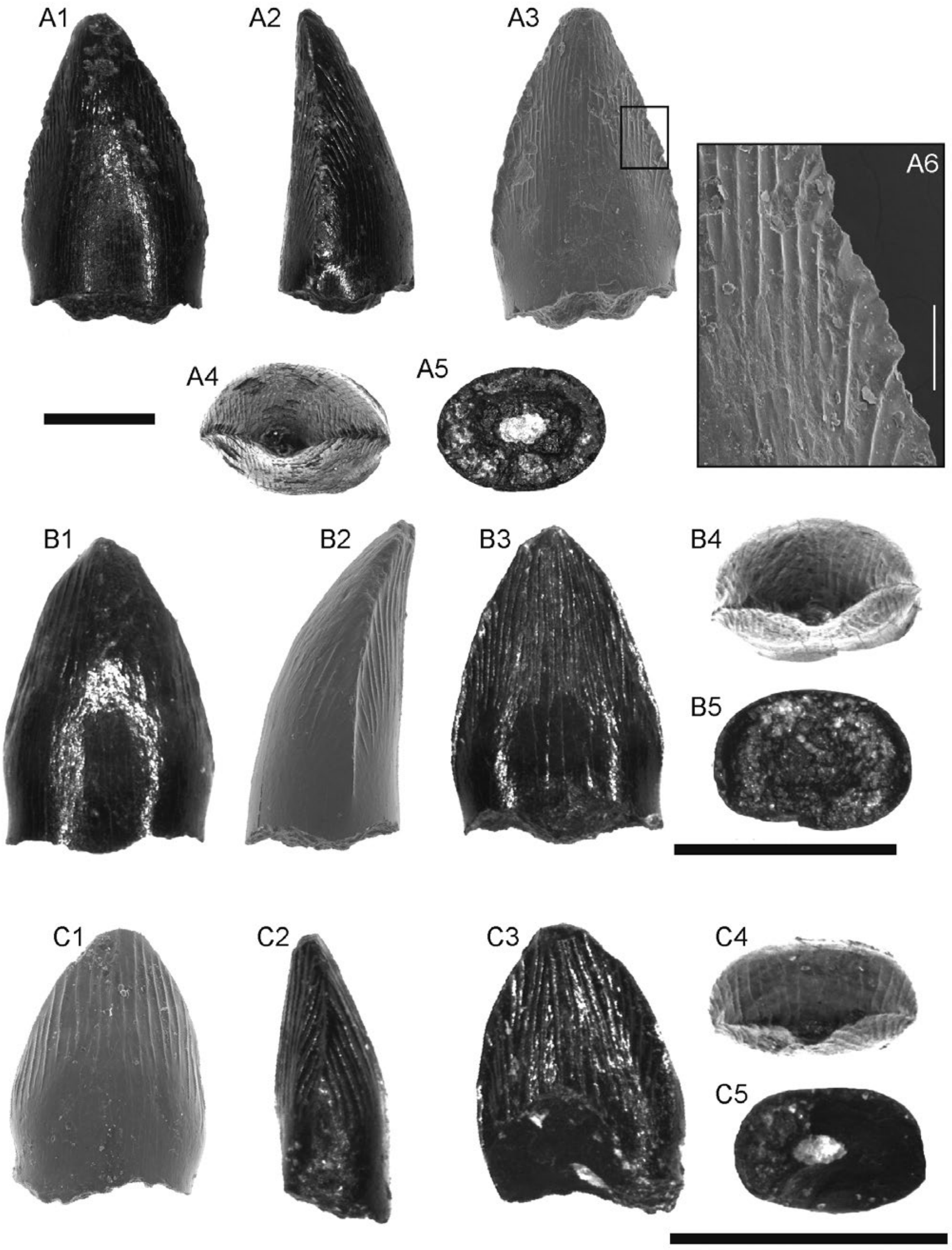

Figure 4. Morphotype 4 teeth ML2522 (A), ML2523 (B) and ML2524 (C) in labial (1), lateral (2), lingual (3), apical (4) and basal (5) views. Scale bars are 1 mm. Close-up of the false denticles seen in ML2522 (A6). Scale bar is 200 µm. All images are normal-light photomicrographs except for A3, A6, B2 and C1, which are SEM photomicrographs.

ridges may form small, false denticles on the carinae (Schwarz-Wings *et al.*, 2009; Puértolas-Pascual *et al.*, 2015b). Within the above-mentioned genera, the presence of pseudoziphodont teeth is exclusive to *Theriosuchus* and *Sabresuchus* (Lauprasert *et al.*, 2011; Tennant *et al.*, 2016). In contrast, the carinae

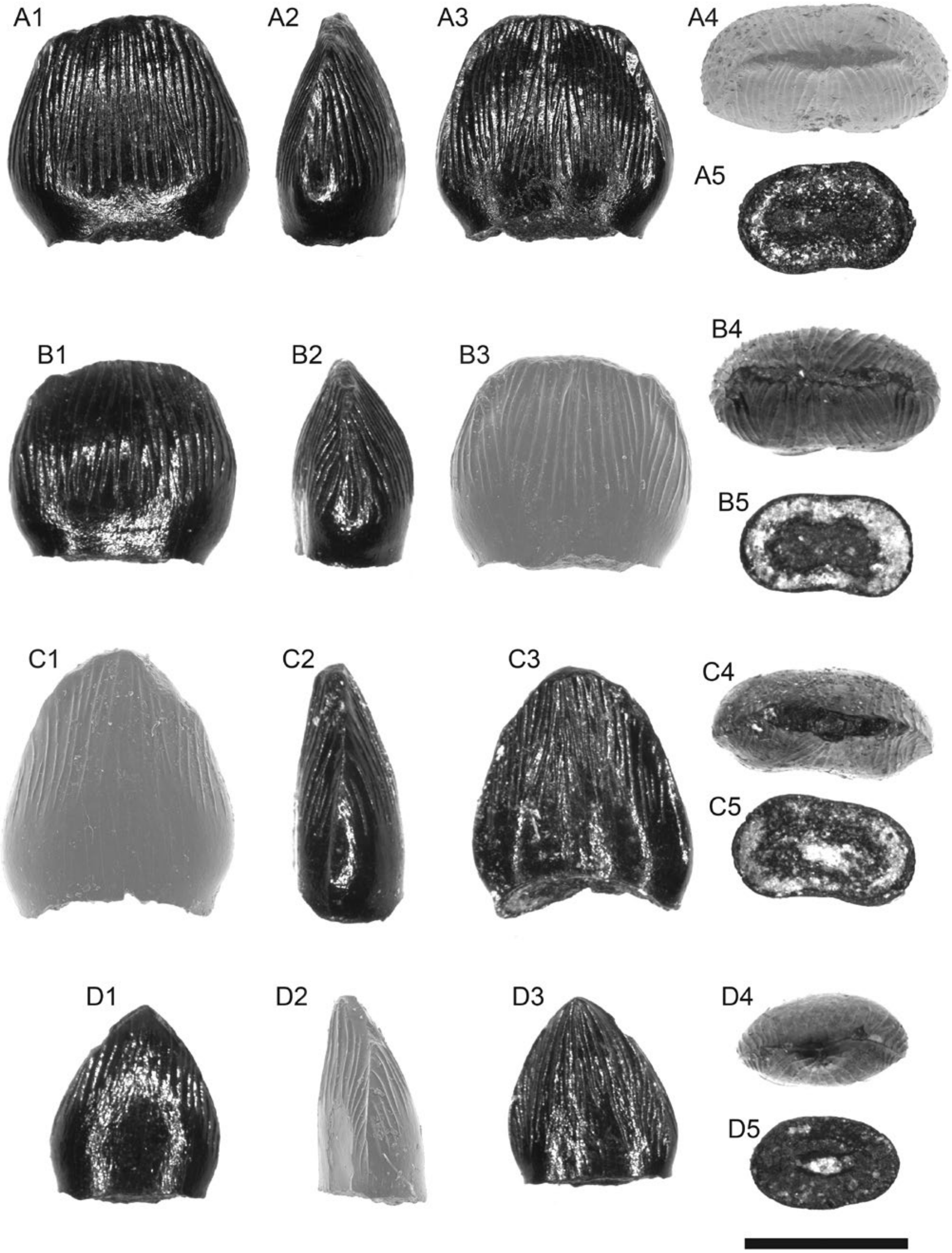

Figure 5. Morphotype 5 teeth ML2532 (A), ML2533 (B), ML2534 (C) and ML2535 (D) in labial (1), lateral (2), lingual (3), apical (4) and basal (5) views. Scale bar is 1 mm. All images are normal-light photomicrographs except for A4, B3, C1 and D2, which are SEM photomicrographs.

of *Knoetschkesuchus* are totally smooth (Schwarz & Salisbury, 2005; Schwarz *et al.*, 2017). In addition, dentition combining conical, lanceolate and leaf-shaped teeth has previously been attributed to *Sabresuchus* and *Theriosuchus* in other crocodylomorph faunal assemblages (Schwarz-Wings *et al.*, 2009; Lauprasert *et al.*, 2011; Salisbury & Naish, 2011; Gasca *et al.*, 2012; Martin *et al.*, 2014b; Puértolas-Pascual *et al.*, 2015b; Marmi *et al.*, 2016; Tennant *et al.*, 2016; Young *et al.*, 2016; Blanco *et al.*, 2018, 2019).

The teeth described in this study can be attributed to one or more of the genera *Theriosuchus*, *Sabresuchus* and *Knoetschkesuchus*. Attribution to the Late Jurassic atoposaurids *Alligatorium* and *Alligatorellus*, which both have smooth-surfaced teeth lacking ridges (Wellnhofer, 1971; Tennant *et al.*, 2016), can be discounted, because all the Valmitão teeth attributed to atoposaurids have ridges on at least the lingual surface. Moreover, the presence of leaf-shaped teeth and pseudoziphodont teeth precludes attribution of these to *Knoetschkesuchus*, and these morphotypes may represent more than one taxon. The Valmitão assemblage may thus reflect higher atoposaurid diversity than previously thought, as has been proposed for other fossil assemblages (Tennant & Mannion, 2014; Puértolas-Pascual *et al.*, 2015b; Tennant *et al.*, 2016; Schwarz *et al.*, 2017). This indicates that in addition to *Knoetschkesuchus guimarotae* there were other atoposaurids in Portugal during the Late Jurassic. The revision of skeletal remains recovered from the Oxfordian Alcobaça Formation, attributed initially to *Theriosuchus* sp. (Malafaia *et al.*, 2010), may cast further light on this hypothesis.

GONIOPHOLIDIDAE? COPE, 1875

GONIOPHOLIDIDAE INDET.

(FIGS 6–7)

Referred material: ML2422 to ML2472; 33 isolated slender conical teeth; 18 broad conical teeth.

Description

Morphotype 6, slender conical (Fig. 6): The teeth have a long, slender, conical shape, which can be triangular or more acuminate, with a lingually curved apex (13° to 41°) and a weak mesiodistal constriction at the base of the crown in some teeth. Their height range is between 1.931 mm and 3.337 mm and their width range is between 0.96 mm and 1.18 mm, their H/W ratio ranging from 1.79 to 2.94. Their cross-section is slightly labiolingually compressed with Lb/Mb ratios from 0.72 to 0.99, resulting in a subcircular to ovoid base of the crown. The labial surface is convex toward the base of the crown, whereas the lingual surface is faintly flattened. The lingual and labial surfaces are separated by mesial and distal carinae. These carinae are adjacent to a basiapical groove on the lingual side. On both surfaces, the enamel is composed of subparallel basiapical ridges: six to ten on the lingual surface, seven to nine on the labial surface. These ridges are more marked on the lingual surface than on the labial surface, which consequently appears smoother. On the lingual face, the ridges extend from the base to the apex of the crown, whereas they only extend over the upper two-thirds of the crown on the labial surface. On both lingual and labial surfaces, the ridges join each other toward the apex, with the lateralmost ones parallel to the mesial and distal margins. In contrast, a few teeth exhibit smooth enamel on both surfaces (Fig. 6E).

Morphotype 7, broad conical (Fig. 7): The teeth have a broad, conical shape, which is lingually curved in the largest specimens (between 23° to 38°) and blunter in the smallest. Their height range is between 2.09 mm and 4.54 mm, and their width range is between 1.88 mm and 2.47 mm high, with an H/W ratio from 1.11 to 2.10. Their cross-sections are slightly labiolingually compressed with Lb/Mb ratios from 0.75 to 0.96, resulting in a subcircular to ovoid base of the crown. The labial surface is convex toward the base in lateral view, whereas the lingual surface is lingually curved in larger teeth, to straight in smaller teeth. Apart from their broad shape, they are similar to the slender, conical teeth, although they exhibit more striations (nine to ten on the lingual surface, 11 to 12 on the labial). The labial ridges of the biggest teeth are smoother at the base of the crown (bottom one-third of the total height).

