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Two new theropod egg sites from the Late Jurassic Lourinhã Formation, Portugal

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Two new Late Jurassic (uppermost Late Kimmeridgian) dinosaur eggshell sites are described, Casal da Rola and Porto das Barcas, both near Lourinhã, central-west Portugal. Casal da Rola yields eggshells with an obliquiprismatic morphotype comparable to those from a nest with the associated fossil embryos from Paimogo, tentatively assigned to the theropod *Lourinhanosaurus antunesi*. The Porto das Barcas eggshells have a dendrospherulitic morphotype with a prolatocanaliculate pore system. This morphotype was also recognised in eggshells from a clutch with associated *Torvosaurus* embryos at the Porto das Barcas locality. A preliminary cladistic analysis of eggshell morphology suggests theropod affinities for the Casal da Rola eggs, but is unable to resolve the phylogenetic position of the Porto das Barcas eggs. The eggshells at both sites are preserved in distal flood plain mudstones and siltstones. Carbonate concretions within the deposits indicate paleosol development.

Keywords: Late Jurassic; Portugal; theropods; dinosaur eggs

Introduction

Although many dinosaur eggs and eggshells are known from the Cretaceous, they are relatively rare in older deposits (e.g. Hirsch 1989; Mikhailov 1997). Jurassic egg sites are known from the Late Jurassic of the USA (Hirsch 1994; Turner and Peterson 2004), the Middle Jurassic of France (Garcia et al. 2006) and the Early Jurassic of South Africa (Kitching 1979; Zelenitsky and Modesto 2002; Reisz et al. 2012) and China (Reisz et al. 2013). Older egg sites are known only from the Late Triassic of Argentina (Bonaparte and Vice 1979).

The Lourinhã region, in central-west Portugal, is rich in Late Jurassic dinosaur nest sites and well-preserved eggs. Several Kimmeridgian–Tithonian localities have been reported (Kohring 1993; Mateus et al. 1997; Antunes et al. 1998; Mateus, Mateus, Antunes, et al. 1998; Mateus, Taquet, Antunes, et al. 1998; Castanhinha et al. 2008, 2009; Araújo et al. 2013). These discoveries increase the diversity of nesting environments in which eggs have been discovered, expand the disparity of morphotypes known from the Lourinhã Formation and, most importantly, provide valuable information on the poorly known pre-Cretaceous egg fossils. This article aims to taxonomically assign and describe fossil eggshells from two sites in the Lourinhã area: Porto das Barcas and Casal da Rola (general coordinates are 39.2N, 9.3 W). In the area, direct connections between eggs and embryos are known from two sites, both attributable to theropods: the *Lourinhanosaurus* nest from Paimogo (Mateus et al. 1997, 2001; Mateus, Mateus, Antunes, et al. 1998; Mateus, Taquet, Antunes, et al. 1998; de Ricqlès et al. 2001; Cunha et al. 2004; Castanhinha et al. 2008, 2009) and the *Torvosaurus* egg clutch from Porto das Barcas (Araújo et al. 2013). Fossil evidence of theropods from the area includes *Ceratosaurus* (Mateus and Antunes 2000a), *Torvosaurus* (Mateus and Antunes 2000b), *Aviatyrannis jurassica* Rauhut (2003), *Allosaurus europaeus* Mateus et al., 2006, *Lourinhanosaurus antunesi* Mateus, 1998, *Richardoestesia* (Hendrickx and Mateus, 2013), plus an unknown genus of Abelisauridae (Hendrickx and Mateus 2013) as well as many others such as Troodontidae (Zinke 1998), and open nomenclature genera cf. *Archaeopteryx* (Weigert 1995), cf. *Compsognathus*, cf. *Dromaeosaurus* (Zinke 1998).

Materials and methods

Well-preserved eggshell specimens were selected from both localities (Casal da Rola, ML1194, only eggshells, and Porto das Barcas, ML1842, one fossil egg and the corresponding eggshells) and cleaned using 10% hydrogen peroxide and either an ultrasound bath or a soft brush. Selected samples were prepared for 30-μm thin sections, using epoxy resin EpoThin 5 (resin) and 1.95 (hardener), for radial and tangential sections. We made two tangential

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and two radial thin sections of the Casal da Rola specimens and four tangential and three radial thin sections of the Porto das Barcas specimens. Pictures were taken using a polarised light microscope (PLM) Labomed CXL POL and a Leica CLS 100 × binocular microscope.

The inner and outer surfaces of eggshell fragments were imaged using a JEOL JSM T330A scanning electron microscope (SEM) at the Universidade Nova Lisboa (FCT-UNL). Fragments were also cut radially, polished and then etched with 10% formic acid for 30 s to provide a better view of the radial surface.

In order to measure the pore dimensions of the eggshells, pictures were taken using binocular and macro lenses. The diameter of each pore was measured with GIMP 2.8.2 image software in order to determine pore area and total pore area against total sample area.

Traditionally, eggshell fragments are used to estimate eggshell curvature, which in turn provides an estimate of overall egg size (Sauer 1968; Williams 1981). The methodology employed here is slightly different. This technique is based on the assumption that the arithmetic mean radius of an ellipsoid should be the same as the measured mean radius of the eggshell samples. On Casal da Rola eggshells, three measurements were taken on each eggshell fragment ($N = 27$) with a digital caliper (error ± 5 μm): eggshell thickness (t) and the width (W) and height (h) across an orthogonal plane at the longest dimension of the eggshell fragment (see Figure 1). In order to get the arc height (H), the thickness of the eggshell (t) is subtracted from the measured height (h).

The radius of curvature (R) of an arc is given by

$$R = \frac{W^2}{8H} + \frac{H}{2}. \quad (1)$$

To approximate the shape of the egg, we compared a sphere with mean radius R to produce a prolate ellipsoid with a mean radius r, the semi-axes (a, b) being dependent on the elongation index (EL).

