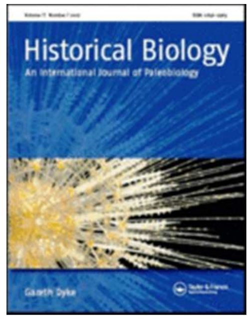

Unusually thick dinosaur eggshell fragments from the Late Cretaceous of The Iberian Range, Spain.

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Unusually thick dinosaur eggshell fragments from the Late Cretaceous of Spain.

Julio Company

Departamento de Ingeniería del Terreno, Universidad Politécnica de Valencia, 46022 Valencia, Spain

Unusually thick dinosaur eggshell fragments from the Late Cretaceous of Spain.

Recent fieldwork carried out in the south-eastern branch of the Iberian Range (Valencia province, Spain) has produced a large collection of dinosaur eggshell fragments of unusual thickness. The specimens, up to 4.8 mm thick, were recovered from palustrine grey marls of the upper Campanian-lower Maastrichtian Sierra Perenchiza Formation, which constitutes the deposits of a wetland paleoenvironment. The eggshell fragments exhibit a characteristic compactituberculate ornamentation, a tubospherulitic organization, and a complex canaliculate respiratory system. The external tuberculate surface of the shell and the internal microstructure permit to refer the studied specimens to *Megaloolithus* aff. *siruguei*, the most common megaloolithid oospecies in the Iberian Peninsula and Southern France. The biostratigraphic range of *Megaloolithus siruguei* matches the temporal distribution of titanosaurid dinosaurs in the Iberian Range, which are tentatively considered to be potential producers.

Keywords: dinosaur eggshells, Megaloolithidae, *Megaloolithus* aff. *siruguei*, Late Cretaceous, Spain.

Introduction

The Upper Cretaceous continental deposits of the Iberian Peninsula and Southern France (Ibero-Armorican Island) have produced an extensive record of dinosaur remains since the 19th century (Allain & Pereda-Suberbiola 2003; Csiki-Slava et al. 2015; Canudo et al. 2016). The most productive localities are principally concentrated in the Pyrenean domain (Spain and France), Provence and Occitan (south-eastern France), and the Iberian Range (eastern Spain). This record includes skeletal remains as well as abundant oological and ichnological material. Up to eight different eggshell taxa have been defined in the Ibero-Armorican domain (Vianey-Liaud et al. 2003), albeit nowadays not all them are considered valid oospecies (for a complete revision, see Sellés, 2012; Fernández and Koshla, 2013).

Recent fieldwork carried out in the foothills of the Sierra de Malacara (southwestern Iberian Range, Valencia province, Spain) has yielded abundant dinosaur eggshell fragments of the megaloolithid type. The fragments, of unusual shell thickness, greatly exceeds the usual parameters described for the megaloolithid structural type (Vianey-Liaud et al. 1994). The aim of the present work is to provide a detailed description of the microstructure of the recovered specimens, to determine their taxonomic position within the family Megaloolithidae, and to chronostratigraphically test the main hypothesis about the identity of the producer dinosaur group.

Locality and stratigraphy

The material described herein was collected from pale grey-pink pedogenic marls exposed in a 20-metres roadcut of deposits of the Late Cretaceous Sierra Perenchiza Formation in the southern part of the Iberian Range (eastern Spain), next to the Yegüeros creek, approximately 8 km west of the village of Buñol, Valencia province (Figure 1). The Sierra Perenchiza Formation constitutes a late Campanian-early Maastrichtian carbonate succession of interbedded palustrine marls and limestones with strong evidence of pedogenic modification (Vilas et al. 1982; Alonso et al. 1991; Garcia et al. 2004). These facies represent the sediments of seasonal wetlands, heavily modified by vegetation and by subaerial exposure (Freytet & Plaziat 1982; Wright & Platt 1995, Alonso-Zarza & Wright 2010).

Neighbouring outcrops of the Sierra Perenchiza Formation, located about 20 km to the north, have yielded a rich vertebrate assemblage composed largely of dinosaurs, crocodiles, pterosaurs, and aquatic chelonians. Microvertebrate remains have also been recovered by screen-washing the sediments, including bony fish, squamates and amphibians, together with tiny eggshell fragments, freshwater invertebrates (gastropods, ostracodes, and bivalves), and charophyte remains (Company 2004; Company & Szentesi 2012).