Remarks: The tooth morphologies described here are characteristic of Goniopholididae (Averianov, 2000; Krebs & Schwarz, 2000; Salisbury, 2002; Schwarz, 2002; Schwarz-Wings *et al.*, 2009; Kuzmin *et al.*, 2013; Puértolas-Pascual *et al.*, 2015b). Nevertheless, these morphologies can be observed in other crocodylomorphs with generalist dentition, and in the anteriorly located teeth of taxa with heterodont dentition (Puértolas-Pascual *et al.*, 2015b). Despite this, all teeth belonging to Goniopholididae are conical in form, with weak, labiolingual compression and an acute, curved apex and more or less developed carinae, according to the size of the crown. The enamel ridges also vary according to the size of the crown (Schwarz-Wings *et al.*, 2009). The strongly curved teeth observed in a supposedly juvenile Goniopholis individual (Salisbury, 2002) would suggest that small morphological differences could be related to ontogenetic differences within the genus, or might refer to different species of Goniopholididae (Schwarz-Wings *et al.*, 2009).

Slender to fluted conical teeth with parallel basiapical ridges are also observed in Pholidosauridae (Pouech *et al.*, 2006; Néraudeau *et al.*, 2012; Oreska *et al.*, 2013; Vullo *et al.*, 2014; Martin *et al.*, 2016b; Gônet *et al.*, 2019) and these could, therefore, match some of the teeth ascribed to morphotypes 6 and 7. *Sarcosuchus* (Early Cretaceous, Africa and South America) has false-ziphodont dentition and an

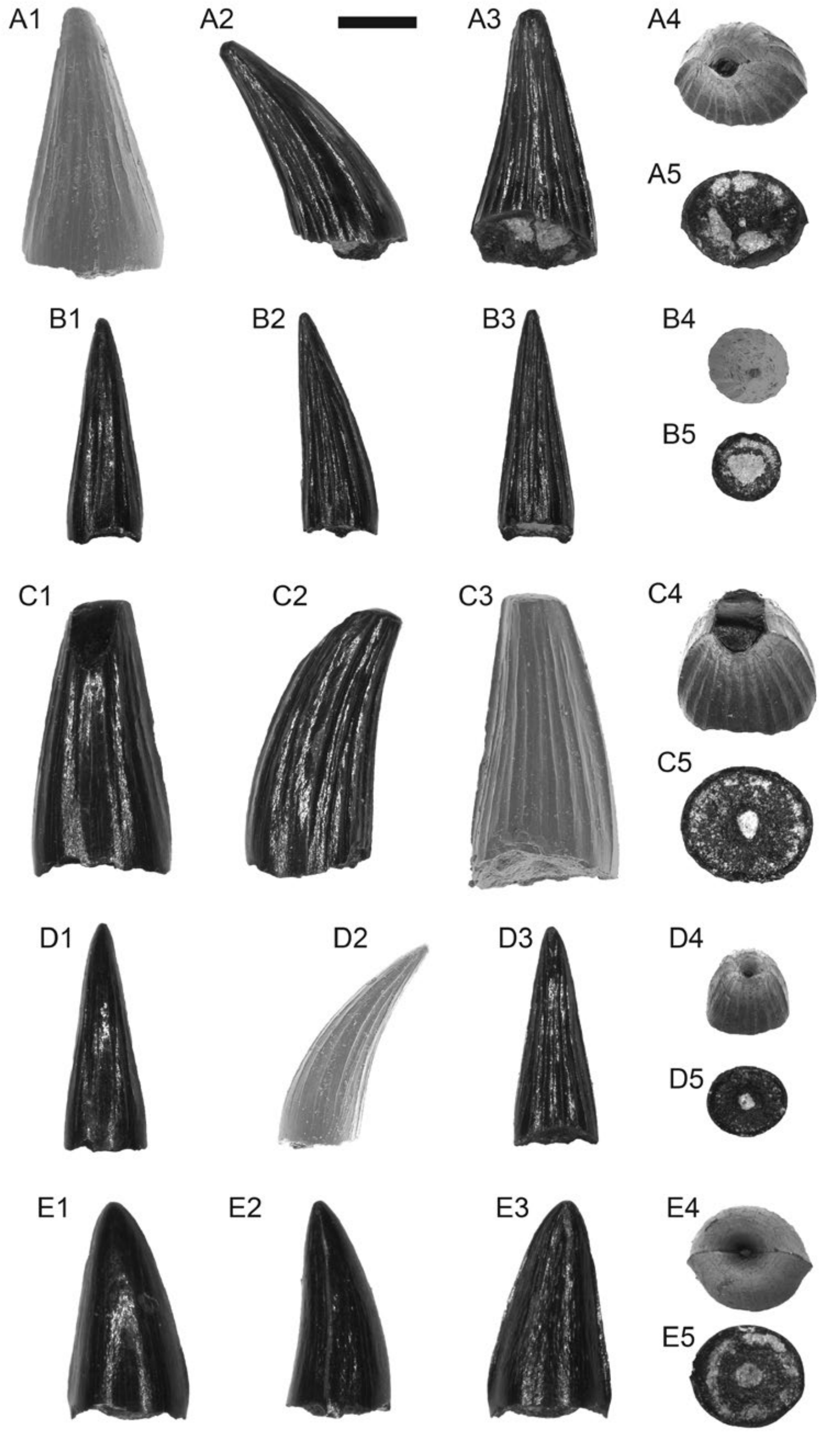

Figure 6. Morphotype 6 teeth ML2422 (A), ML2423 (B), ML2424 (C), ML2525 (D) and ML2626 (E) in labial (1), lateral (2), lingual (3), apical (4) and basal (5) views. Scale bar is 1 mm. All images are normal-light photomicrographs except for A1, B4, C3 and D2, which are SEM photomicrographs.

anastomosing enamel surface (Buffetaut & Taquet, 1977; Sereno *et al.*, 2001), and *Pholidosaurus* (Early Cretaceous, Europe) possesses ornamented teeth with well-marked longitudinal ridges that can hardly be differentiated from the carinae (Martin *et al.*, 2016b). These two taxa can thus be ruled out. In contrast,

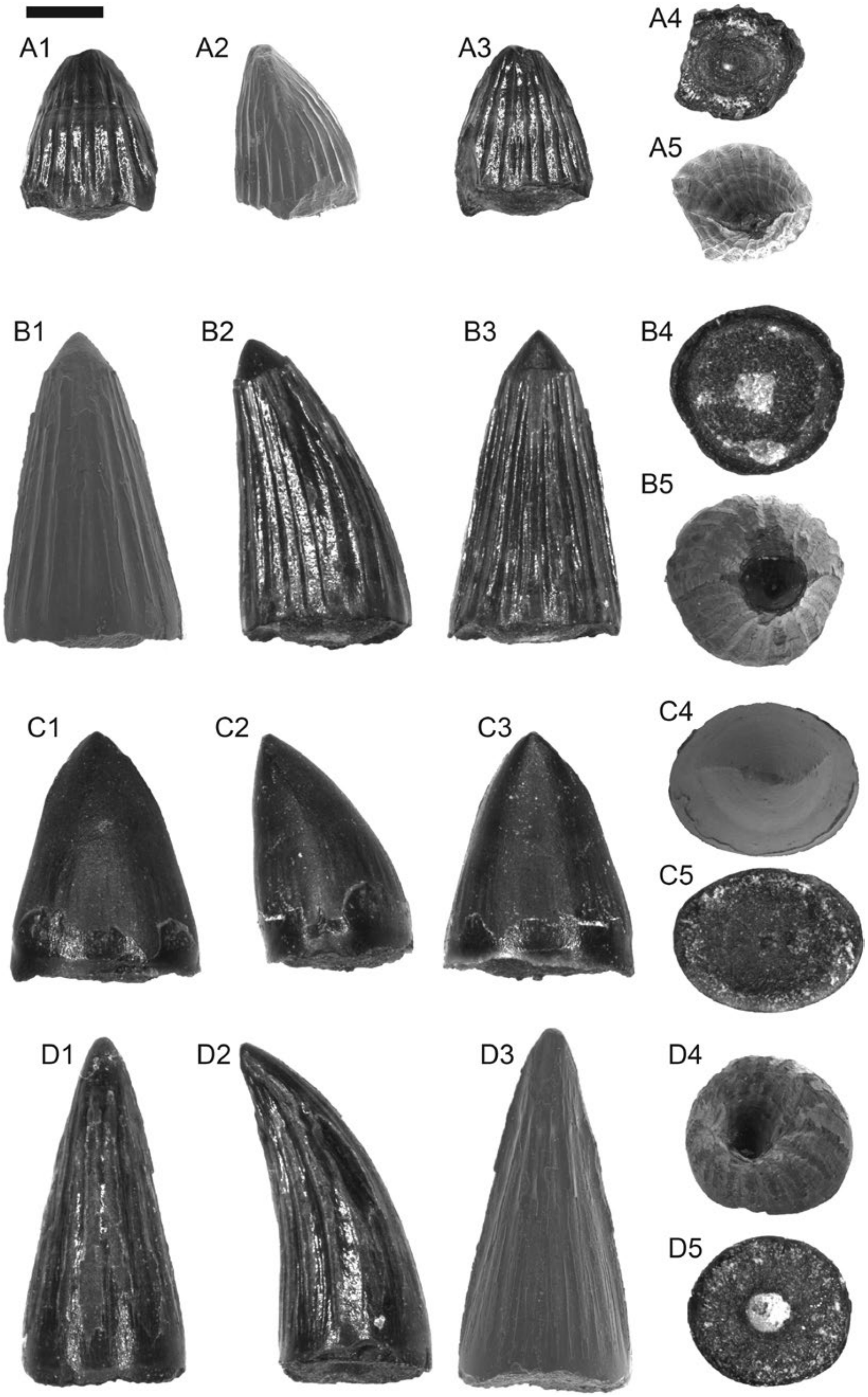

Figure 7. Morphotype 7 teeth ML2455 (A), ML2456 (B), ML2457 (C) and ML2458 (D) in labial (1), lateral (2), lingual (3), apical (4) and basal (5) views. Scale bar is 1 mm. All images are normal-light photomicrographs except for A2, B1, C4 and D3, which are SEM photomicrographs.

the dental morphology of other pholidosaurids, such as *Terminonaris* (Late Cretaceous, North America; Wu *et al.*, 2001; Adams *et al.*, 2011), *Oceanosuchus* (Early and Late Cretaceous, France; Hua *et al.*, 2007) and maybe *Chalawan* (Late Jurassic–Early Cretaceous, Thailand; Martin *et al.*, 2014a), *Elosuchus*

(Early Cretaceous, North Africa; de Broin, 2002) and *Meridiosaurus* (Late Jurassic, Uruguay; Fortier, Perea, & Schultz, 2011), could fall within morphotypes 6 and 7. However, all these taxa were recovered from more modern deposits and/or different continents than the Valmitão vma. Taking all Pholidosauridae described in the fossil record into account, *Anglosuchus* (Bathonian, England) and *Crocodilaemus* (Kimmeridgian, France) have a closer geographic distribution and are older or contemporary, but their attribution is only putative (Fortier *et al.*, 2011). Given the absence of Pholidosauridae in the fossil record of Portugal to date, Goniopholididae is thus the most parsimonious taxonomic assignment for these morphotypes.

Broad conical teeth have two overall shapes, which could depend on their position in the tooth row. The taller, curved teeth correspond with more anterior positions, probably in the anterior to mid-part of the jaw, whereas the blunter ones represent posterior locations. A conservative approach prevents us from attaining a more rigorous identification of these teeth, despite the fact that all the specimens with this morphology reported from the Late Jurassic of Portugal until now have belonged to *Goniopholis* (Krebs & Schwarz, 2000; Schwarz-Wings *et al.*, 2009; Malafaia *et al.*, 2010).

BERNISSARTIIDAE DOLLO, 1883

BERNISSARTIIDAE INDET.

(FIGS 8–9)

Referred material: ML2478 to ML2496; one isolated conical tooth; 18 isolated molariform teeth.

Description

Morphotype 8, conical (Fig. 8): Only one tooth of this morphotype was recovered (Table 1). Although the apex is not preserved, the tooth is 1.28 mm wide and seems to be conical and broad in labial and lingual views, with the base of the crown constricted. Its cross-section is labiolingually compressed with an Lb/Mb ratio of 0.89, resulting in a subcircular base of the crown. The lingual surface is convex, whereas the labial surface is flatter. Both mesial and distal margins are rounded. On both surfaces, it has parallel basiapical striations or ridges, extending two-thirds of the distance to the base of the crown on the labial surface and three-quarters of the distance to the base on the lingual surface. Since the apex is not preserved, the total length of the ridges cannot be determined. The enamel is covered by 14 ridges on the labial surface and 19 ridges on the lingual surface.