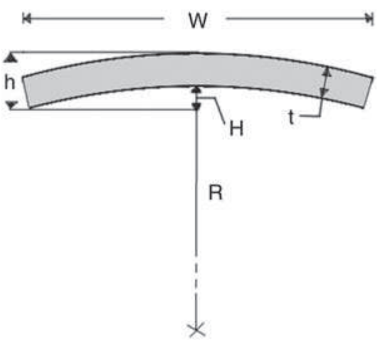

Figure 1. Schematic overview of eggshell curvature measurement method: width (W), height across an orthogonal plane of the eggshell (h), eggshell thickness (t), arc height (H) and resulting radius (R).

The mean radius of the ellipsoid (r) is given by

$$r = \frac{(2a + b)}{3}, \quad (2)$$

where a is the radius of rotation of the ellipsoid and b is the semi-length of the axis of symmetry (Chambat & Valette 2001). The equation for the EL is

$$\mathrm{EL} = \frac{b}{a} \text{ then } b = \mathrm{EL}{\cdot}a. \quad (3)$$

After this, b can be substituted for $E.a$ and assuming $r = R$;

$$\text{Solving (2) for } a : \mathrm{a} = \frac{3{\cdot}r}{(2 + \mathrm{EL})}, \quad (4)$$

with values for a and b found, the egg length and width are equal to $2b$ and $2a$ for a given EL.

Geology and age

Upper Jurassic strata in the Lusitanian Basin record a marine to terrestrial syn-rift succession, where the depositional systems were controlled by basin setting and synsedimentary tectonic activity (Leinfelder 1993). In the Lourinhã region (Figure 2), the informally established Lourinhã Formation (Hill 1989) is a continental, siliciclastic and regressive unit that is dominated by fluvial sequences with occasional marine incursions (Pena dos Reis et al. 2000). The Lourinhã Formation spans the Kimmeridgian and Tithonian, possibly extending into the Berriasian (Alves et al. 2003).

A transgressive event during the Late Kimmeridgian to Early Tithonian led to the deposition of the Sobral Member, which has a total thickness of around 80 m and shows three distinctive marly layers with characteristic brackish water fauna throughout (Figure 3). The razor-shaped bivalve *Gervillia sobralensis* Sharpe, 1850 is restricted to the base of the member (Leinfelder 1986). About half-way up the Sobral Member, a maximum flooding surface is recognised with *Protocardia gigantea* Schneider et al., 2010, a species restricted to this layer and basin, known as the Kimmeridgian–Tithonian boundary based on Sr-isotope stratigraphy (Schneider et al. 2010).

At the top of the Sobral Member, the occurrence of the trigoniidae bivalve *Myophorella lusitanica* Sharpe, 1850 is restricted to the southern Arranhó II Member which is of Early Tithonian age (Schneider et al. 2008).

The locality of Casal da Rola was discovered in 1997 about 1 km south of Lourinhã. The approximately 10-m-thick section consists of marls containing *G. sobralensis*, *Eomiodon securiformis* Sharpe, 1850 and *Isognomon lusitanicus* Sharpe, 1850 at the base. The layer containing

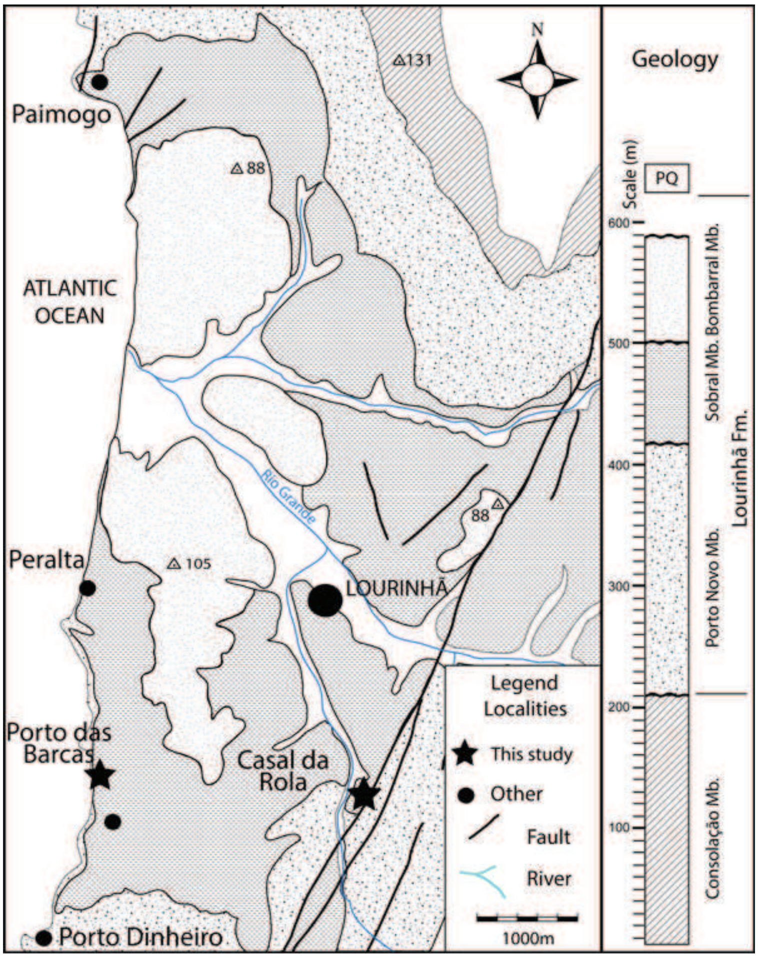

Figure 2. Geological map of Lourinhã region showing lithostratigraphy, unit thickness, and different egg and eggshell localities (modified from Manuppella et al. 1999).

the eggshells is underlain by mudstones, siltstones and a fine-grained sandstone unit. The egg bed consists of mudstone and siltstone with carbonate concretions. Some eggshell clusters are preserved within a carbonate matrix. No whole eggs were recovered since all shell fragments were obtained by surface collection and sieving. The taxonomic composition of the bivalve assemblage indicates that the site is located at the base of Sobral Member.