The paleoecological association and the sedimentological traits of these deposits place the Sierra Perenchiza fossil localities in a palustrine paleoenvironment at the end of the Cretaceous, settled in the western Tethyan margin of the Iberian coastline.

Materials and methods

More than 100 eggshell fragments were recovered by surface prospecting in a single collecting site of approximately 500 square meters. They range from small pieces of few millimetres up to larger pieces of 3.5–4 cm in size. Even smaller fragments were recovered by screen-washing a bulk sample of sediment (ca. 25 kg), which also produced tiny fragments of crocodile eggshells, abundant charophyte remains, ostracodes and fragmentary freshwater gastropods. Neither complete eggs nor dinosaur skeletal remains were found in the locality. The specimens are relatively equally well-preserved, without noticeable signs of abrasion, and display a similar external appearance, so it is presumed that the fragments had not been subject to significant transportation and come from the same nesting area.

Eggshell fragments were cleaned with 30 sec. ultrasonic baths. The process was monitoring using a stereomicroscope. Shell thickness of each specimen was estimated as the mean of three different measurements taken with a digital micrometer. Radial thin sections of the specimens were prepared following standard petrographic methods. The sections were studied under a petrographic microscope (Olympus BXTR BX40), in both normal and polarized light. Images were captured with a mounted digital camera (Sony Cybershot TM QX-100) and edited with Adobe© Photoshop CS5©. Surface ornamentation and microstructural organization of smaller Au, Pd-coated fragments were examined using a scanning electron microscope (Philips XL30 ESEM FEG). Nomenclature and definitions of eggshell microstructure used here are mainly based on Mikhailov (1997). Specimens have been temporarily deposited in the collections of the Polytechnic University of Valencia (Valencia, Spain).

Systematic palaeontology

Oofamily Megaloolithidae Zhao, 1979

Oogenus *Megaloolithus* Vianey-Liaud, Mallan, Buscail and Montgellard, 1994

Megaloolithus aff. *siruguei* Vianey-Liaud, Mallan, Buscail and Montgelard, 1994

Figs. 2 & 3

Description

The eggshell fragments are composed of a single structural layer of calcite with a well preserved surficial ornamentation (Figure 2). The eggshell thicknesses ranges from 1.8 to 4.8 mm, with an average of 3.45 mm (n = 125). The outer surface displays a distinct compactituberculate ornamentation, consisting mostly of relatively rounded to polygonal nodes which constitute the top of the shell units (Figures 2a-c). Occasionally, neighbouring nodes coalesce, forming small chains. The average node diameter is about 0.59 mm, ranging from 0.34 to 0.90 mm in size. The pore openings are located in the internodular spaces (Figures 2b-c). They are subcircular in shape and have diameters ranging from 50 to 250 µm approximately.

In radial section, the eggshells consist of a single structural layer composed of fan-shaped shell units of acicular calcite. Arched accretionary lines run from the base to the top of the units (Figures 2e-f, Figure 3). The crystal units are spherulitic and extremely high and narrow (average height/width ratios range from 4.4:1 to 6.1:1). A few units are fused upwardly. In general, the shell units do not have parallel margins, as their borders diverge at angles between 20º and 25º (Figure 2f).

The respiratory system is multicanaliculate (Mikhailov 1997). It consists of a branching network of relatively straight, vertical primary canals with occasional (transverse) anastomoses, forming a complex three-dimensional respiratory system (Figure 2f). This eggshell structural type correlates with a high gas conductance, characteristic of nesting in humid environments (Mikhailov 1997, López-Martínez et al. 2000; Deeming, 2006; Jackson et al., 2008; Tanaka and Zelenitsky, 2013). Many of the vertical canals have been enlarged into galleries, filled posteriorly by diagenetic, coarse sparry calcite cement during diagenesis (Figure 2f, Figure 3). The contour of these cavities is irregular, suggesting dissolution of the boundaries of the shell units (Bravo et al., 2006; Moreno-Azanza et al. 2016).