Morphotype 9, molariform (Fig. 9): The teeth are molariform, with bulky, low, rounded crowns, a blunt apex and a mesiodistal constriction at the base of the crown. Their height ranges from 0.71 mm to 1.48 mm and their width from 0.98 mm to 2.55 mm, with an H/W ratio from 0.58 to 0.80. In basal cross-section, they are labiolingually compressed, with an Lb/Mb ratio from 0.39 to 0.55, resulting in an elliptical to reniform base of the crown. Some teeth exhibit a weak groove on the lingual surface. The labial surface is more convex than the lingual surface. Most of the teeth lack carinae on both mesial and distal margins, but carinae are present in some (Fig. 9C, E). The teeth have parallel basiapical striations on both surfaces extending over the upper two-thirds of them, but some

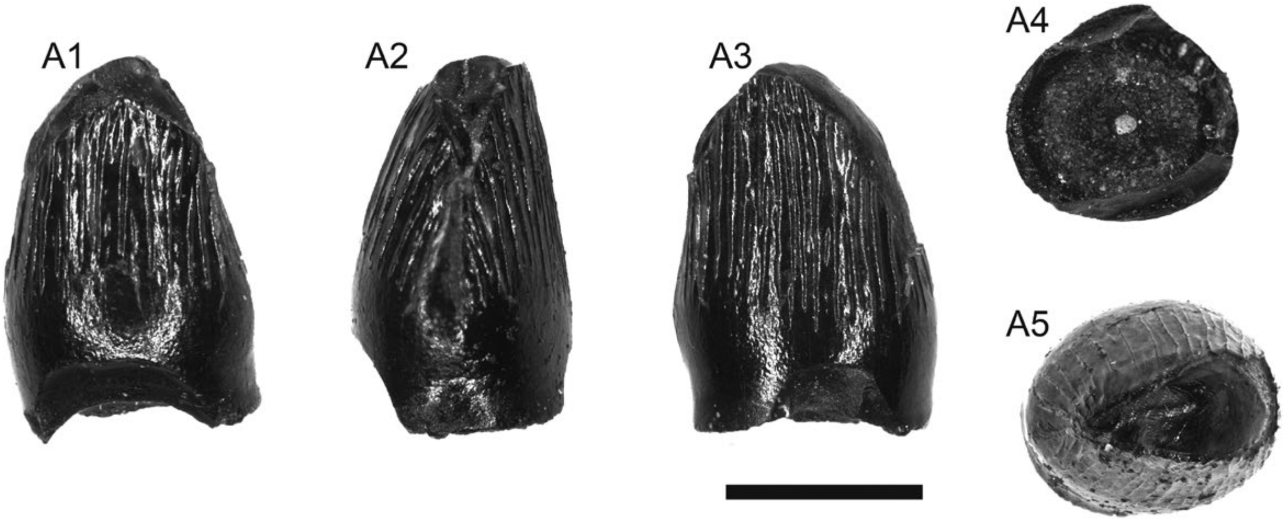

Figure 8. Morphotype 8 tooth ML2478 in labial (1), lateral (2), lingual (3), basal (4) and apical (5) views. Scale bar is 1 mm. All images are normal-light photomicrographs.

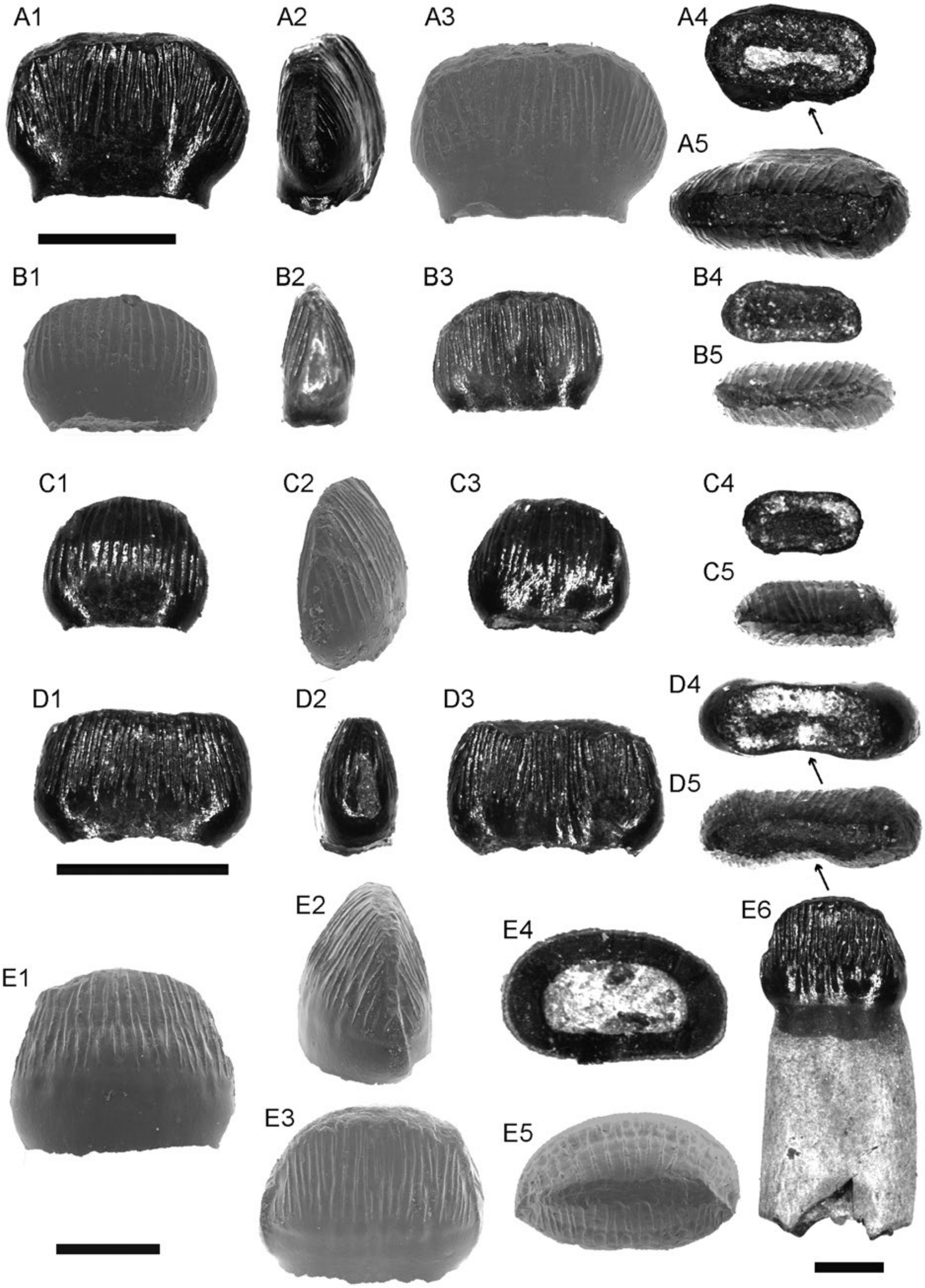

Figure 9. Morphotype 9 teeth ML2479 (A), ML2481 (B), ML2482 (C), ML2483 (D) and ML 2480 (E) in labial (1), lateral (2), lingual (3), basal (4) and apical (5) views. E6 shows ML2480 in lingual view with the root preserved. The arrows point the lingual groove that can be observed in some specimens. Scale bars are 1 mm. All images are normal-light photomicrographs except for A3, B1, C2, E1–E3 and E5, which are SEM photomicrographs.

teeth exhibit ridges from the base of the crown to the apex. The enamel is covered by 19 to 30 ridges on the labial surface and 17 to 32 ridges on the lingual surface. The apex presents wear facets in all the teeth, even though the wear differs from one tooth to another: The ML2479 (Fig. 9 A) apex is strongly worn and the wear extends from the apex to almost the base of the crown on the mesial and distal margins, whereas ML2480 and ML2482 (Fig. 9C, E) display an apex that is faintly worn in comparison to ML2479 and the wear facet is limited to only the apex margin.

Remarks: Conical teeth with a subcircular cross-section have been considered to come from the anterior part of the dentition in Bernissartiidae, whereas molariform teeth occupy middle and posterior positions (Buffetaut & Ford, 1979; Schwarz-Wings *et al.*, 2009; Puértolas-Pascual *et al.*, 2015b; Sweetman *et al.*, 2015). Although incomplete, the morphotype 8 tooth from Valmitão does not seem to be as pointed and elongated as described for the anteriormost teeth of *Bernissartia* and other bernissartiids (Buffetaut, 1975; Sweetman *et al.*, 2015), but its broad, conical shape makes it similar to the acuminate bulbous teeth observed in the mid-region of the maxilla in *Koumpiodontosuchus* (Sweetman *et al.*, 2015)

Molariform crowns with a reniform or kidney-shaped cross-section are characteristic of Bernissartiidae, as exemplified by the above-cited taxa *Bernissartia* and *Koumpiodontosuchus*, and are associated with a durophagous diet, as suggested by the wear facets observed on the apex of the teeth (Buffetaut & Ford, 1979; Sanz-López *et al.*, 1984; Schwarz-Wings *et al.*, 2009; Ullmann *et al.*, 2012; Puértolas-Pascual *et al.*, 2015b; Sweetman *et al.*, 2015). Bernissartiid molariform teeth can be distinguished from atoposaurid teeth, such as those of *Theriosuchus*, by their blunt, tribodont crowns and the presence of parallel basiapical ridges (Salisbury & Naish, 2011; Sweetman *et al.*, 2015; Tennant *et al.*, 2016). Nevertheless, this morphology is also seen in taxa not closely related to Bernissartiidae, such as the hylaeochampsids *Unasuchus* and *Acynodon*, the alligatoroids *Brachychampsa*, *Albertochampsa* and *Allognathosuchus*, and the extant crocodylian *Osteolaemus* (e.g. Buffetaut & Ford, 1979; Brinkmann, 1992; Puértolas-Pascual *et al.*, 2015b; Jouve *et al.*, 2019). Some isolated teeth with this morphology and unworn crowns have been attributed to *Bernissartia*, and teeth in the *Bernissartia* holotype were described with a longitudinal carina (Buffetaut & Ford, 1979; Norell & Clark, 1990). This suggests that in less eroded or unworn teeth, such as ML2480 and ML2482, the carina may be preserved, supporting their attribution to this morphotype and to bernissartiids.

Bernissartiid remains are common in many Cretaceous localities: Bornholm in Denmark and Skåne in Sweden (Schwarz-Wings *et al.*, 2009), Swanage and the Isle of Wight in Great Britain (Buffetaut & Ford, 1979; Salisbury, 2002; Sweetman *et al.*, 2015), Cherves-de-Cognac in France (Pouech *et al.*, 2006), Teruel, Uña, Pio Pajarón, Buenache de la Sierra, Vallipón, and La Cantalera in Spain (Sanz-López *et al.*, 1984; Brinkmann, 1989, 1992; Buscalioni *et al.*, 2008; Puértolas-Pascual *et al.*, 2015b) and Bernissart in Belgium (Dollo, 1883; Buffetaut, 1975). Bernissartiid skeletal remains are currently unknown prior to the Cretaceous. However, isolated teeth from the Guimarota vertebrate microfossil assemblage, and from the Purbeck-type bonebeds of Chassiron in France, have been assigned to *Bernissartia* sp. (Brinkmann, 1989; Krebs & Schwarz, 2000; Vullo *et al.*, 2014), providing the only Jurassic records for this clade.

MESOEUCROCODYLIA INDET.

(FIG. 10)

Referred material: ML2473 to ML2477, five isolated teeth.

Description

Morphotype 10, ziphodont: The teeth are conical and lingually curved (14° to 15°), with a sharp apex and slight distal curvature (7° to 13°). Their height ranges from 3.60 mm to 3.65 mm and their width from 1.28 mm to 1.83 mm, with an H/W ratio from 2.00 to 2.35. Their cross-sections are labiolingually compressed, with an occasional labially shifted centre, and with an Lb/Mb ratio of 0.69 to 0.78, resulting in a lenticular base of the crown. The lingual surface is flat to weakly concave labially, whereas the labial surface is convex labially toward the base. The two surfaces are separated by acute and crenulated carinae, where small, true denticles can be observed, especially in the lower half of the carinae. The denticles are irregular in size and shape (Fig. 10C7–C10). The enamel on both sides is smooth, but some teeth exhibit shallow ridges on the upper part, forming faint and diffuse striations.