The Porto das Barcas locality also lies near Lourinhã. The fossil egg material lay embedded in an isolated sandstone block from a sandstone layer in the above lying cliffs, which overlies an erosive and transgressive surface marked by *I. lusitanicus* and *G. sobralensis* bivalves, and in turn is overlain by a channel bed. The Kimmeridgian–Tithonian boundary is recognisable at the top of the 40-m cliff, so the egg-bearing unit is Late Kimmeridgian. Both the Casal da Rola and Porto das Barcas localities are coeval.

Systematics

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Oofamily PRISMATOOLITHIDAE Hirsch, 1994

Original diagnosis after Hirsch (1994)

Dinosauroid prismatic basic type morphotype, prismatic morphotype obliquicaniculate or angusticaniculate pore system. Outer shell surface smooth to undulating. Elongate ellipsoid or ovoid eggs. Medium shell thickness 0.8–1.0 mm.

Oogenus *Preprismatoolithus* Zelenitsky and Hill, 1996

Original diagnosis after Zelenitsky and Hill (1996)

Dinosauroid basic type; angustiprismatic to obliquiprismatic morphotype; obliquicaniculate or angusticaniculate

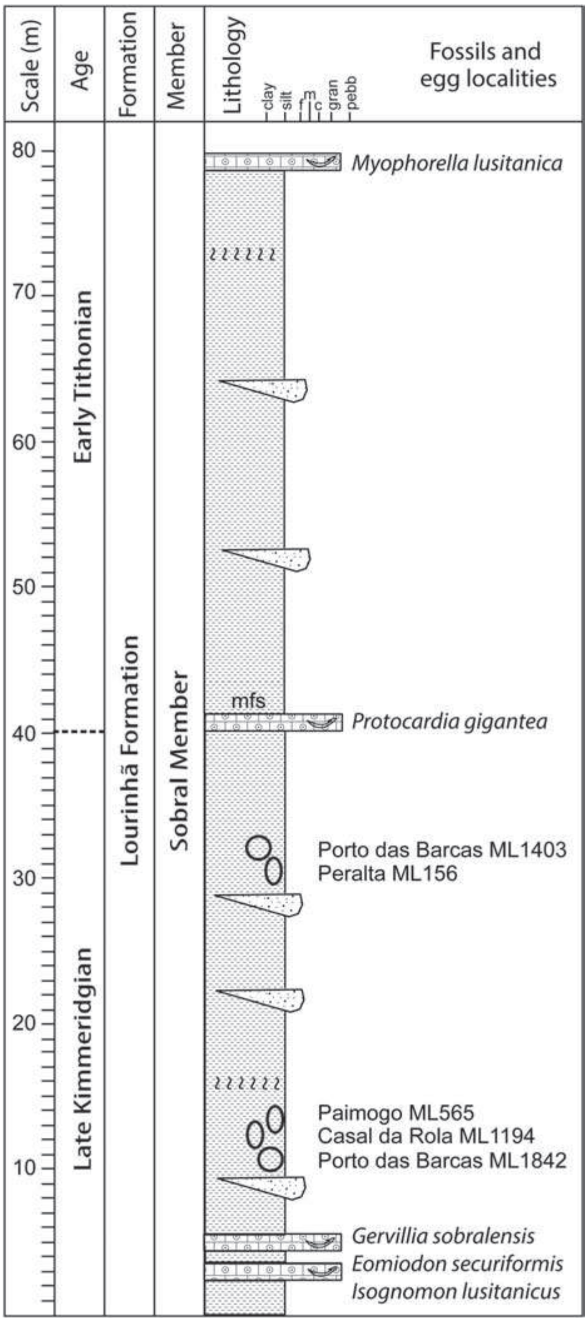

Figure 3. Stratigraphic log of Sobral Member (modified from Ribeiro and Holwerda 2012; Ribeiro and Mateus 2012).

pore system; outer surface smooth to undulating or with fine sculpturing; eggshell thickness 0.3–1.22 mm; eggs are elongate, ellipsoidal or oval shaped; $E = 1.8–2.7$.

Age and formation

Late Kimmeridgian, Lourinhã Formation, lower part of Sobral Member.

Material and taphonomy

Hundreds of eggshell fragments (ML1194) were found in a siltstone layer in a steep cliff under dense vegetation. Therefore, only loose fragments were collected at the surface or by sieving. No preserved egg structures or embryo remains were found.

Locality

Casal da Rola, Lourinhã, Portugal.

Description

External surface is smooth with sparse nodes. In the inner surface of well-preserved samples, complete mammillary units are visible (Figures 4(A),(C),(D),(F), 6(A)). The eggshell thickness is 0.87 mm [standard deviation (SD) ± 0.06; $N = 27$]. Under PLM, a mammillary zone is well defined, accounting for 1/3 to 1/4 of the eggshell thickness. The mammillary units measure 250–350 μm in height and change gradually upwards into a prismatic layer, with a columnar extinction pattern visible under polarised light (Figure 4(B)). In radial view, horizontal growth lines are also visible (see Figure 4(B); gl). Under a microscope, a third zone of variable thickness is also visible (Figure 4(B); dl), consisting of recrystallised or secondary deposits, which also appear inside the pores, parts of the inner surface, or even on the edges of the eggshell. We interpret this extra layer as calcite, given that the eggshells themselves are composed of calcite, and they are preserved in carbonate-rich soils.