The inner surface of the shell is covered by irregular mamillae in different degrees of dissolution (Figure 2d). The *membrana tesacea* is mostly missing in the examined specimens; only rare remnants persist covering the base of the spherulites (Figure 3). Occasional extra-spherulites are dispersed throughout the shell (Figure 2f).

Discussion

The external compactituberculate ornamentation, along with the tubospherulitic (discretispherulitic) organization and the canaliculate pore system of the eggshell fragments permit to refer the studied specimens to the oofamily Megaloolithidae (Zhao, 1979; Vianey-Liaud et al. 1994).

Megaloolithid eggs are widely distributed in the Upper Cretaceous deposits of the Ibero-Armorican landmass of the European archipelago (Iberian Peninsula and southern France), as well as in other Laurasian and Gondwanan paleoprovinces, and thus have a worldwide distribution (Powell, 1992; Grigorescu et al. 1994; Sahni et al. 1994;Vianey-Liaud et al. 1994, 2003; Mikhailov, 1997; Calvo et al. 1997; Vianey-Liaud & Lopez-Martinez 1997; Mohabey 1998; Chiappe et al. 1998; Garcia 2000; Garcia & Vianey-Liaud 2001a, 2001b; López-Martínez 2003; Garcia et al. 2003; Grellet-Tinner et al. 2004; Jackson 2007; Grigorescu et al. 2010; Griebeler & Wermer 2011; Grellet-Tinner et al. 2012; Fernández & Khosla 2015).

The most striking feature of the studied specimens is their unusual shell thickness, often exceeding 3.5 mm and reaching a maximum value of 4.8 mm, which are noticeably greater than the corresponding values of the different megaloolithid taxa, that rarely reach 3.0 to 3.5 mm in thickness (Vianey-Liaud et al. 1994; Sellés 2012 and references therein). Only four valid Late Cretaceous megaloolithid species are considered to be medium- to thick-shelled taxa (Sellés et al, 2012), and exhibit high (i.e., >3:1) length-to-width ratios of the shell units: *Megalolithus cylindricus*, *M. khempuriensis*, *M. megadermus*, and *M. siruguei*. Whereas *M. khempuriensis* and *M. megadermus* eggs are restricted to the Upper Cretaceous beds of Lameta Formation, in India (Mohabey 1998), *M. cylindricus*, has also been reported from South America (Kholsa & Sahni 1995; Fernández & Khosla 2015). Thus, all three oospecies have a Gondwanan distribution. By contrast, *M. siruguei* is a Laurasian taxon, exclusively documented in the European archipelago. *M. siruguei* constitutes the most common megaloolithid oospecies in the Upper Cretaceous of the Iberian Peninsula and southern France (Moratalla 1993; Vianey-Liaud et al. 1994, 2003; López-Martínez et al. 2000; Garcia & Vianey-Liaud 2001; Bravo et al 2005, 2006; Vila et al. 2009, 2010, 2011; Sellés 2012; Sellés et al. 2013; Sellés & Vila 2015).

Regarding *M. megadermus*, some authors consider it an invalid, pathologic ootaxon (Sellés 2012), while others consider it a valid species (Mohabey, 1998;

Fernández, 2013; Fernández & Khosla 2015). The general features of *M. megadermus* (Mohabey, 1998) resemble those of the Valencia eggshells, especially the strong shell thickness, the coarse compactituberculate ornamentation, and the proportions of the elongate, fan-shaped shell units. Nevertheless, the absence of a complex (i.e. multicanaliculate) respiratory system in *M. megadermus*, prevents from placing the Valencian specimens in this ootaxon. *M. cylindricus* exhibits “regular”, never-fused cylindrical shell units, more rounded and well-separated ornamental nodes, and simple, vertical respiratory canals (Khosla & Sahni 1995), features not seen in the studied samples. Moreover, the taxonomical validity of *M. cylindricus*, has been recently questioned (Mohabey 1998; Khosla and Sahni 1995). Finally, *M. khempuriensis* also differs from the Valencian specimens in the reduced thickness of the shell and in lacking a complex pore system organization (Mohabey 1998).