Remarks: Teeth with true denticles on the carinae are termed ziphodont (Prasad & de Lapparent de Broin, 2002; Puértolas-Pascual *et al.*, 2015b), and have been attributed to mesoeucrocodylian taxa without monophyletic relationships. The irregular shape and size of the denticles and the lingual curvature of the tooth crowns differ from the mesiodistal curvature and denticle morphology observed in theropod teeth, confirming their crocodylomorph identity. However, the presence of denticles, which reflects a dentary specialization, cannot be used for taxonomic classification (Turner, 2006; Andrade & Bertini, 2008; Puértolas-Pascual *et al.*, 2015b), but the presence of

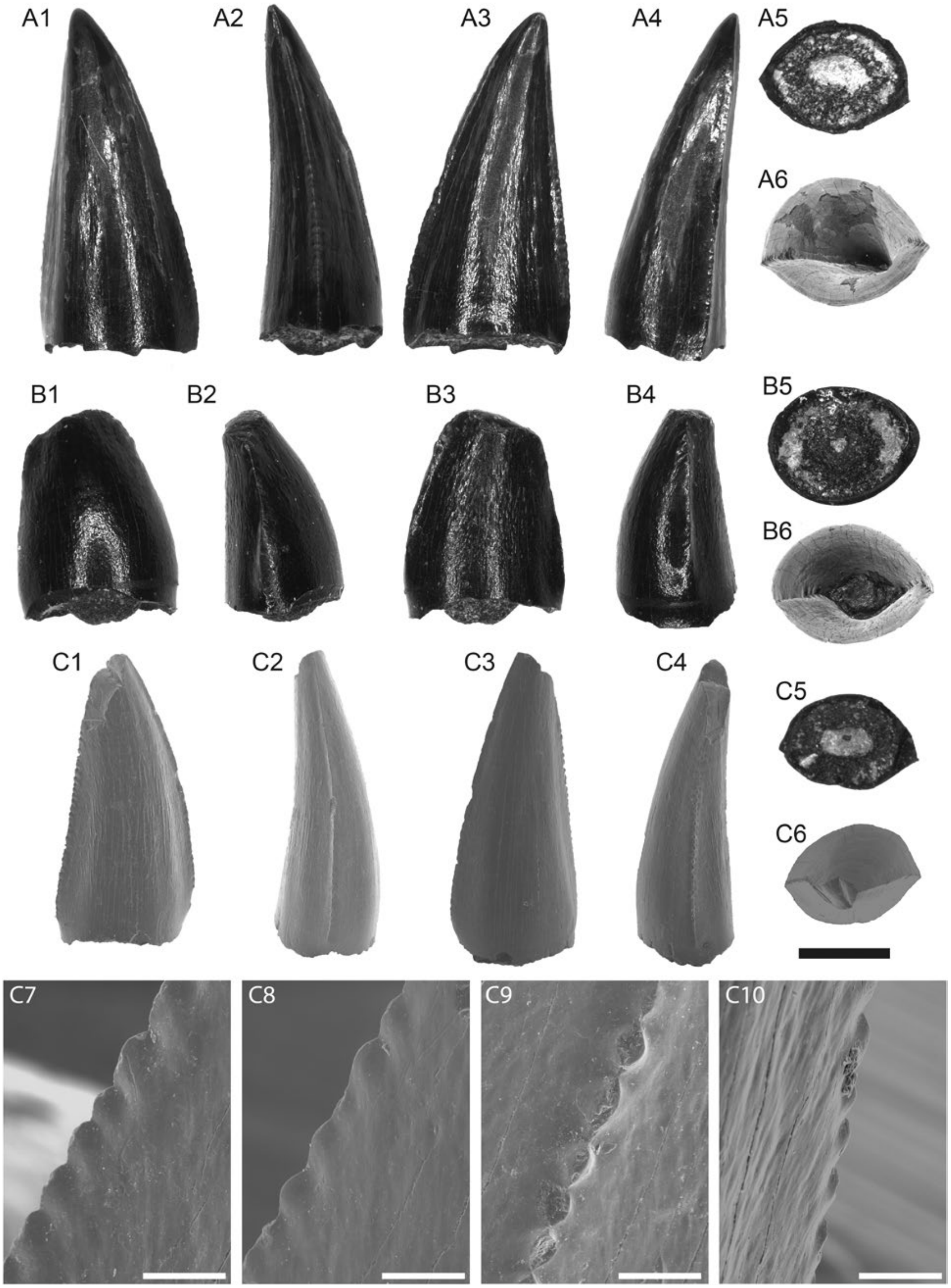

Figure 10. Morphotype 10 teeth ML2473 (A), ML2474 (B) and ML2475 (C) in labial (1), lateral (2 and 4), lingual (3), basal (5) and apical (6) views. Scale bar is 1 mm. Close-ups of ML2475 denticles in labial (7, 8), lateral (9) and lingual (10) views. Scale bars are 100 µm. All images are normal-light photomicrographs except for C1–C4 and C6–C10, which are SEM photomicrographs.

serrations, not seen in other elements in the assemblage, distinguishes these teeth from those described above and from other above-mentioned taxa. Similar ziphodont teeth have been observed in undetermined crocodyliforms from the La Cantalera assemblage in Spain (Puértolas-Pascual *et al.*, 2015b) and the

Wessex Formation in Great Britain (Sweetman, 2016). Judging by its shape and the presence of denticles, this morphology also differs from that observed in the material from Guimarota attributed to *Lisboasaurus estesi*, because our specimens lack the median groove on the labial surface, the blunt apex and the conical to triangular shape usually observed in the latter taxon (Schwarz & Fechner, 2008). This morphology also differs from the morphology observed in the dentary and maxillary teeth of one of the other Guimarota taxa, *Lusitanisuchus mitracostatus*, whose maxillary teeth are ornamented and do not exhibit denticles, and whose dentary teeth are spatulate (Schwarz & Fechner, 2004). The presence of this morphotype, which cannot be assigned to any known taxon from the Late Jurassic of Portugal, further adds to the diversity of the Lourinhã Formation.

REVIEW OF THE *LUSITANISUCHUS MITRACOSTATUS* DENTITION

In studying the teeth from the Valmitão vertebrate microfossil assemblage, a striking issue was the apparent absence of teeth from *Lusitanisuchus* and *Lisboasaurus* in the sample, two known taxa from the nearby contemporary site of Guimarota. However, there is a lack of detailed photographs in previous publications (Buscalioni *et al.*, 1996; Schwarz & Fechner, 2004, 2008). Teeth belonging to these taxa might, therefore, be present in the Valmitão vma, but not identifiable. From the figures in these previous works, *Lisboasaurus* teeth, which are characterized by a conical to triangular shape with a blunt apex and a median groove on the labial side, seem to be clearly different from those recovered at Valmitão. However, *Lusitanisuchus* teeth are similar to a morphotype assigned to atoposaurids in this study (morphotype 5). In order to confirm or rule out the presence of these taxa in the Valmitão vertebrate microfossil assemblage, the material from Guimarota housed in the Geological Museum of Lisbon was studied. Unfortunately, *Lisboasaurus* material is not stored in the collection, so we have not had an opportunity to study it and are, therefore, unable to comment on it here.

CROCODYLOMORPHA HAY, 1930 (*SENSU* CLARK, 1986)

MESOEUCROCODYLIA WHETSTONE & WHYBROW, 1983 (*SENSU* BENTON & CLARK, 1988)

FAMILY *INCERTAE SEDIS*

LUSITANISUCHUS MITRACOSTATUS (SEIFFERT, 1970)

(FIGS 11–13)

Referred material: MG26081 (IPFUB Gui Croc 7505); MG28911 (IPFUB Gui 75 6.03); (IPFUB Gui Croc 7516); MG26103 (IPFUB Gui Croc 8002); (IPFUB Gui Croc 8009).

Locality, horizon and age: Guimarota Mine (Leiria, Portugal); Alcobaça Formation; Kimmeridgian.

Description

Anterior premaxillary and maxillary teeth (Fig. 11): IPFUB Gui Croc 8009 has three teeth preserved, whereas the other specimens have only one preserved. Because they are incomplete, the position in the tooth series cannot be determined. The root is exhibited in MG26103. Their height ranges from 1.014 mm to 2.373 mm and their width from 0.608 mm to 0.882 mm, with an H/W ratio from 1.668 to 2.690. The teeth are conical, with a broad, pointed apex. They do not seem compressed, suggesting a subcircular cross-section, with a faint constriction at the base of the crown. The teeth are weakly posteriorly curved. Both distal and mesial margins seem to exhibit a faint carina with no denticles observed. The enamel on both labial and lingual surfaces is covered by subparallel ridges converging toward the apex, forming basiapical striations (Seiffert, 1973; Schwarz & Fechner, 2004; pers. obs.).

Dentary teeth (Figs 12, 13): Three teeth are preserved in MG28911 and three more alveoli without teeth are preserved. However, their position cannot be determined because the dentary is not completely preserved. MG26081 is almost complete, with two teeth preserved in the last positions. The previous two alveoli do not preserve teeth; then two more teeth are preserved, with one broken. The most anterior alveoli are not preserved. The root is exhibited in one tooth in MG28911. The height of the teeth ranges from 0.703 mm to 1.215 mm and their width from 0.54 mm to 0.993 mm, with an H/W ratio from 1.200 to 1.392. The teeth are spatulate, with a sagittate (arrowhead-shaped) to truncate (straight and horizontal) apex, similar to a human incisor. They are labiolingually compressed, and there is a faint constriction visible at the base of the crown. Both labial and lingual surfaces are planar, and the edge of the apex is sharp. The enamel on both lingual and labial surfaces is covered by ridges forming basiapical striations, extending toward the apex to form vertical false denticles. These denticles are irregular in size; the lateralmost ones are small and barely visible, whereas the centralmost one is pointing outward from the apex, forming a small tip. No denticles are observed on the distal and mesial carinae of the teeth. In the lower part, ridges form parallel basiapical striations, but in the upper

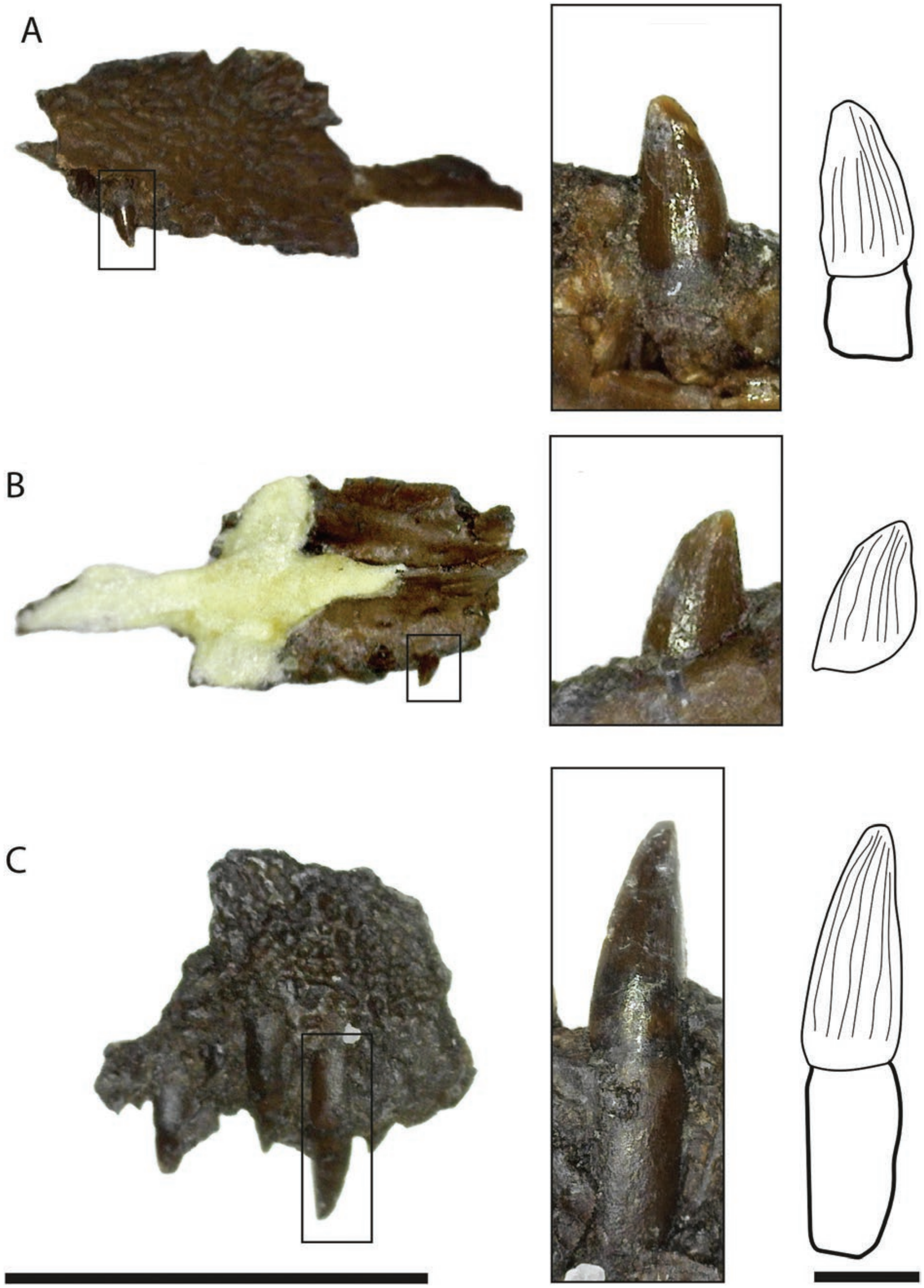

Figure 11. A–B, *Lusitanisuchus mitracostatus* left premaxilla–maxilla MG26103 (IPFUB Gui Croc 8002) in labial (A) and lingual (B) views with enlargements and schematic drawings of one tooth to illustrate tooth morphology. C, *Lusitanisuchus mitracostatus* right maxilla (IPFUB Gui Croc 8009) in labial view with enlargement and schematic drawing of one tooth to illustrate tooth morphology. Scale bar for the general views (left) is 1 cm, scale bar for enlargements and drawings (right) is 2 mm for A and B and 1 mm for C.