The pore system is obliquicaniculate or angusticaniculate (see Mikhailov et al. 1996), displaying a circular section (Figures 4(A), 6(A)). The pores have a mean diameter of 160 μm (SD ± 41) ($N = 37$) measured in five sections from tangential surfaces with a total area of 142 mm^2. The average pore area is 0.021 mm^2 and the average density is 26 pores cm^{-2}. Pore distribution is uneven, making the relative pore area of about 0.55%. The measured eggshells show a mean radius of 57 mm (SD ± 16) ($N = 27$).

Discussion and comparison

The eggshells from Casal da Rola are similar in some respects to those from Paimogo (see Mateus et al. 1997; Antunes et al. 1998), a coeval locality eight kilometres north of Casal da Rola that contains eggs and embryos. The Paimogo eggs (ML565) have been tentatively ascribed to the theropod *L. antunesi* (Mateus et al. 1998) based on embryonic material (Mateus et al. 2012). The eggshells from Paimogo have a smooth external surface with an average shell thickness of 0.92 mm. The eggshell microstructure is distinctly prismatic, with narrow units with

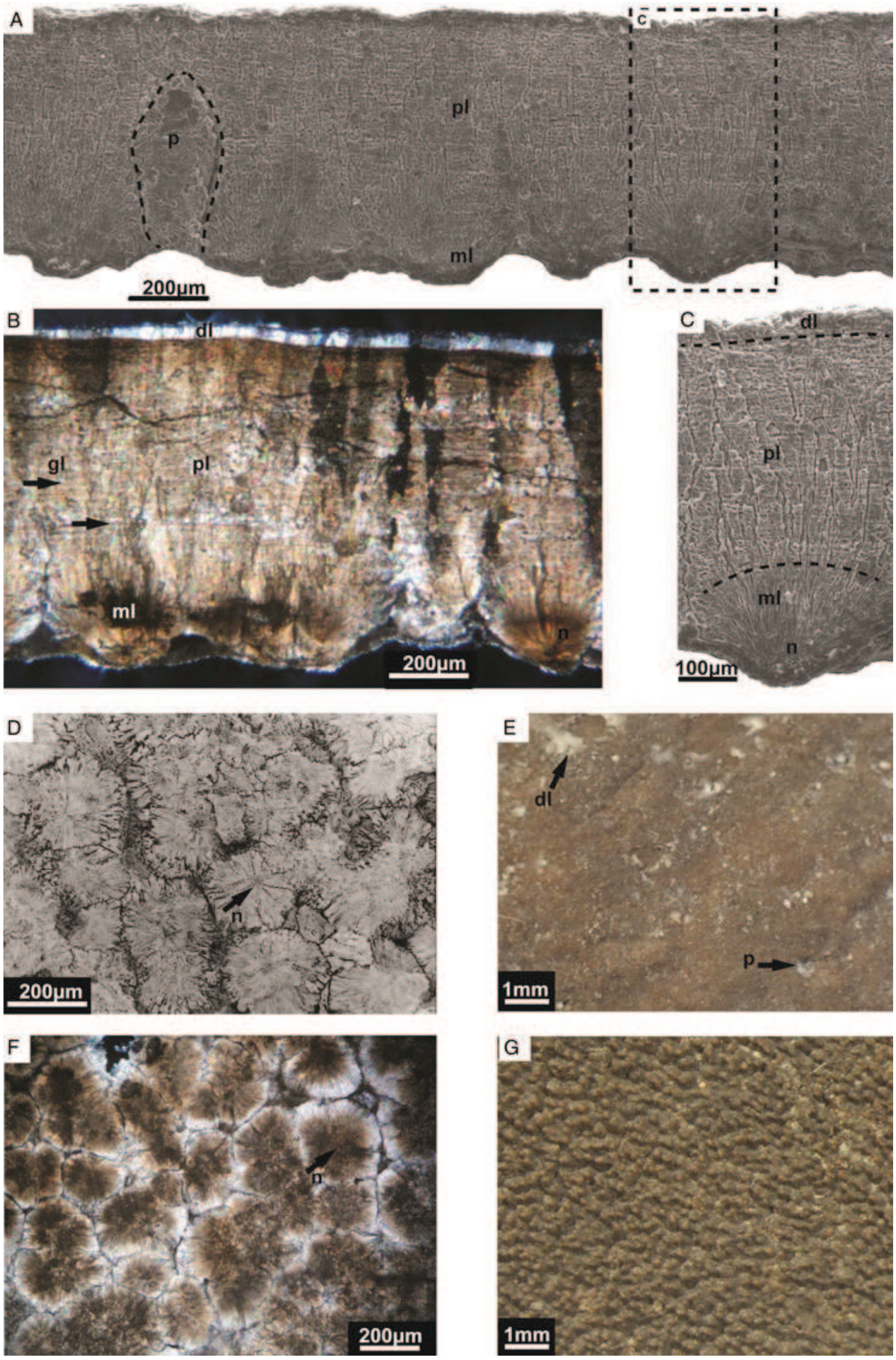

Figure 4. Prismatic eggshells from Casal da Rola (ML1194). A, SEM surface image of polished and etched radial section; B, PLM image of radial section; C, close-up of shell unit; D, SEM image of inner surface; E, macro image of outer surface; F, tangential section under PLM at mammillae level; G, macro image of inner surface; pore (p), prismatic layer (pl), diagenetic layer (dl), growth lines (gl), mammillary layer (ml), nucleation centre (n).

semi-round mammillae, accounting for 1/4 of total shell thickness. Diagenetically altered material dominates the external surface and fills the pores (Antunes et al. 1998). The pore system is obliquicaniculate or angusticaniculate, composed of simple and round pores with an average diameter of 180 µm. Pore density varies from 10 pores cm^{-2} in the equatorial zone to 40 pores cm^{-2} in the polar zones, with a pore relative area of 0.5%. The eggs are ellipsoidal to oval in shape, 130 × 94 mm in size, with an average EL of 1.4 based on complete eggs. Some of these anatomical features are also observed in the Casal da Rola specimens. In particular, both the Casal da Rola and Paimogo eggshells have similar thickness (0.87–0.92 mm), external ornamentation (smooth), pore systems (obliquicaniculate or angusticaniculate), pore diameters (160–180 μm) and pore relative area (0.50–0.55%). Eggshells from both localities also share a similar microstructure with two distinct zones, a mammillary zone and a columnar zone.