The only thick-shelled megaloolithid oospecies provided with a three-dimensional pore system is *M. siruguei* –and its junior synonym *M. multituberculata* (Vianey-Liaud et al. 1994; Sellés 2012; Bravo & Gaete 2015). Even though the *M. siruguei* type material and the large number of specimens recovered elsewhere display lower values of shell thickness, ranging between 1.84 and 3.18 mm (Vianey-Liaud et al. 1994; López-Martínez et al. 2000; Vianey-Liaud et al. 2003; Bravo et al. 2005; Vila et al. 2009, 2010, 2011; Sellés 2012; Sellés et al. 2013), in certain Campano-Maastrichtian Iberian localities (La Rosaca and La Tejera sites, Burgos province), extremely thick megaloolithid eggshell fragments of up to 5.46 mm have also been referred to by this ootaxon (Izquierdo et al. 2001; Bravo et al. 2006; Moreno et al. 2016). Despite certain differences of ornamentation and shape of the shell units that these specimens display (Bravo et al. 2006, p. 229; Moreno-Azanza et al. 2006, p.5/17), given the morphological variability usually observed in fossil oospecies, they have been ascribed to this Late

Cretaceous oospecies. The close similarity between the Valencian samples and the abovementioned specimens is indisputable. Additionally, the taphonomic history of the eggshells from both localities followed a similar pattern resulting in an enlargement of some pore canals in dissolution galleries, later filled with equant (blocky) calcite spar, combined with the appearance of extra-spherulites of diagenetic origin (Moreno-Azanza et al., 2016).

Other Upper Cretaceous megaloolithid oospecies reported in the Ibero-Armorican Island are *Megaloolithus aureliensis* (= *M. Peralta*), *Megaloolithus mamillare* (= *M. baghensis*, recently renamed *Fusioolithus baghensis* in Fernández & Khosla (2015)), and *Megaloolithus jabalpurensis* (= *M. patagonicus*) (Vianey-Liaud et al. 2003; Bravo et al. 2005; Vila et al. 2011; Sellés 2012; Sellés et al 2013; Bravo & Gaete 2015). The shells of these taxa clearly differ from those of the studied specimens in their general microstructure: they all display thinner shells composed of shorter and wider spherulitic units, that are frequently fused producing coalescent nodes on the external surface, and lack the complex multicanaliculate respiratory system characteristic of *M. siruguei*.

Therefore, in accordance with the microstructural features observed in the eggshell material from Valencia, and taking into account the well-known morphological variability observed inside each taxa of the oofamily Megaloolithidae (Mikhailov 1997) which has allowed a profusion of invalid oospecies (Vianey-Liaud et al. 2003; Sellés 2012; Fernandez & Khosla 2015; Bravo & Gaete 2015), the recently discovered megaloolithid material from the Sierra Perenchiza Formation in Valencia province fits in the range of variation of the thick-shelled variety of *M. siruguei* (Bravo et al. 2005; Moreno-Azanza et al., 2006), and is hereafter assigned to *Megaloolithus* aff. *siruguei*.

This small oological sample from Valencia province provides important information on the oodiversity of dinosaur faunas in one of the most meridional areas of the European archipelago just before the Cretaceous–Paleocene event, improving the data provided by coeval localities of the south-central and south-eastern Pyrenees and the Iberian Range.

Megaloolithus siruguei record in the Iberian Peninsula and association with titanosaurian dinosaurs

There is a general consensus that the megaloolithid eggs were laid by titanosaurian sauropods (Powell, 1992; Calvo et al. 1997; Mikhailov 1997; Grellet-Tinner et al. 2012), especially after the discovery of sauropod embryonic remains inside megaloolithid eggs in Argentina (Chiappe et al. 1998, 2003; Grellet-Tinner et al. 2004). The occurrence in Romania of Upper Cretaceous (upper Maastrichtian) nesting horizons with clutches of megaloolithid eggs (*Megaloolithus* cf. *siruguei*) associated with hatchling and embryo remains of the basal hadrosaur *Telmatosaurus transsylvanycus* (Grigorescu et al. 1994, 2010) calls in doubt that megaloolithid-type eggs are exclusive of sauropods.