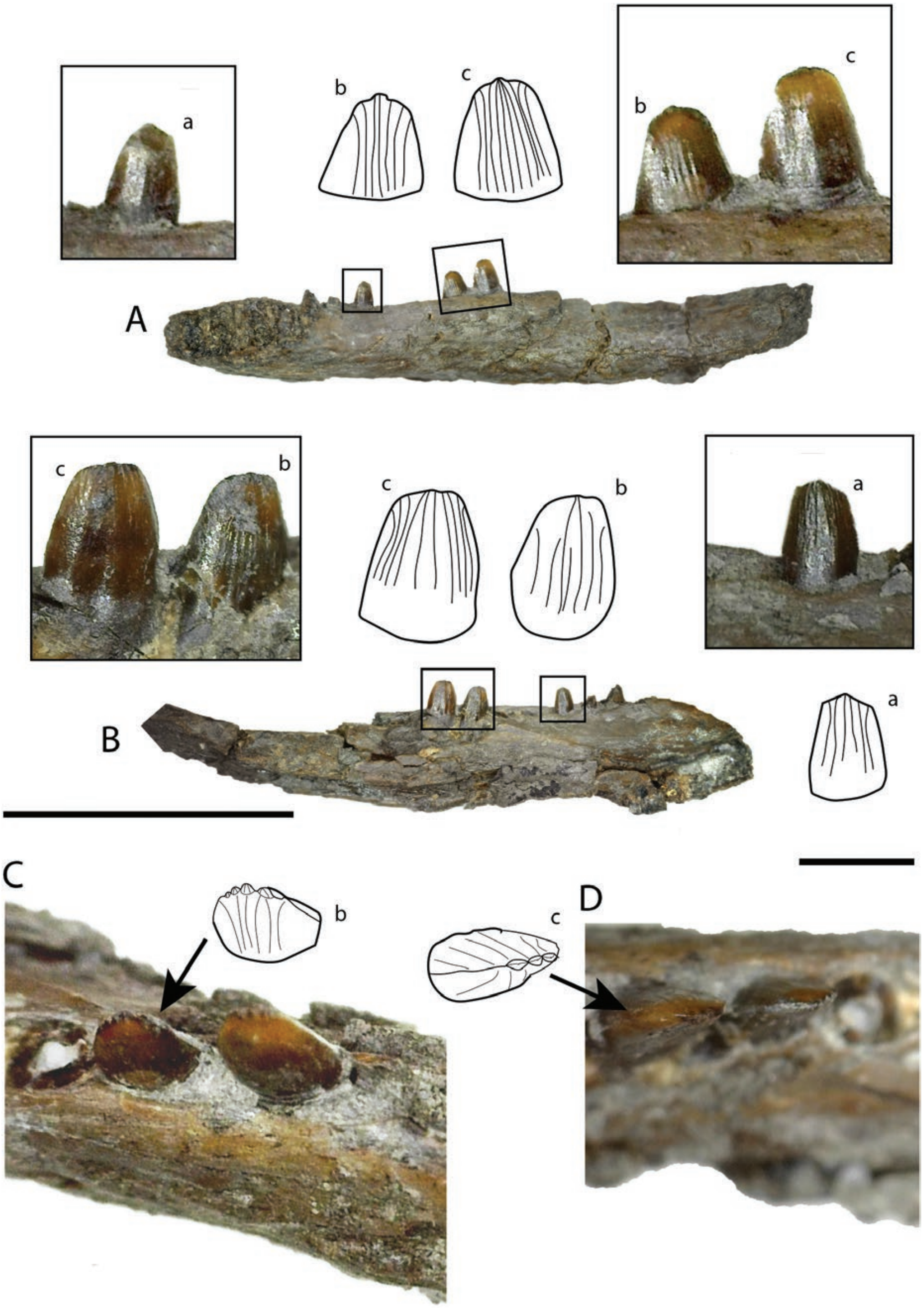

Figure 12. *Lusitanisuchus mitracostatus* left dentary MG26081 (IPFUB Gui Croc 7505) in labial (A), lingual (B), apicolabial (C) and apicolingual (D) views, with enlargements and schematic drawings of three teeth (from anterior to posterior: a, b and c) to illustrate tooth morphology. Scale bar for the general views (left) is 1 cm. Scale bar for the enlargements and drawings (right) is 1 mm.

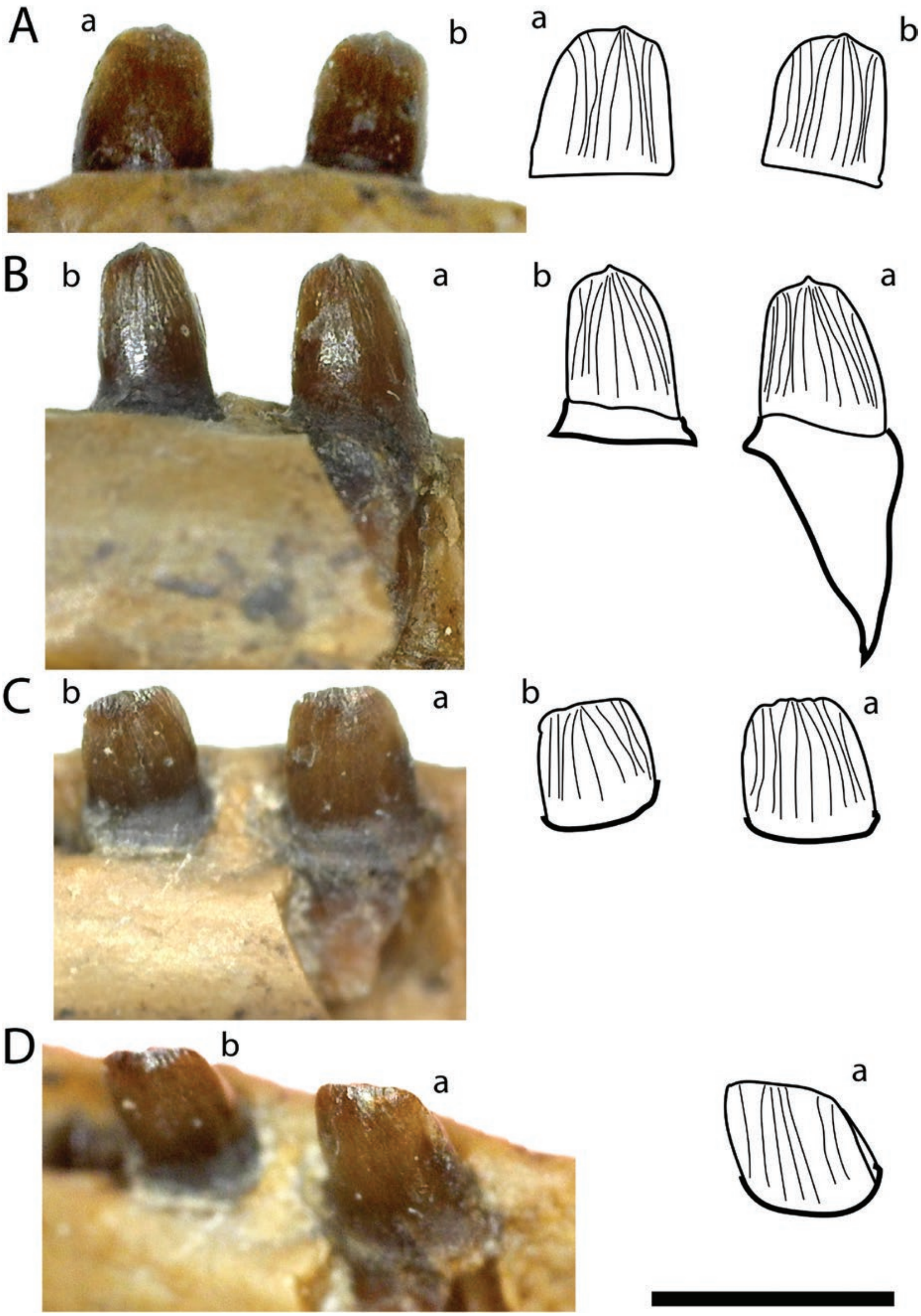

Figure 13. Enlargement of the teeth of the *Lusitanisuchus mitracostatus* dentary MG28911 (IPFUB Gui 75 6.03) (from anterior to posterior: a and b) and schematic drawings to illustrate tooth morphology, in labial (A), lingual (B) and apicolingual views (C, D). Scale bar is 1 mm.

part, the central ridges converge toward the small tip of the apex, whereas the lateralmost striations have a flabelliform distribution and extend toward the margins and the edge of the apex, forming small lateral denticles (Seiffert, 1973; Schwarz & Fechner, 2004; pers. obs.).

Remarks: The conical morphotype of the premaxillary and anterior maxillary teeth in *Lusitanisuchus mitracostatus* is commonly observed in Crocodylomorpha. Their overall shape and the ornamentation of the enamel are similar to teeth of morphotype 7, attributed to goniopholidids and usually associated with generalist feeding behaviour (Buffetaut & Ford, 1979; Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2011; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015b), even though they are smaller and broader, as shown by their H/W ratios. The conical teeth of *L. mitracostatus* can also be compared with teeth of morphotype 2, attributed to atoposaurids, showing a similar shape and proportion, but the labial basiapical ridges in morphotype 2, when present, are more strongly marked than in *L. mitracostatus*. Material with better exposed teeth will enable us to confirm the difference between these two morphotypes.

The morphology of the dentary teeth differs from that observed in other mesoeucrocodylians (Schwarz & Fechner, 2004), including atoposaurids, despite the similar ornamentation suggesting a particular ecological specialization. This morphology also differs from the molariform teeth characteristic of bernissartiids: the edge of the apex is sharper in *Lusitanisuchus mitracostatus* and comprises small denticles, whereas it is blunt and smooth in bernissartiids, the enamel in bernissartiids is more ornamented and some teeth observed in *L. mitracostatus* have a more pointed apex than is observed in Bernissartiidae. Not being multicuspids, they also differ from the spatulate teeth observed in *Simosuchus* and *Uruguaysuchus* (Buckley *et al.*, 2000) and they differ from those observed in *Acynodon* by being less broad and more labiolingually compressed (Buscalioni *et al.*, 1997; Martin, 2007; Delfino *et al.*, 2008; Blanco *et al.*, this volume). Given the preservation of the dentaries, no substantial difference could be observed in the tooth series between anterior and posterior teeth.

DISCUSSION

TAPHONOMY

Most of the crocodylomorph teeth collected from the Valmitão vma sediments are well preserved, showing little or no sign of transport. Most of them have wear facets and sometimes broken apices. This indicates that they were shed teeth – lost during the normal process of tooth replacement that occurs in crocodylomorphs (Kieser *et al.*, 1993). Some provide evidence of having been digested. This could have originated as a result of predation or from having been swallowed by their owner when they were shed. The predominance of shed teeth suggests that the Valmitão assemblage is located close to the habitat of the crocodylomorphs (Schwarz-Wings *et al.*, 2009). However, some teeth show traces of abrasion, having partially or completely lost the enamel (Fig. 7C) or are broken, and only one tooth has the root preserved (Fig. 9E). This suggests that some teeth may have been transported over short distances (Schwarz-Wings *et al.*, 2009). Further, no other crocodylomorph remains but osteoderms were recovered from the sample (see Supporting Information, Data S1), although crocodylomorphs are known from the Lourinhã Formation (Puértolas-Pascual & Mateus, 2019). This mixture of parautochthonous and allochthonous specimens suggests that accumulation by transport played a role in the formation of the Valmitão vma.

The crocodylomorph teeth from the Valmitão assemblage seem to have belonged to small animals (Fig. 14). Indeed, the average size is 2.11 mm in the sample studied, with 3.08 mm for the teeth attributed to goniopholidids, 3.62 mm for the ziphodont teeth, 0.99 mm for the teeth attributed to bernissartiids and 1.52 mm for the teeth attributed to atoposaurids. Atoposaurids and bernissartiids are small crocodylomorphs, reaching a total adult body length of around 500–600 mm (Schwarz-Wings *et al.*, 2009; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015b; Schwarz *et al.*, 2017). However, the crown height ranges from 2mm to 10 mm for atoposaurids and from 3 mm to 6 mm for bernissartiids (Puértolas-Pascual *et al.*, 2015b). This suggests that the Valmitão assemblage is composed of only juvenile bernissartiids and of both juvenile and subadult atoposaurids. By contrast, goniopholidids are large crocodylomorphs, reaching an adult body length of about 4 m and with centimetric high teeth (Salisbury *et al.*, 1999; Buscalioni *et al.*, 2008; Puértolas-Pascual *et al.*, 2015b) ranging from 7 mm to 26 mm (Averianov, 2000; Wings *et al.*, 2010; Kuzmin *et al.*, 2013; Puértolas-Pascual *et al.*, 2015a; Martin *et al.*, 2016a), which suggests that the specimens found in the Valmitão vma are all juvenile.

The crocodylomorph teeth reported here were mostly recovered from the 1 mm and 0.5 mm residue fractions of the Valmitão sediments, and clasts exceeding 5 mm in length are rare in the assemblage. This suggests a taphonomic bias towards small elements in the formation of the accumulation, possibly reflecting the low energy of the fluxes responsible for the accumulation of the specimens (Schwarz-Wings *et al.*, 2009). However, the small size of the teeth could also be an indication that the Valmitão ecosystem was dominated by small crocodylomorph taxa. Small crocodylomorphs have been previously reported from the Lourinhã Formation (Puértolas-Pascual & Mateus, 2019).