Despite that no partial or complete eggs were found, the size and shape of the Casal da Rola eggs were estimated using the mean radius of curvature of well-preserved eggshells. Making the mean radius of a prolate ellipsoid (r) equal to the measured mean radius ($R = 57$ mm) and using the estimated EL$(=1.4)$ from the Paimogo nest, we estimated an egg dimension of approximately 140 × 100 mm, which is similar to the dimensions obtained from the complete eggs. SD (± 16 mm) shows a range of curvatures, indicating that the eggs were oval rather than spherical in shape.

If there were a mathematical correlation between any independent trait (e.g. SD) and the EL, and if the result for Casal da Rola is similar to 1.4 (Paimogo Index), then the eggs from Casal da Rola would have been similar in size to those in the Paimogo nest.

Other nesting localities contain eggshells that are comparable to the Casal da Rola material. *Preprismatoolithus coloradensis* (Hirsch 1994), from the Upper Jurassic Morrison Formation, is a basic obliquiprismatic eggshell, with a thickness of 0.8–1.0 mm, although some eggs are slightly smaller in size, approximately 110 × 60 mm. *Prismatoolithus levis* Zelenitsky and Hill, 1996, from the Oldman Formation in Alberta, Canada, and Two Medicine Formation in Montana (Upper Cretaceous), is also attributed to theropods (Zelenitsky et al. 1996; Varricchio et al. 2002). *Prismatoolithus levis* is similar to *Preprismatoolithus coloradensis* in terms of eggshell thickness, but has different prismatic layer to mammillary layer thickness ratios, and an angusticaniculate pore system.

Assignment of the Casal da Rola eggshells to the oofamily Prismatoolithidae (Hirsch 1994) and oogenus *Preprismatoolithus* (Zelenitsky and Hill 1996) is based on shared morphologic characteristics, including prismatic basic type, eggshell microstructure, pore system and eggshell thickness. Despite these similarities, there may be differences in the EL and estimated egg size.

***Dinosauria* Owen, 1842**
***Theropoda* Marsh, 1881**
***Torvosaurus* Galton and Jensen, 1979**

Parataxonomy

Oofamily PHACELOOLITHIDAE Zeng and Zhang, 1979 (synonym of Dendroolithidae Zhao and Li, 1988)

Age and formation

Late Kimmeridgian, Lourinhã Formation, lower part of Sobral Member.

Material and taphonomy

One isolated egg (ML1842) was highly deformed in a fine-grained sandstone block, and several corresponding eggshell fragments (mostly taken from the egg). The block was found at the base of a cliff, but was traced to the original sandstone layer due to its lithological similarities.

Locality

Porto das Barcas (ML1842), Lourinhã area, Portugal. Not to be confused with Porto das Barcas egg clutch ML1403 (Araújo et al. 2013).

Description

The egg is flattened and broken into two parts. The measured length and width are 23 cm and 15 cm respectively (Figure 5(A)). The geometry and curvature of the egg were not preserved, and plastic post-mortem deformation prevents both accurate measurement of the original shell curvature and reliable estimation of the egg shape.

The inner surface of the preserved eggshell fragments in tangential view is smooth with polygonal-shaped mammillae and acicular internal structure radiating from the nucleation centre towards the outer part (Figure 5(B)–(D), (F)). The nucleation centres are spaced about 100–200 μm apart. In radial view (Figures 5(C), (D), 6(B)), wedge-shaped shell units, which broaden towards the outer surface and interconnect, display a distinct fanning pattern outwards to the edges of the shell units (Figures 5(C),(D), 6(B)). The mammillary layer in radial view seems to show a slight differentiation from the rest of the shell units. Growth lines are visible as arched lines (Figure 5(C)).

In tangential view, the outer surface is obscured by a coating of sand (Figure 5(E)) derived from the sandstone layer in which the fossil was embedded. Despite this sandy coating, examination of tangential and radial sections