In the Iberian Peninsula, the most extensive record of eggshells, eggs, and clutches belonging to the family megaloolithidae comes from the Upper Cretaceous continental deposits of the south Pyrenean domain (Vila et al. 2011; Sellés et al 2013; Sellés & Vila 2015; Bravo & Gaete 2015), which consist of a continuous stratigraphic record of transitional and continental sediments ranging up to1000-m-thick from the late Campanian to the Paleogene (Oms et al. 2007; Vila et al 2011). The oological record often co-occurs with a rich record of both dinosaur skeletal remains and ichnological sites.

According to recent reviews, between 150 and 200 dinosaur localities have been identified in the foothills of the southern Pyrenees (Sellés & Vila 2015; Oms et al. 2016; Canudo et al. 2016). The faunal composition of the sites illustrates a clear predominance of titanosaurian sauropods and hadrosaurid ornithopods over ankylosaurians and theropod dinosaurs (Riera et al. 2009; Vila et al. 2016; Canudo et al. 2016). Even though titanosaurs are almost continuously present from the basalmost terms of the sedimentary sequence (late Campanian) to the Cretaceous/Paleogene boundary, there is a gradual decline in the abundance of remains towards the end of the Maastrichtian (albeit there is an apparent increase in their taxonomical diversity: Vila et al. 2012). Meanwhile, the hadrosaurids, which are completely absent from the late Campanian to the early Maastrichtian, increases gradually their presence, and become the dominant group at the end of the Maastrichtian (Riera et al 2009; Vila et al. 2016; Canudo et al. 2016). Similarly, any member of Megaloolithidae is present throughout all the sedimentary sequence, and *M. siruguei* eggs and eggshells tend to be more frequent in Upper Campanian to lower Maastrichtian deposits (Vianey-Liaud & López-Martínez 1997; López-Martínez et al 2000; Garcia & Vianey_Liaud 2001b; López-Martínez 2003; Vila et al. 2009, 2010, 2011; Sellés 2012; Sellés et al. 2013; Sellés & Vila 2015), just when the sauropod (i. e., titanosaurian) skeletal record is more abundant. The last occurrence of *M. siruguei* is located in the lower part of the late Maastrichtian, near the C31r-C31n reversal (Vila et al. 2011; Sellés et al. 2013), which chronologically marks the first appearance of the hadrosaurids in the Ibero-Armorican domain (Riera et al. 2009; Canudo et al. 2016). Up to now, no *M. siruguei* remains have been reported from the younger sediments that have produced the rich hadrosaurid fauna of the Ibero-Armorican domain.

Megaloolithid eggs and eggshells are not only present in the Pyrenean realm, but also in other geological domains of the Iberian Peninsula, as the Iberian Range. The Iberian Range is a large NW–SE fold belt generated, like the Pyrenees, as a result of the Alpine compression in the eastern part of the Iberian Peninsula. Exposures of Late Cretaceous continental deposits occur along the northwestern and south-eastern margins of the range (Vilas et al. 1982; Alonso et al. 1991) where at least three different continental formations have produced oological remains. Hundreds of megaloolithid eggshell fragments have been recovered from Campanian-Maastrichtian strata in Burgos, Cuenca and Valencia provinces (Gutiérrez & Robles 1976; Moratalla 1993; Izquierdo et al. 2001; Company, 2004; Bravo et al. 2006; Moreno-Azanza et al. 2016). The occurrence of megaloolithid eggs and titanosaurian remains has been documented in each of these stratigraphic formations.