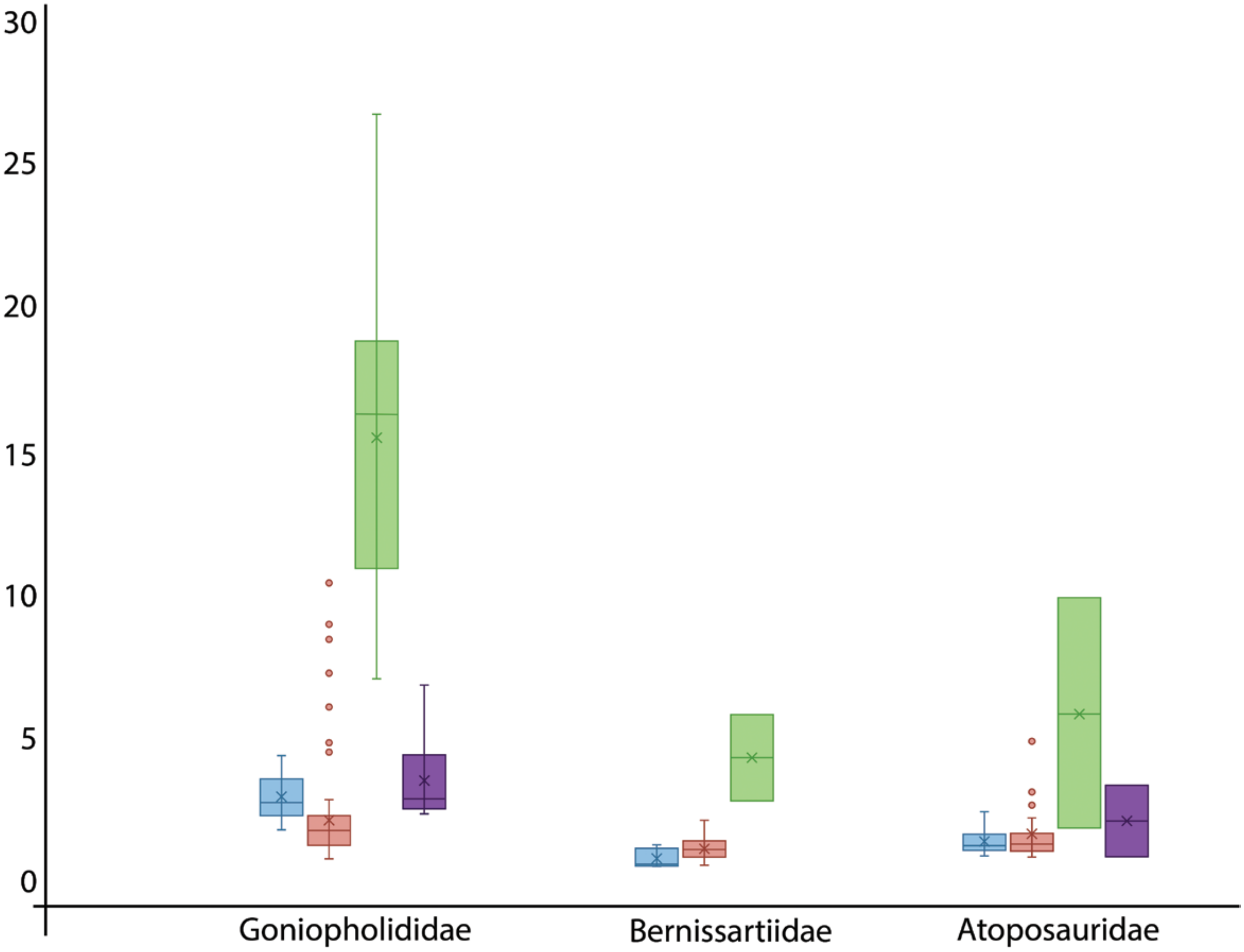

Figure 14. Comparison of the maximum height (in mm) of the crocodylomorph teeth recorded from Valmitão (blue) and La Cantalera in Spain (red), and in adult (green) and juvenile specimens (purple). The red dots for La Cantalera represent the outliers. Data from: Averianov, 2000; Wings *et al.*, 2010; Kuzmin *et al.*, 2013; Puértolas-Pascual *et al.*, 2015a, b; Martin *et al.*, 2016.

PALAEOECOLOGY AND THE FEEDING HABITS OF THE VALMITÃO VMA CROCODYLOMORPHS

The teeth described in this analysis can be sorted into nine different morphotypes, from which four ecomorphotypes based on ecological niches can be determined: ecomorphotype A, indicating a diet based on small arthropods (insects, crustaceans, soft-bodied) and occasional small vertebrates such as mammals and amphibians (Owen, 1879; Buscalioni & Sanz-López, 1988; Puértolas-Pascual *et al.*, 2015b), similar to extant juvenile crocodilians (Brinkmann, 1989; Schwarz & Salisbury, 2005; Schwarz *et al.*, 2017); ecomorphotype B, for generalist feeders, with a diet based on shelly and soft prey items, similar to modern alligators (Schwarz, 2002; Schwarz *et al.*, 2017); ecomorphotype C, for durophagous feeders, with a diet based on animals with shells, such as snails or mollusks, and crushing feeding behaviours (Melstrom & Irmis, 2019); and ecomorphotype D, for carnivorous predators.

The five conical tooth morphotypes (morphotypes 2, 3, 6, 7 and 8) are the most abundant in the studied sample (*N* = 77, 61.6%; Fig. 15). Conical teeth are common in several crocodylomorph clades, being present mainly in generalist taxa, but also forming the anterior dentition of most heterodont taxa (Buffetaut & Ford, 1979; Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2011; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015b). However, differences in the shape of the cross-section and the enamel ornamentation pattern were observed, allowing the teeth to be separated into the different morphotypes and the ecomorphotypes with which they are associated. Teeth from morphotypes 2 and 3 (*N* = 25, 19.84%) are attributed to ecomorphotype A, associated here with Atoposauridae. Teeth from morphotypes 6 and 7 (*N* = 51, 40.48%) are attributed to ecomorphotype B, here assigned to Goniopholididae. The only tooth from morphotype 8 (0.79%) is attributed to ecomorphotype C, consistent with Bernissartiidae.

Morphotypes 4 and 5 are represented by 25 teeth (19.84%; Fig. 15). These are associated with the high dietary plasticity (Tennant *et al.*, 2016) of ecomorphotype A. Other authors have even suggested herbivorous (Brinkmann, 1992), ovivorous (Kirkland *et al.*, 1994) or piscivorous diets (Thies, Windolf, & Mudroch, 1997) for these dental morphotypes.

Morphotype 9 is represented by 18 teeth (14.29%; Fig. 15). Because of its peculiar shape among crocodylomorphs, it has been suggested this morphotype could be closely linked to a specific ecological diet, rather than resulting from phylogenetic relationships, and it has been associated with ecomorphotype C (Buffetaut & Ford, 1979; Puértolas-Pascual *et al.*, 2015b).

Morphotype 10 is the scarcest, apart from morphotypes 1 and 8, represented by only five teeth (4%; Fig. 15). This morphology is found in a broad range of mesoeucrocodylian taxa, such as *Iberosuchus*, *Sebecus*, *Pristichampsus*, *Hamadasuchus*, *Araripesuchus* and *Ischyrochampsa*, as well as undetermined mesoeucrocodylians. It suggests a highly predatory terrestrial lifestyle (Turner, 2006; Andrade & Bertini, 2008; Puértolas-Pascual *et al.*, 2015b, 2016; Sweetman, 2016) and can be related with ecomorphotype D.

No feeding behaviours have been proposed for *L. mitracostatus*, which has been described as a small-adult-sized undetermined mesoeucrocodylian (Schwarz & Fechner, 2004) and should, therefore, fit ecological niches for similar-sized taxa. Morphotype 1, and the morphologies of the teeth observed in MG28911 and MG26081, are similar to what is observed in many herbivorous dinosaur clades (Weishampel & Norman, 1989). However, the dental arcade differs from the herbivorous crocodylomorphs *Mariliasuchus amarali* de Souza Carvalho & Bertini, 1999 and *Iharkutosuchus* (Ősi *et al.*, 2007), which exhibit stronger incisiform to conical anterior teeth, and more blunt molariform posterior teeth (Ősi *et al.*, 2007; Andrade & Bertini, 2008; Nobre *et al.*, 2008) than the conical teeth observed in IPFUB Gui 8009 and MG26103. There are no molariform teeth in *L. mitracostatus*. Nor is there extensive tooth wear or a tooth battery that would suggest a herbivorous diet (Barrett, 2000). Furthermore, the jaw does not seem adapted for a detrivorous diet since the teeth are vertical on the dentary and would not allow the scraping of sediments. Morphotype 1 and the teeth observed in MG28911 and MG26081 share a similar flabelliform ornamentation, false denticles and labiolingual compression with morphotypes 4 and 5, observed in atoposaurids, but the overall shape and the presence of a tip on the truncate, sharp apex distinguish them. Because of this similarity, and because of the presence of the tip on the apex, it is here proposed that *L. mitracostatus* can be associated with ecomorphotype A. However, more complete cranial material is required in order to gain a better understanding of the feeding behaviour of *L. mitracostatus*.

Of note is the diversity of dental ecomorphotypes observed in the Valmitão vma. Northern South America and South-East Asia currently have the highest crocodylian diversity, with up to six and four living species, respectively, whereas no more than two or three usually occur sympatrically (Scheyer *et al.*, 2013). In contrast, sympatric crocodylomorph assemblages with higher diversity are known from the Eocene of Messel in Germany (Micklich, 2007), the Mio–Pliocene of Urumaco in Venezuela (Scheyer *et al.*, 2013; Scheyer & Delfino, 2016) and the Maastrichtian of Molí del Baró-1 and L'Espinau in Spain (Marmi *et al.*, 2016; Puértolas-Pascual *et al.*, 2016; Blanco *et al.*, 2019), at each site of which at least seven different species have been recovered. On a bigger scale, the Tremp Formation in Spain yields as many as ten different taxa (Blanco *et al.*, 2019), whereas the Barremian of the Wealden Group of the Isle of Wight records 11 species (Sweetman, 2011a, 2016). Even so, in some of the richest localities, with most crocodylomorph species living at the same time and in the same area, the three or four tooth ecomorphotypes for ecological niches and feeding behaviours observed in each case are equal to, or less diverse than, those observed in the Valmitão vma. This implies that the species diversity at the Valmitão site is underestimated. Five taxa are reported here, but there were probably more. Systematic studies of the faunal composition based on the tooth morphotypes are here supported as a good proxy for highlighting the hidden crocodylomorph diversity in assemblages (Marmi *et al.*, 2016; Sweetman, 2016; Blanco *et al.*, 2018, 2019).

Because feeding and access to food are essential parameters in the fitting of organisms to the ecological niche they occupy, the morphological diversity of dentition observed within atoposaurids has been proposed as one of the potential drivers of their evolution in the Middle to Late Jurassic (Young *et al.*, 2016). The observations made from the Valmitão assemblage are consistent with this proposal and support the biogeographical and taxonomic variation seen in previous studies, suggesting that Atoposauridae were already diverse by the end of the Late Jurassic in Europe (Tennant & Mannion, 2014;

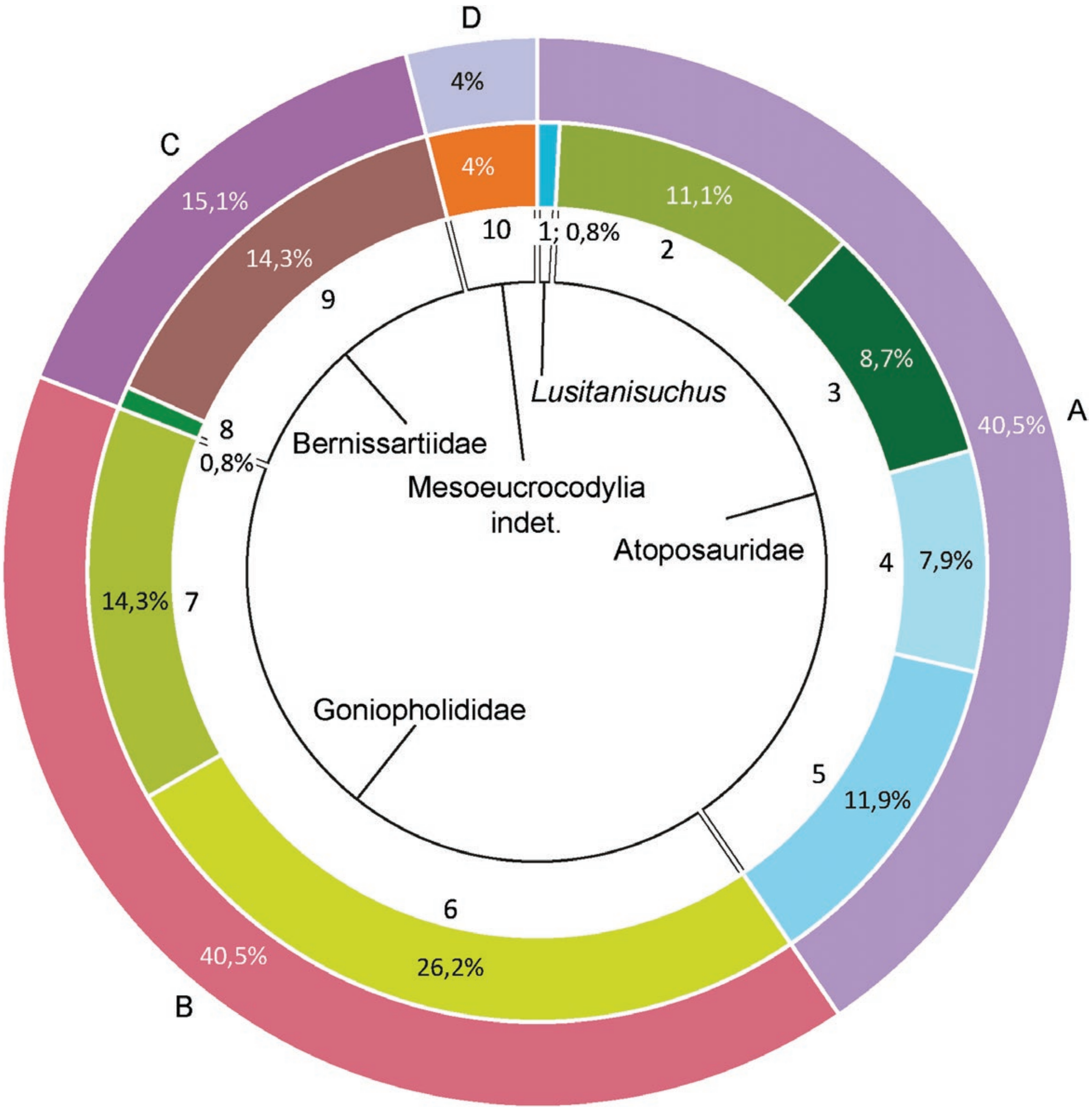

Figure 15. Distribution of the teeth according their morphotypes (1–10) and their ecomorphotypes (A–D), and the corresponding taxa to which they are thus attributed.