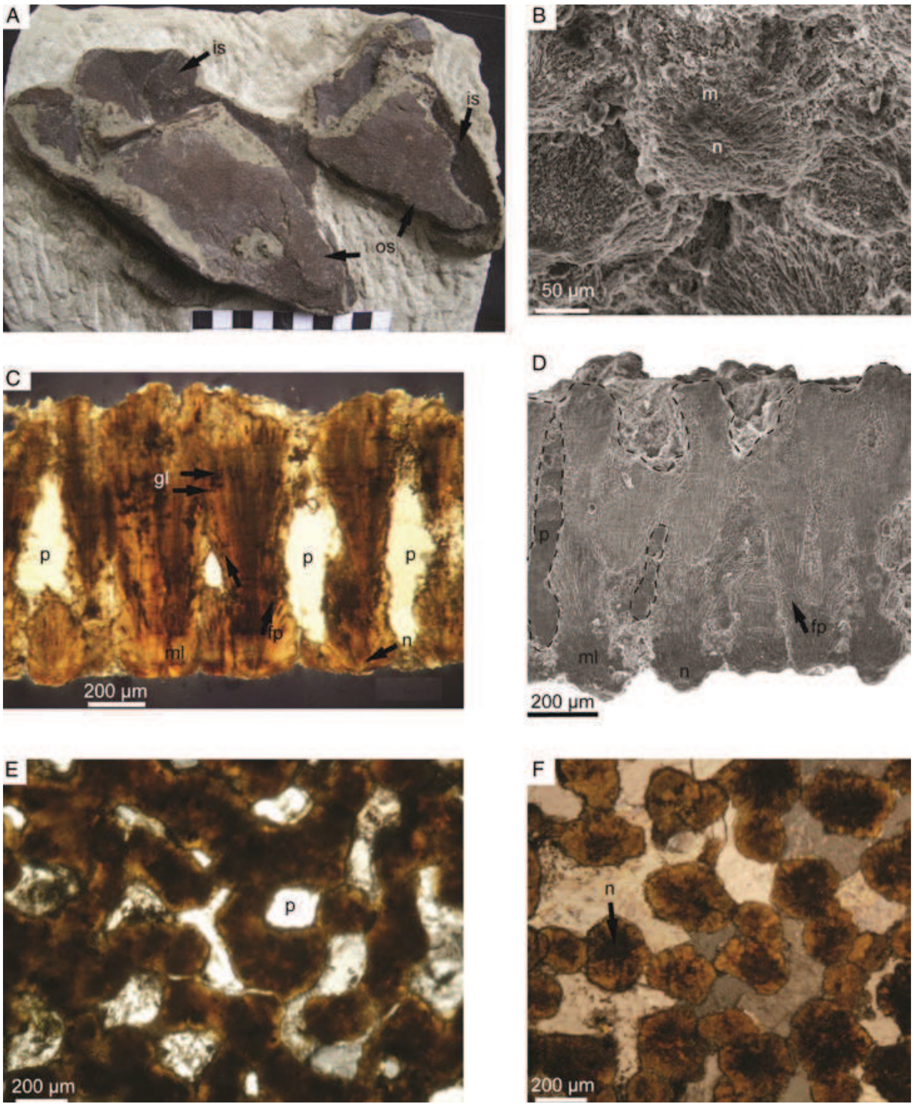

Figure 5. Spherulitic eggshells from Porto das Barcas (ML1842). A, isolated egg (scale = 10 cm); B, SEM image of lateral edge of inner surface with mammillae showing radiating pattern from nucleation centre outwards; C, PLM image of surface of radial section; D, SEM image of surface of radial section; E, PLM image of tangential section across outer shell; F, PLM image of tangential section across the mammillae; outer surface (os), inner surface (is), distinct fanning pattern (fp), pore with calcite infill (p), mammillary layer (ml), growth lines (gl), mammilla (m), nucleation centre (n).

under PLM reveals protruding ridges on the outer surface (Figures 5(E), 6(B)). Erosion was not measured. Both inner and outer surfaces display interconnected pores, forming an anastomosing system (Figure 5(E),(F)). The pore canals can also be seen to interconnect throughout the shell in radial view (Figures 5(C),(D), 6(B)). They are irregularly shaped and round to elongated in tangential view, with diameters ranging from 50 to 250 μm for more regular pores and 600 × 100 μm for elongated pores. Accordingly, the area of the pores is highly variable, averaging 0.019 mm^2 (SD ± 0.014). The percentage of pore area to total surface area is estimated at 14%.

Discussion and comparisons

Most features of the Porto das Barcas ML1842 eggshell morphology, and the fact that there is no conspicuous columnar extinction pattern make assignment to spherulitic dinosauroid type most logical. Even though the acicular crystallisation patterns in the mammillae are associated with turtle eggs (e.g. Fang et al. 2003), other characteristics of this eggshell point to a dinosauroid type.

The eggshells from Porto das Barcas are similar to those from Portugal described by Kohring (1993) and Araújo et al. (2012, 2013). The Porto das Barcas egg clutch (ML1403) with the associated fossil embryos is the

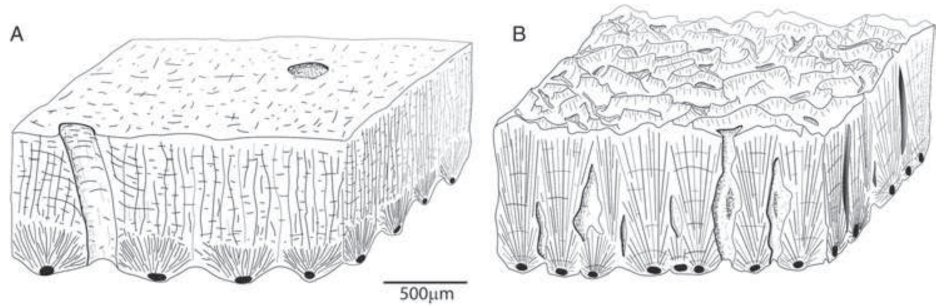

Figure 6. Schematic 3D view of eggshells. A, Casal da Rola (ML1194); B, Porto das Barcas (ML1842).

most morphologically similar. Kohring (1993) mentions a spherulitic eggshell type with a thickness of 0.9–1.1 mm and similar prolatocanaliculate pore system from the slightly older Porto Dinheiro locality, about 2 km south. An eggshell clutch (ML1403) found 600 m south of the isolated egg preserves associated with neonate theropod embryos that have been assigned to *Torvosaurus* (Araújo et al. 2013). These eggs share the same range of eggshell thickness (0.9–1.2 mm), ridged outer surface ornamentation, inner surface ornamentation with acicular crystallisation in the mammillae, wedge-shaped irregular shell units with distinct fanning pattern, prolatocanaliculate pore system, irregular pore area and high porosity.