The stratigraphic distribution of Upper Cretaceous eggshells and dinosaur skeletal remains in the Iberian Range is very similar to that in the Pyrenean record. Eggshell fragments of *M. siruguei* (Moratalla 1993; Izquierdo et al. 2001; Bravo et al. 2006) and titanosaurian remains (Izquierdo et al. 2001; Company et al. 2009; Ortega & Pérez-García, 2009; Ortega et al. 2015) occur only in late Campanian-early Maastrichtian formations. The first appearance of hadrosaurid remains in the Iberian Range is dated to the end of the Maastrichtian (Company 2004), far from the last occurrence of *M. siruguei*. Therefore, the co-occurrence of titanosaur remains and *M. siruguei* material in in coeval deposits of the Iberian Range matches with that observed in the southern Pyrenees and gives support to the extended acceptance that there is a close relationship between titanosaur sauropods and megaloolithid eggs. Therefore, the oological material from Valencia is tentatively assigned to titanosaurian dinosaurs.

In sum, none of the late Campanian-early Maastrichtian dinosaur localities from the Ibero-Armorican Island that have yielded *M. siruguei* material and titanosaur remains have provided hadrosaurid fossils. Late Maastrichtian formations, which have produced hadrosaurid remains, have not yielded *M. siruguei* eggshells. This disparity makes it highly improbable that this oospecies, at least in the Iberian domain, was laid by hadrosaurid dinosaurs. This fact does not contradict that other megaloolithid-type eggs belong to hadrosaurs, given their direct associations in Central Europe.

Conclusions

The dinosaur eggshell fragments recently recovered from the Upper Cretaceous beds of the Iberian Range, Valencia province (Spain) can be referred to the oofamily Megaloolithidae. The egg fragments are close similar to and exhibit the main microstructural features of *Megaloolithus siruguei* from southern France, south-central Pyrenees and other egg-producing localities of the Iberian Range. Even though these fragments display thicker shells than the type material, analogous eggshells from diverse Late Cretaceous Iberian localities have been referred to as the above-mentioned oospecies. In accord with recent discoveries and the chronostratigraphic distribution of dinosaur groups in the Iberian Range, the egg material is likely to have been laid by titanosaurian sauropod dinosaurs.

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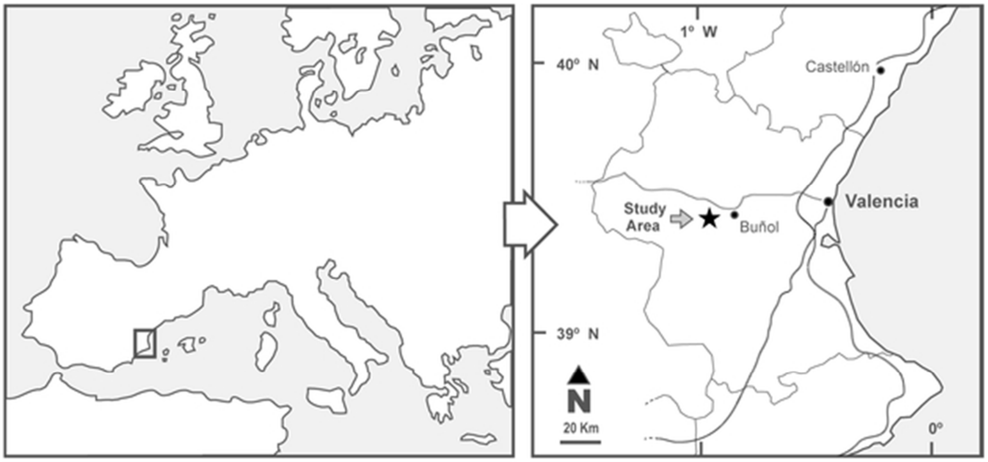
511 Figure 1. Sketch maps showing the locality from which the specimens were collected. Inset shows the position of the sketch map of Valencia province showing the location (star) of the collecting site, in the vicinity of Buñol village (exact location on file at DGPC, Generalitat Valenciana).

515 Figure 2. *Megaloolithus* aff. *siruguei* from the Late Cretaceous Sierra Perenchiza Formation (Valencia province, Spain). (a–c), SEM photographs of the outer eggshell surface, showing the compactituberculate ornamentation composed of densely packed nodes (a–b). Note the occasional coalescence of the nodes (b). White arrows mark the position of the pore apertures (b–c). (d), SEM photograph of the inner surface showing partially dissolved mamillae. (e), SEM photograph in radial view showing the shape of the fan-shaped units made of acicular calcite crystals radiating from the nucleation centres. (f), Polarized light microscope photograph of a radial thin section showing the highly elongated fan-shaped units, with a few fused units (red arrow). Growth lines are markedly convex and end at the margins of the shell units. Note the presence of extra-spherulites (green arrows) and the prolatocanaliculate canal system sometimes linked by transverse channels (blue arrows).Anastomosed canals are coloured for a better view. Scale bar in (c) = 1 mm.