Tennant *et al.*, 2016; Schwarz *et al.*, 2017). This high trophic diversity, in the context of freshwater crocodylomorphs (Wilberg *et al.*, 2019) that were relatively small in size, represents an adaptation in an ecosystem otherwise dominated by dinosaurs, where predatory niches were already occupied by medium- and large-sized predators, such as the theropods *Lourinhanosaurus*, *Allosaurus* and *Torvosaurus* (Mateus *et al.*, 2006).

PALAEOECOLOGICAL DIFFERENCES BETWEEN THE VALMITÃO VMA AND THE GUIMAROTA MINE ASSEMBLAGE

The apparent absence of *Lisboasaurus* and the scarcity of *Lusitanisuchus* in the Valmitão vma were unexpected given their relative abundance in the similarly aged Guimarota Mine, suggesting that they were relatively uncommon in the Lourinhã Formation. Even though they are slightly different, the conical teeth observed in IPFUB Gui Croc 8009 and MG26103 share similarities with morphotypes 2 and 7. It is thus possible that a certain degree of uncertainty concerning less well-preserved teeth could have led to the misinterpretation of some teeth by the authors.

Lisboasaurus teeth are characterized by their conical to triangular shape, their blunt apex and the median groove on the labial side, and this morphology has not been observed in any of the teeth from the Valmitão vma. *Lisboasaurus* has been a problematic taxon, with fragmentary material (Milner & Evans, 1991; Buscalioni *et al.*, 1996; Schwarz & Fechner, 2008), and the original material from Guimarota could not be accessed and redescribed during this study. More complete material with a complete tooth arcade may thus shed further light on the tooth morphology and the tooth series of *Lisboasaurus*.

Another important difference between the crocodylomorph assemblages of Valmitão and Guimarota is the absence in the former of the large marine thalattosuchian *Machimosaurus hugii*, isolated teeth of which have been reported from different localities of the Lourinhã Formation and in Guimarota, which also provided skeletal remains (Krebs & Schwarz, 2000; Young *et al.*, 2014).

As suggested by the dominance of terrestrial taxa such as dinosaurs and squamates, together with freshwater amphibians in the assemblage, and considering that all the crocodylomorphs reported here are freshwater taxa (Wilberg *et al.*, 2019), the Valmitão vma can be assumed to have been deposited in a freshwater environment, probably with oxbow lakes as previously interpreted (Gowland *et al.*, 2017), where marine inputs, as evidenced by the presence of bivalves, were limited. However, we should take into account that *Machimosaurus hugii* teeth are usually centimetric in size (Young *et al.*, 2014), i.e. well over the dominant bioclast size found in the Valmitão vma, so a taphonomic bias cannot be ruled out.

Comparison of the crocodylomorph fauna from Valmitão vma with other Mesozoic vmas

Compared to other Mesozoic assemblages in Europe (Fig. 16), the Valmitão crocodylomorph fauna is similar in composition, in that it comprises the four ecomorphotypes described above, even though these ecomorphotypes are not always all represented in the same site in other localities (Schwarz-Wings *et al.*, 2009). Also, conical teeth are often the most highly represented morphology due to their omnipresence among different taxa and ecomorphotypes. However, significant differences in the relative abundance of each ecomorphotype can be seen between localities (Fig. 17).

In the Valmitão vma, ecomorphotypes A and B are equally represented (40.48%), followed by ecomorphotype C (15.08%) and ecomorphotype D (3.97%). This supports the interpretation of Valmitão as a continental environment, as atoposaurids have been proposed to be terrestrial and semi-aquatic crocodylomorphs (Thies *et al.*, 1997; Tennant *et al.*, 2016; Young *et al.*, 2016), suggesting an ecological partitioning with goniopholidids (Tennant & Mannion, 2014).

Quarry 9 in the Morrison Formation (United States, Kimmeridgian–Tithonian in age) is famous for providing an important vertebrate microfossil assemblage that displays significant mammal diversity (Marsh, 1880, 1887). Over 1000 crocodylomorph teeth have been recorded and attributed to both *Goniopholis* sp. and *Macelognathus vagans* (Carrano & Velez-Juarbe, 2006), suggesting that ecomorphotype B was the only one represented in this ecosystem, although it has been interpreted as a fully continental, lacustrine palaeoenvironment (Carrano & Velez-Juarbe, 2006).

The Purbeck-type bonebeds of Chassiron (France, Tithonian in age) yield a rich and diverse vertebrate microfossil assemblage, which includes at least six crocodylomorph taxa (Vullo *et al.*, 2014). From these bonebeds, isolated teeth have been recorded from which the presence of ecomorphotypes A, B, and C can be inferred in equal abundance, as well as a piscivorous ecomorphotype, here associated with the thalattosuchian *Steneosaurus* (Vullo *et al.*, 2014). This assemblage was deposited in a continental lacustrine environment subject to salinity fluctuations (Vullo *et al.*, 2014).

The vertebrate microfossil assemblage from Cherves-de-Cognac (France, Berriasian in age) exhibits an impressive diversity, with 24 vertebrate families represented, including four crocodylomorph ones (Pouech *et al.*, 2006). Although no quantitative data have been provided on the morphotypes observed and the number of teeth recorded for each one, the presence of the three ecomorphotypes A, B and C can be inferred. The Cherves-de-Cognac assemblage was deposited in a lagoon environment that developed under hypersaline to freshwater conditions (El Albani *et al.*, 2004; Mazin *et al.*, 2006).

Even though conical teeth of undetermined ecomorphotype and without taxonomic attribution (Fig. 17A) are fairly well represented (38.56%) in the Scandinavian assemblages of Bornholm and Skåne (Berriasian–Valanginian in age), there is a considerable predominance of ecomorphotype A (58.56%; Fig. 17B). Teeth from ecomorphotype C are extremely rare (2.89%) and ecomorphotype D is not recorded (Schwarz-Wings *et al.*, 2009). This would suggest that Scandinavia was a mainly continental environment in the Early Cretaceous, although the predominance of ecomorphotype A may be biased by

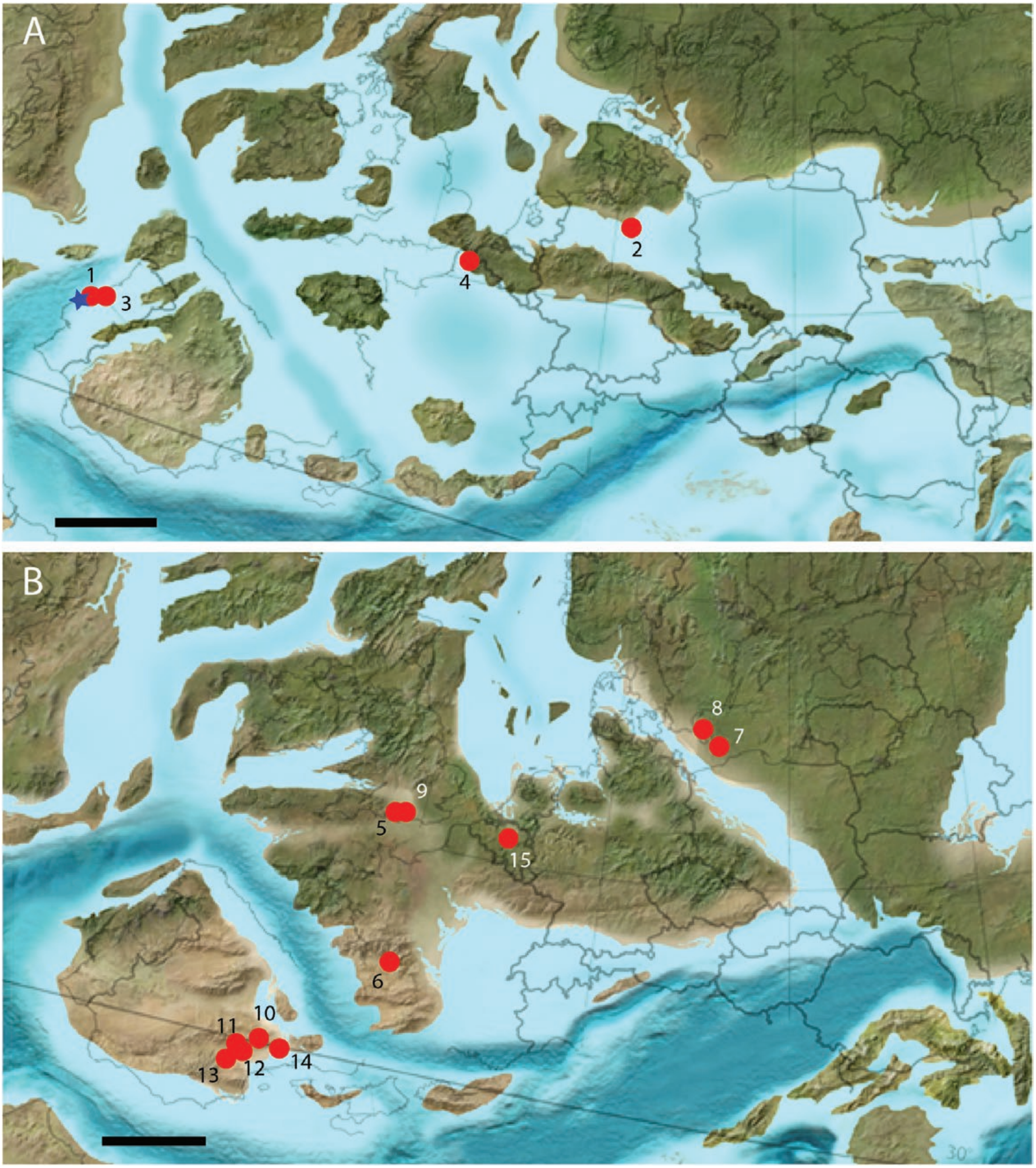

Figure 16. Palaeogeographic maps of Europe with Upper Jurassic (A) and Lower Cretaceous (B) localities yielding mesoeucrocodylian assemblages with *Goniopholis*, *Theriosuchus* and *Bernissartia*. Blue star indicates the locality of Valmitão, Lourinhã Formation (Ribamar, Portugal). 1. Guimarota Mine, Alcobaça Formation (Leiria, Portugal). 2. Langenberg/Oker, Langenberg Formation (Germany). 3. Andrès, Alcobaça Formation (Pombal, Portugal). 4. Montrouge and La Rochette II, the Formations généreuses (Boulogne-sur-Mer & Wimille, France). 5. Swanage, Purbeck Limestone Group (Dorset, England). 6. Cherves-de-Cognac, gypsum and marlstone units equivalent to Purbeck Limestone Group (France). 7. Arnager, Rabekke

misidentification on the part of the authors, and the absence of ecomorphotype B cannot be ruled out, even though it is not supported here.

The Angeac assemblage (France, Hauterivian–Barremian in age) is another microvertebrate site that yields more than 1000 teeth, mainly attributed to Goniopholididae and Pholidosauridae (Néraudeau *et al.*, 2012; Gônet *et al.*, 2019), this ecosystem thus being dominated by ecomorphotype B. The Angeac assemblage has been interpreted as a floodplain deposit with a continental paleoenvironment and scarce marine influence (Néraudeau *et al.*, 2012), which is congruent with the relative abundances of crocodylomorph tooth ecomorphotypes.