The most similar eggshell type reported in the literature, besides the Portuguese findings, is the oogenus *Dendroolithus* Zhao and Li, 1988, from China that is placed into the oofamily Phaceloolithidae Zeng and Zhang, 1979 (synonym of Dendroolithidae Zhao and Li, 1988).

The original diagnosis of Oogenus *Dendroolithus* Zhao and Li, 1988 after Zhao and Li (1988) and Fang et al. (2003) is as follows:

> Eggs are small to medium size (6–20 cm), spherical to slightly oval. The eggshell has a dendrospherulitic morphotype, with shell units irregularly shaped. The shell units display a fanning pattern. The shell displays a prolatocanaliculate network throughout the eggshell. The outer surface ornamentation is irregular with crests and the pores irregularly dispersed between the crests. Eggshell thickness is about 1.5 mm.

The *Dendroolithus* eggshell type is described as having narrow shell units which interlock towards the outer surface, and an interconnecting prolatocanaliculate pore system (Zhao and Li 1988; Mikhailov et al. 1994; Zhao 1994). Therefore, this parataxon resembles more closely the morphology of ML 1842. *Dendroolithus* is known from Cretaceous deposits of China and Mongolia (Zhao and Li 1988; Mikhailov et al. 1994; Zhao 1994; Fang et al. 2003; Tanaka et al. 2012) and from the Late Jurassic of Portugal (Kohring 1993; Araújo et al. 2013), making this eggshell type more widespread than previously thought.

Comparisons between the Late Cretaceous Mongolian and Chinese oospecies *Dendroolithus* are difficult because each has a different shell thickness range and external ornamentation. *Dendroolithus wangdianensis* Zhao and Li, 1988 has a shell thickness of 1.7–2.1 mm, whereas *Dendroolithus verrucarius* Mikhailov et al. 1994 has a shell thickness range of 1.8–3.8 mm, with a second layer of spherulitic units. *Dendroolithus microporosus* Mikhailov et al. 1994 has a shell thickness of 2.0–2.7 mm and comparatively small eggs (about 6 × 7 cm) with smooth external ornamentation. *Dendroolithus dendriticus* Fang, Lu and Cheng, 1998 has a rugose outer surface and smooth inner surface, with a shell thickness of 1 mm. The shell units are wide and interconnect towards the outer surface. The mammillae are round with acicular crystallisation, and the pore canals are described as branching.

Assignment of the Porto das Barcas (ML1842) material to the oofamily Phaceloolithidae is based on the following shared features: dendrospherulitic morphotype, rugose outer surface with crests and irregularly spaced pores, prolatocanaliculate pore system, interconnection towards the outer surface and irregular shape and fanning pattern of the shell units (Zhao and Li 1988; Mikhailov et al. 1994; Zhao 1994; Fang et al. 1998, 2003; Tanaka et al. 2012). Within Phaceloolithidae the oogenus *Dendroolithus* is the most similar to the Portuguese eggshells. However, some differences (mainly in fanning pattern with wider prisms and thinner eggshells in ML1842) are sufficient to warrant erection of a new oogenus. We have chosen not to assign a new oogenus because the embryonic remains in ML1403 allow definitive identification of the egg producer: the theropod *Torvosaurus*.

The *Dendroolithus* egg type was initially assigned to either sauropods or ornithopods by Fang et al. (1998), Mikhailov et al. (1994) and Zhao (1994); but embryonic remains show that *Dendroolithus* and Phaceloolithidae were associated with therizinosaurs (Cohen et al. 1995; Mikhailov 1997; Tanaka et al. 2012). The Portuguese findings also strengthen the connection of Phaceloolithidae to theropods, particularly *Torvosaurus* and therizinosaurs.

Table 1. Comparative characteristics and measurements from different eggs.

Locality	Ootaxa	Eggshell Thickness (mm)	Egg Dimension (mm)	PL:ML Thickness ratio
Casal da Rola (this study)	*Preprismatoolithus*	0.75–0.99	140 × 100	2:1–3:1
Paimogo, Portugal[a]	*Preprismatoolithus*	0.70–1.14	130 × 94	3:1
Young locality, USA[b]	*Preprismatoolithus coloradensis*	0.7–1.0	110 × 60	3:1
Devil's Collee, Canada[c]	*Prismatoolithus levis*	0.72–0.98	100 × 60	6:1–8:1
Porto das Barcas (this study)	Phaceloolithidae	0.90–1.2	N/A	N/A
Porto das Barcas, Portugal[d]	Phaceloolithidae	1.2	N/A	N/A
Gong An Zhai, China[e]	*Dendroolithus wangdianensis*	1.7–2.1	150 × 120	N/A
Baruungoyot, Mongolia[f]	*Dendroolithus microporosus*	2.0–2.7	60 × 70	N/A
Baruungoyot, Mongolia[f]	*Dendroolithus verrucarius*	1.8–3.8	90–120	N/A

Note: N/A, not applicable, not measurable.
[a] Antunes et al. (1998).
[b] Hirsch (1994).
[c] Zelenitsky and Hill (1996).
[d] Araújo et al. (2013).
[e] Zhao and Li (1988).
[f] Mikhailov et al. (1994).

Table 1 shows characteristics and measurements from our sites and from other sites, as reported in the literature. Figure 6 compares the two types of eggs described here.