528 Figure 3. *Megaloolithus* aff. *siruguei* from the Late Cretaceous Sierra Perenchiza Formation (Valencia province, Spain). Polarized light microscope photograph of a radial section showing the fan-shaped morphology of the elongated shell units and the presence of extended cavities filled with sparry calcite cement. Remains of a membrane partially covers the base of the spherulites (white arrows). Abbreviations: **al**, accretionary lines; **acc**, acicular calcite crystals; **ca**, cavities. Scale bar = 0.5 mm.

534 Fig. 4. (a), map of the main Late Cretaceous megaloolithid, hadrosaur and titanosaur-producing localities in the Iberian Peninsula. (b), chronostratigraphic ranges of megaloolithid oospecies in the Ibero-Armorican realm (data from the Iberian Range in a separate graph. Star marks the chronostratigraphic position of the studied locality). (c),

Stratigraphic distribution of titanosaur and hadrosaur occurences in the northern Pyrenees (grey graphs), southern Pyrenees (black graphs), and the Iberian Range (white graphs). (a, modified from Vissers & Meijer 2012; b, c, modified from Sellés & Vila 2015).



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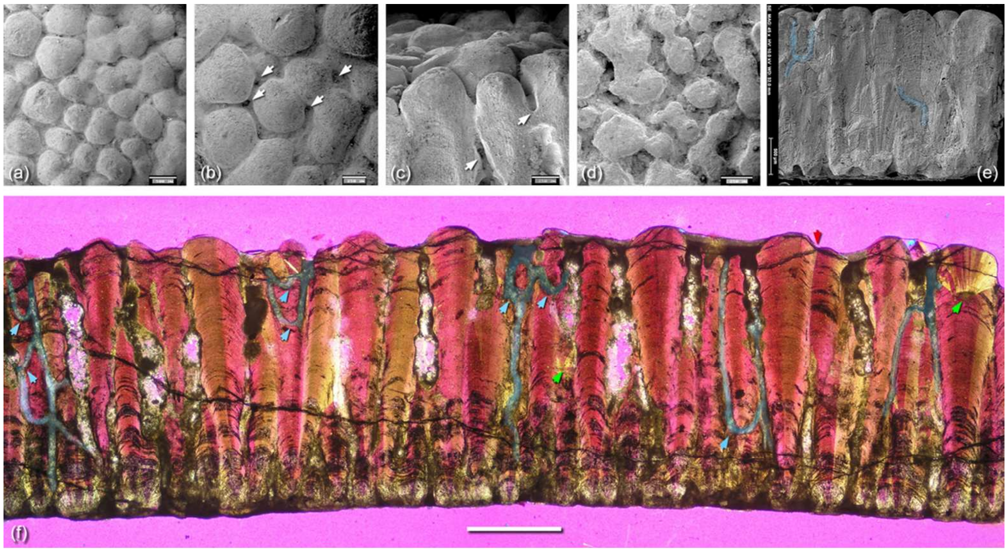