Ecomorphotypes B and C are similar in abundance (46.43% and 45.6%, respectively; Fig. 17B) in the La Cantalera assemblage (Spain, Lower Barremian in age), whereas teeth attributed to ecomorphotype A are underrepresented (7.14%) and ecomorphotype D (0.82%) is the scarcest (Puértolas-Pascual *et al.*, 2015b). This distribution of ecomorphotypes supports the interpretation of the La Cantalera assemblage as a floodplain deposit in a lentic ecosystem with short lacustrine episodes of swamp vegetation (Aurell *et al.*, 2004; Canudo *et al.*, 2010), dominated by terrestrial taxa, suggesting that the site could have been a feeding area for herbivorous dinosaurs (Puértolas-Pascual *et al.*, 2015b).

In contrast to La Cantalera and similar to the Scandinavian sites, the Buenache de la Sierra assemblage (Spain, Upper Barremian in age) is dominated by teeth of ecomorphotype A (43.6%; Fig. 17B) (Buscalioni *et al.*, 2008). Unlike other localities with a predominance of ecomorphotype A, the dominance of ecomorphotype B (24%) towards the ecomorphotype C (16.4%) is not as marked, although a significant number of conical teeth (15.6%) could not be attributed to any ecomorphotype (Buscalioni *et al.*, 2008). The Buenache de la Sierra assemblage is dominated by both obligate and amphibious taxa and has been interpreted as a swamp environment (Buscalioni *et al.*, 2018), supposedly wetter than La Cantalera (Puértolas-Pascual *et al.*, 2015b). Although atoposaurids are semi-aquatic, the interpretation of the ecomorphotypes does not strongly support the palaeoenvironmental interpretation. This may be due either to a taphonomic or a sampling bias. Alternatively, teeth of ecomorphotype A were misinterpreted by the authors as teeth of ecomorphotype C in La Cantalera, or vice versa in Buenache de la Sierra. It is notable that the authors did not observe any teeth from morphotypes 2 or 3 in La Cantalera, or from morphotype 8 in Buenache de la Sierra (Fig. 17A).

The Wealden Group of the Isle of Wight (England, Barremian in age) yields a vertebrate microfossil assemblage (Sweetman, 2011a) with 11 crocodylomorph species recorded to date (Salisbury & Naish, 2011; Sweetman, 2016). Quantitative data are not provided regarding the different morphotypes observed among the isolated teeth, or their abundance in the assemblages. However, it can be inferred that the four ecomorphotypes A, B, C and D are represented, and possibly more could be present (Sweetman, 2016). The group was deposited in a floodplain setting (Stewart, 1981, 1983; Sweetman, 2016) and has been interpreted as a continental lacustrine paleoenvironment (Sweetman, 2011b).

The Cloverly Formation (United States, Aptian in age) yields a large number of vertebrate microfossil assemblages in which crocodylomorph teeth have been recorded (Oreska *et al.*, 2013; Carrano *et al.*, 2016). Ecomorphotype A is the most frequent (48.02%; Fig. 17B), whereas ecomorphotype B (25.82%) and ecomorphotype C (5.43%) are underrepresented and ecomorphotype D is absent (Oreska *et al.*, 2013; Carrano *et al.*, 2016). However, a significant number of teeth (20.72%) were not attributed to any ecomorphotypes and only taxonomically attributed to crocodyliforms. The Cloverly Formation assemblages are dominated by terrestrial taxa, and semi-aquatic taxa are not diverse there (Carrano *et al.*, 2016). The relative abundance of crocodylomorph tooth ecomorphotypes recorded in the Cloverly Formation assemblages is congruent with the interpretation of a continental lacustrine paleoenvironment, with a setting near a coastal margin (Oreska *et al.*, 2013; Carrano *et al.*, 2016).

The Tremp Formation (Spain, Maastrichtian in age) also yields relevant vertebrate microfossil assemblages (Marmi *et al.*, 2016), in which up to ten crocodylomorph taxa have been identified (Blanco *et al.*, 2018, 2019). Although different morphotypes from those of Valmitão were observed, mostly due to the temporal and spatial gap, the four ecomorphotypes A, B, C and D were represented (Fig. 17B), together with a piscivorous ecomorphotype (Blanco *et al.*, 2019). Ecomorphotype B (56.13%) is by far the most abundant,

Formation (Bornholm, Denmark). 8. Eriksdal, Annero Formation (Skåne, Sweden). 9. Isle of Wight, Wessex Formation (England). 10. Galve, El Castellar Formation and Camarillas Formation (Teruel, Spain). 11. Uña, Uña Formation (Cuenca, Spain). 12. Pio Pajarón, Uña Formation (Cuenca, Spain). 13. Buenache de la Sierra, La Huérguina Limestone Formation (Cuenca, Spain). 14. Vallipón and La Cantalera, Artoles Formation and Blesa Formation (Teruel, Spain). 15. Bernissart, Sainte-Barbe clays (Belgium). Modified from Schwarz-Wings *et al.* (2009); palaeomaps from Colorado Plateau Geosystem. Scale bars are 400 km.

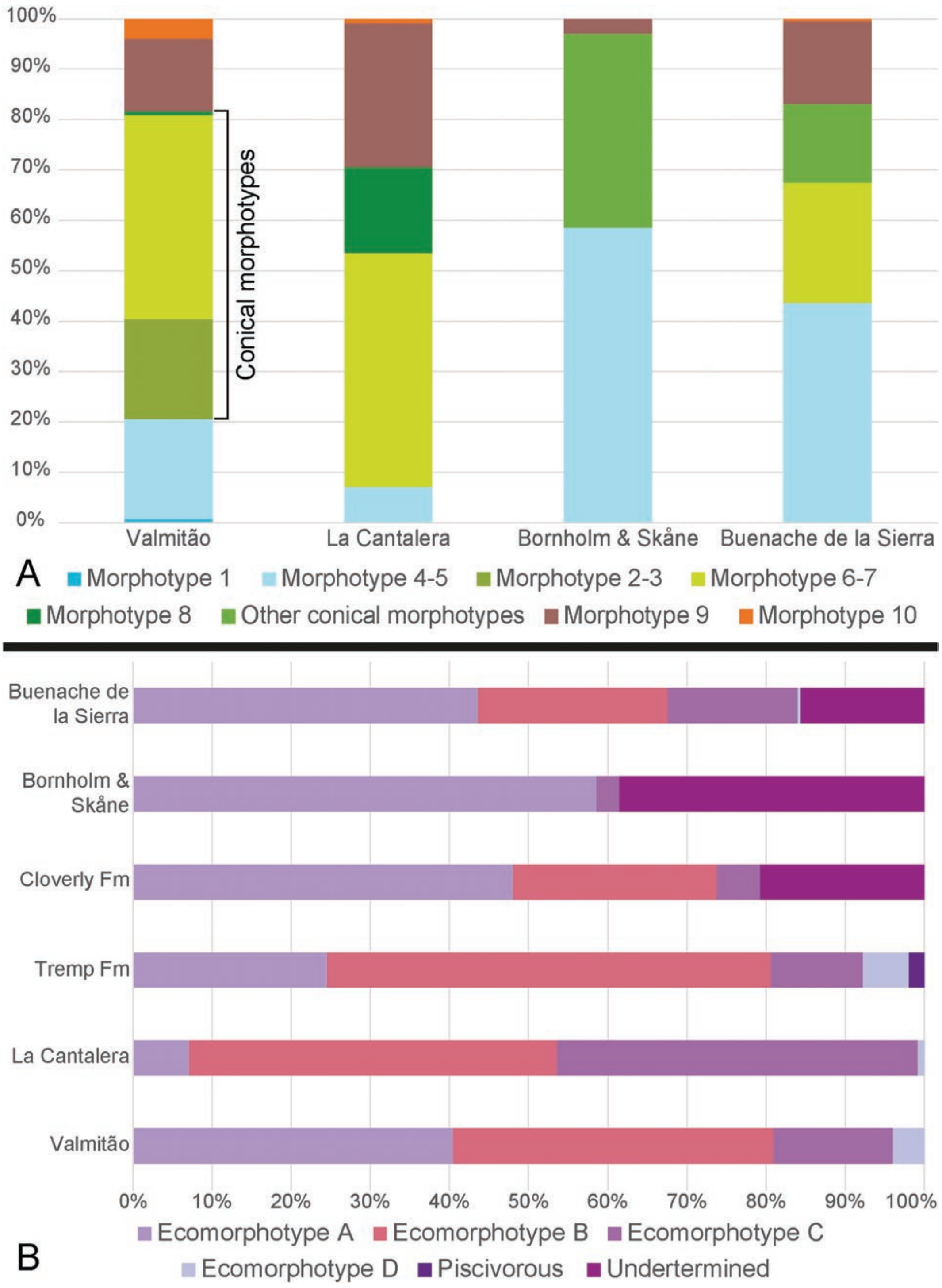

Figure 17. Crocodylomorph tooth distribution from the La Cantalera (Puértolas-Pascual *et al.*, 2015b), the Bornholm & Skåne (Schwarz-Wings *et al.*, 2009) and the Buenache de la Sierra (Buscalioni *et al.*, 2008) assemblages, also with assemblages from the Cloverly Formation (Oreska *et al.*, 2013; Carrano *et al.*, 2016) and the Tremp Formation (Blanco *et al.*, this volume), compared with the Valmitão vma, according to tooth morphotypes (A) and their ecomorphotypes (B).

whereas ecomorphotypes C (11.61%) and A (24.52%) are underrepresented and ecomorphotype D (5.81%) and the piscivorous ecomorphotype (1.94%) are scarce (Blanco *et al.*, 2019), suggesting a floodplain deposit in a continental lacustrine paleoenvironment. Using different vmas, the authors inferred environmental preferences for each taxon according to the depositional environment (Blanco *et al.*, 2019).

Further studies are needed to confirm whether these dietary signals correlate with differences in the proportions of arthropods and small vertebrates in the corresponding ecosystems. Including the crocodylomorph teeth, the Valmitão vma yields 427 vertebrate remains, of which 283 could be identified and attributed to a low taxonomic rank, resulting in four obligate taxa, six amphibious taxa and nine facultative taxa. The preliminary list of the elements picked can be found in the Supporting Information, Data S1).

CONCLUSION

As part of a systematic sampling of the vertebrate microfauna of the Lourinhã Formation, sediments from the locality of Valmitão were sampled and sieve residues picked. A new collection of 126 crocodylomorph teeth is here described. These were identified in order of abundance as belonging to Goniopholididae, Atoposauridae, Bernissartiidae, an undetermined mesoeucrocodylian taxon and *Lusitanisuchus mitracostatus*.

Compared to the contemporary Portuguese locality of Guimarota Mine, the absence of big marine crocodylomorphs, such as *Machimosaurus hugii*, in conjunction with the palaeofaunal composition of the assemblage, suggests a more continental environment for Valmitão vma, dominated by terrestrial and amphibious taxa. The apparent scarcity of *Lusitanisuchus mitracostatus* and the absence of *Lisboasaurus estesi* suggest that these animals were rare components in Valmitão, although a certain degree of uncertainty concerning less well-preserved teeth could have led to the misinterpretation of some conical teeth by the authors.

The teeth were classified according to four different ecomorphotypes, associated with four different feeding habits: (A) spatulate, broad-leaf-shaped, lanceolate to conical teeth associated with arthropods and small-vertebrate feeders, (B) conical teeth associated with generalist taxa, (C) molariform to conical teeth associated with durophagous taxa and (D) subconical ziphodont teeth associated with carnivorous predators. The Valmitão crocodylomorph assemblage is consistent with assemblages observed in other European Late Jurassic–Early Cretaceous localities as regards the presence of the four ecomorphotypes described. Compared with other Mesozoic vmas, the Valmitão vma is co-dominated by ecomorphotypes A and B, whereas ecomorphotype C is underrepresented and ecomorphotype D scarce. Using crocodylomorph teeth, vertebrate microfossil assemblages bring to light the hidden diversity of this group. Other assemblages with similar ecomorphotype diversity but higher taxonomic diversity suggests that the species diversity at the Valmitão site is underestimated.

ACKNOWLEDGMENTS

We thank the Museu da Lourinhã for hosting this study and allowing the preparation and observation of the specimens. We also thank André Saleiro, who screen-washed the sediments used for this study, and Alexandra Fernandes, André Bonito, Vincent Cheng, Miguel Marx, Helena Oliveira, Roberto Silva, Cátia Ribeiro and Victor Takev, who helped with the picking of the sediments. The authors would like to acknowledge the use of the Servicio General de Apoyo a la Investigación-SAI, Universidad de Zaragoza. We are thankful to the reviewers who helped to improve the manuscript and this study with their comments, and to Rupert Glasgow for revising the English.

FUNDINGS

Eduardo Puértolas-Pascual (SFRH/BPD/116759/2016) and Miguel Moreno-Azanza (SFRH / BPD / 113130 / 2015) hold postdoctoral grants funded by the Fundação para a Ciência e Tecnologia (FCT-MCTES) of Portugal. This work was supported by Fundação para a Ciência e a Tecnologia project PTDC/CTA-PAL/31656/2017.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Supplementary Data 1. List of remains picked from the sediments of the Valmitão vma according the taxa they have been attributed.

Supplementary Data 2. Selected measurements (in mm for lengths, in degrees for angles) of the crocodylomorphs teeth morphotypes. NLgS, number of lingual striations; NLbS, number of labial striations; DoM, Denticles on mesial and distal margins.