Phylogenetic analysis

There are few articles devoted to non-avian dinosaur eggshell cladistic analysis to support phylogenetic relationships among taxa, exist to provide a list of characters and data matrices: Varricchio and Jackson (2004), Grellet-Tinner and Makovicky (2006), Zelenitsky and Therrien (2008), Jin et al. (2010) and Tanaka et al. (2011, 2012). For eggshell-based cladistic analyses on other taxonomical groups: Aves see Lee et al. (1997), Grellet-Tinner (2006) and Zelenitsky and Modesto (2002) and for turtles see Winkler (2006). Varricchio and Jackson (2004) were pioneers in the theropod eggshell phylogeny.

The eggs from Casal da Rola and Porto das Barcas were analysed (in Winclada, Nixon 1999) with the two most recent phylogenetic data matrixes (Jin et al. 2010; Tanaka et al. 2011).

Using the following coding for Jin et al. (2010) data matrix: Casal da Rola (12002 110_1 ?0?20 0??0) and Porto das Barcas (13002 10011 ?0?30 1??0), the result Nelsen consensus tree was mostly resolved (Figure 7), in which the Porto das Barcas eggs (*Torvosaurus*) is a sister taxon of *Dictyoolithus*, and Casal da Rola is a sister taxon of Paimogo's *Lourinhanosaurus* (length = 53 steps; Ci: 55; Ri: 79).

The character coding using the matrix provided by Tanaka et al. (2011) is as follows: Casal da Rola (31??? 00100 101013) and Porto das Barcas (100?? 00001 001001). The resulting Nelsen consensus tree (Ci: 62; Ri: 90; length: 43) with the data matrix of Tanaka et al. (2011) placed Porto das Barcas eggshell (*Torvosaurus*) in a polytomy with *Dendroolithus* and *Faveoolithus* and Casal da Rola in a trichotomy with Paimogo's *Lourinhanosaurus* and *Preprismatoolithus coloradensis*.

Paleobiological implications

Prismatic eggs similar in morphotype and most likely attributable to basal theropods are now known from at least three different sites in Lourinhã. The nesting preferences of basal theropods are virtually unknown due to the lack of fossil evidence. However, they may be inferred, in part, by the phylogenetic brackets, taphonomy and paleoenvironmental reconstructions.

The eggshells from Casal da Rola and Paimogo are considered to be the same species or close taxonomic relatives (Antunes et al. 1998). Eggshells from both localities have a relative pore area higher than that of avian eggs of the same weight (Antunes et al. 1998; Deeming 2006). This suggests a need for maintenance of precise humidity and temperature conditions during incubation, possibly by covering the nest with soil or vegetation.

The Casal da Rola and Paimogo sites share similar depositional settings: overbank deposits of mudstone and siltstone with carbonate nodules, which provide evidence of paleosol development due to seasonal moisture deficit. An extensive paleosol study from the Lourinhã Formation performed earlier by Myers et al. (2012) revealed paleoclimatic conditions for the Late Jurassic of Lourinhã with relatively high mean annual precipitation, temperatures and humidity compared to the present-day values (Myers et al. 2012). However, how the rainfall is distributed throughout the year will have a large impact on the environment, with possibly a pronounced arid season, thus confirming the taphonomic interpretation of the new egg sites from Lourinhã.

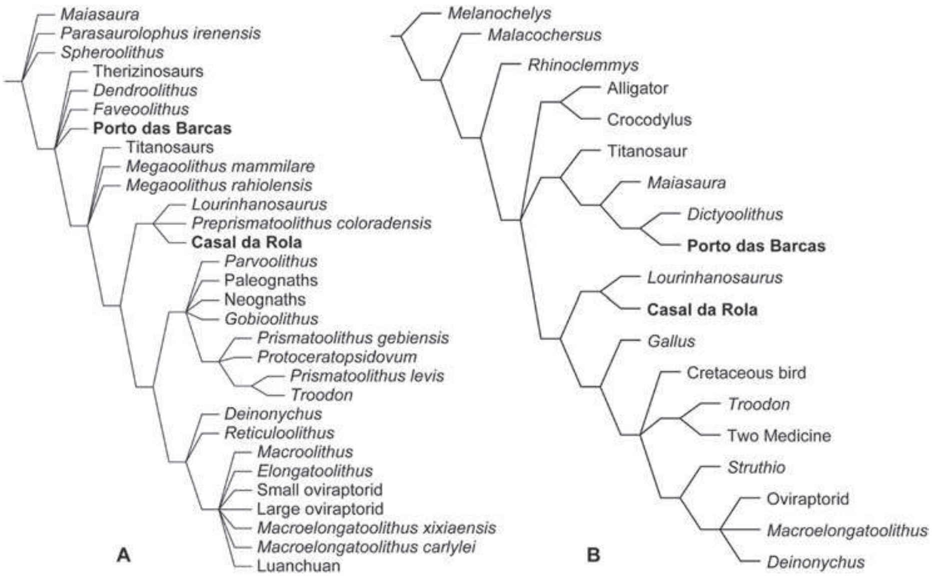

Figure 7. Phylogenetic consensus trees of eggs with the eggshells of the Upper Jurassic Portuguese localities of Casal da Rola (*Lourinhanosaurus*) and Porto das Barcas (*Torvosaurus*) after the data matrixes of A, Tanaka et al. (2011), and B, Jin et al. (2010). See text for discussion.

Conclusions

We conclude that (i) the Casal da Rola eggshell is the same taxon as, or closely related to, the Paimogo eggshell (*Lourinhanosaurus*); (ii) the Casal da Rola, Porto das Barcas and Paimogo localities are preserved in coeval strata of uppermost Late Kimmeridgian age; (iii) the paleoenvironmental setting points to deposition of the eggs in distal alluvial plains in overbank sediments; (iv) the Porto das Barcas eggshells are of the oofamily Phaceloolithidae (close to the oogenus *Dendroolithus*) which represents the first Jurassic occurrence outside Asia and (v) the Porto das Barcas eggshells are attributable to *Torvosaurus* sp.

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