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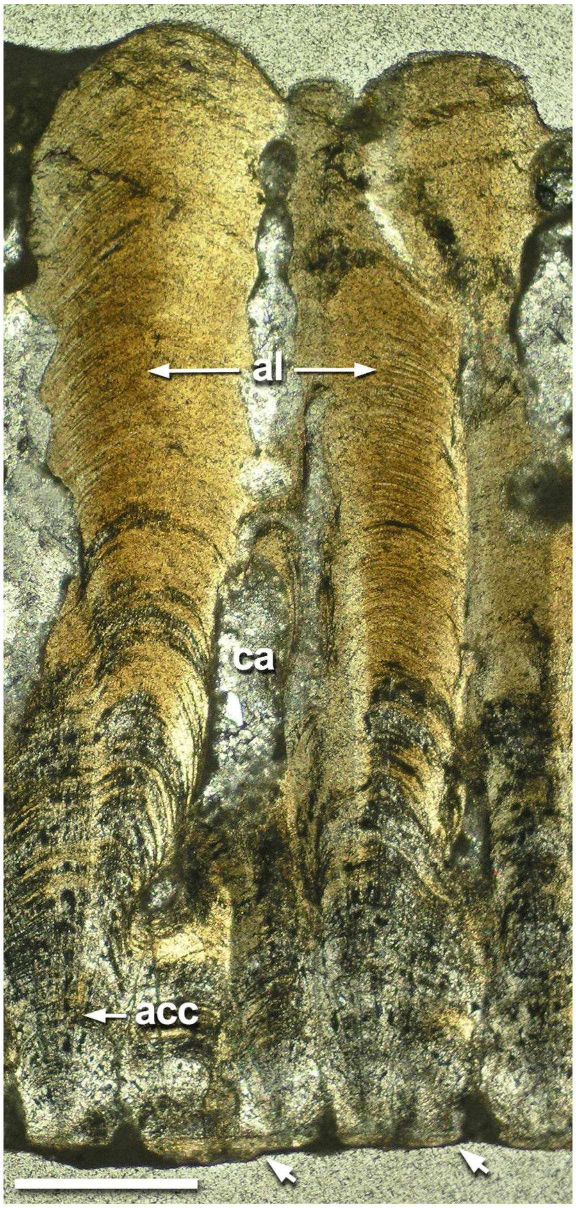

Figure 3. Megaloolithus cf. siruguei from the Late Cretaceous Sierra Perenchiza Formation (Valencia province, Spain). Polarized light microscope photograph of a radial section showing the fan-shaped morphology of the elongated shell units and the presence of extended cavities filled with sparry calcite cement. Remains of a membrane partially covers the base of the spherulites (white arrows). Abbreviations: al, accretionary lines; acc,a cicular calcite crystals; ca, cavities. Scale bar = 0.5 mm.

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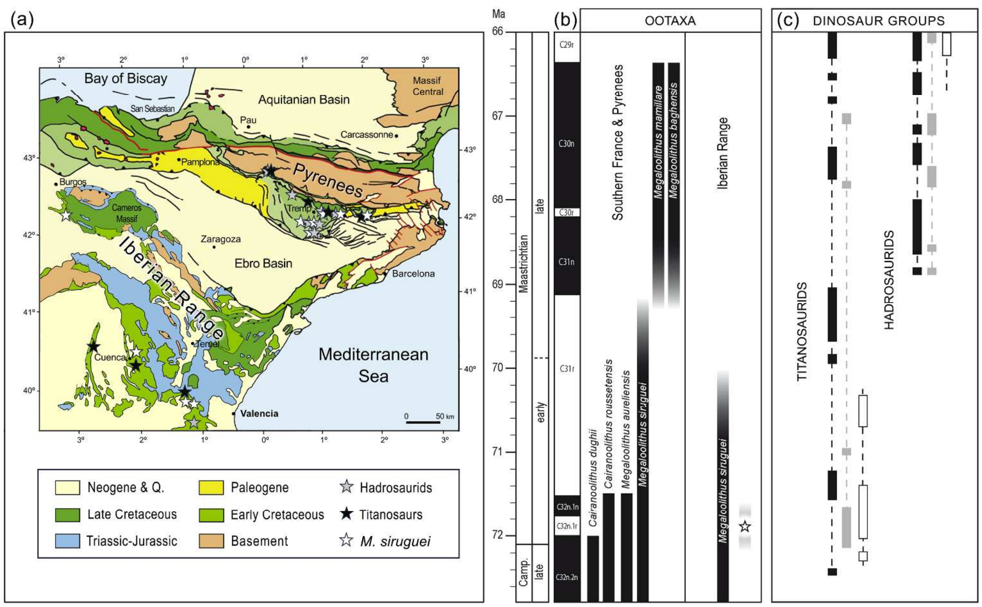

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118x73mm (600 x 600 DPI)