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AN OCCURRENCE OF FOSSIL EGGS FROM THE MESOZOIC OF MADAGASCAR AND A DETAILED OBSERVATION OF EGG SHELL MICROSTRUCTURE

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ABSTRACT—Whereas fossil turtle eggs have a near global distribution and range from Middle Jurassic to Pleistocene, they are rarely documented from the Mesozoic of Gondwana. Here, we report three fossil turtle eggs from the Upper Cretaceous (Campanian) of the Morondava Basin, Madagascar. The spherical eggs range in size from 33.5 to 35.5 mm and have an average eggshell thickness of 440 μm . They can be confidently identified as rigid-shelled turtle eggs by the presence of tightly packed shell units composed of radiating acicular crystals and a shell unit height to width ratio of 2:1. Lack of associated skeletal remains precludes taxonomic identification of the eggs. Although a large vertebrate fauna has been reported from the Upper Cretaceous of Madagascar, these specimens are the first eggs from the Mesozoic of the island.

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

INTRODUCTION

Turtles are unique amongst amniotes because they lay eggs composed of aragonite instead of calcite. This composition is less stable and is more susceptible to diagenetic alteration (Hirsch, 1983), which may account for the relatively small number of fossil turtle eggs that have been described previously (reviewed by Lawver and Jackson, 2014). Although the vast majority of fossil turtle eggs are described from Laurasian continents, specimens are known from every continent except Antarctica (likely a collection bias) and their temporal distribution ranges from Middle Jurassic to Pleistocene (Lawver and Jackson, 2014).

Turtle eggshell consists of a single layer of shell units made up of needle-like aragonite crystals that originate from an organic core within the shell membrane. The degree of mineralization varies widely among turtle eggs and includes pliable, semipliable, and rigid-shelled eggs (Hirsch, 1983). This variation in eggshell mineralization corresponds to variation in the height to width ratios of the shell units and whether the shell units are loosely or tightly spaced and interlocking in structure (Hirsch, 1996). The tightly interlocking structure of rigid-shelled eggs enhances their potential for preservation in the fossil record (Hirsch, 1983).

Numerous vertebrate taxa have been described from Upper Cretaceous rocks of Madagascar. This fauna includes ray-finned fishes, anurans, turtles, snakes, lizards, crocodyliforms, non-avian and avian dinosaurs, and mammals (Krause and Kley, 2010). Although the vast majority of these fossils were collected from the Mahajanga Basin in northwestern Madagascar, other Malagasy basins are beginning to gain attention. Recently, an abelisauroid theropod was described from Upper Cretaceous rocks of the Diego Basin in the northernmost point of Madagascar (Farke

and Sertich, 2013), as well as fishes, rhynchosaurs, aetosaurs, phytosaurs, dinosaurs, and traversodonts from the Triassic and Jurassic of the Morondava Basin (Burmeister et al., 2006, and references therein). Despite this rich fossil record, no Mesozoic eggs have been previously described from Madagascar. Here, three spherical turtle eggs from the Belo Region of the Morondava Basin of western Madagascar are described.

GEOLOGIC BACKGROUND

The western region of Madagascar is characterized by three large sedimentary basins that resulted from rifting between Africa and Madagascar, which was initiated as early as the Permo-Triassic. These basins include the Diego and Mahajanga basins to the north and the larger Morondava Basin to the south (Fig. 1; Walaszczyk et al., 2014). During the Middle Jurassic, Madagascar drifted southward until reaching its current position by the Early Cretaceous (Walaszczyk et al., 2014), and by the Late Cretaceous (Turonian and Campanian) increased subsidence and marine transgression resulted in continuous open marine sedimentation in the Morondava Basin. Within the Morondava Basin, the rock units trend approximately north-south and range in age from Late Carboniferous to Recent, with the oldest units to the east (Nichols and Daly, 1989; Burmeister et al., 2006).

The eggs in this study were discovered and collected by amateurs and lack exact locality information. However, all three eggs were found together and in association with scaphite ammonites and the heteromorph ammonite *Bostrichoceras* in marine rocks, suggesting that they come from the Campanian units of the Belo Region near the Tsiribinha River (Richter, 2008, 2010; Walaszczyk et al., 2014).

METHODS

All three eggs were molded and cast prior to removal of eggshell samples for scanning electron microscopy (SEM),

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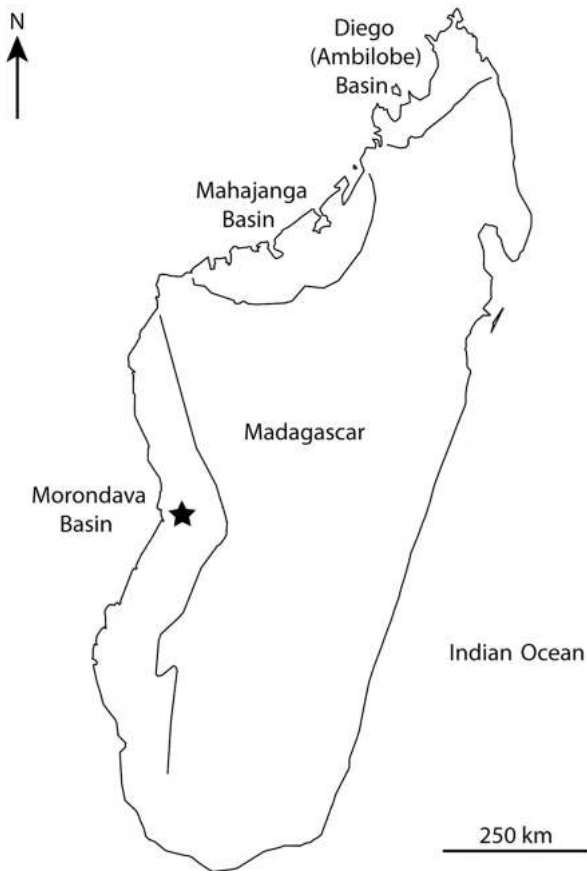


FIGURE 1. Map of Madagascar showing the general area in the Belo region in which the fossil turtle eggs were discovered, indicated by the star. Modified from Rogers et al. (2000).

cathodoluminescence (CL) analysis, and thin sectioning. Radial and tangential thin sections ($30\ \mu\text{m}$ thick) were made following standard procedures and examined under a Nikon Eclipse LV100POL light microscope. Eggshell fragments were mounted on an aluminum stud, coated with $10\ \text{nm}$ of gold, and imaged under a JEOL JSM-6100 SEM at $10\ \text{kV}$. Images included the inner surface and radial views of the eggshell. A radial, thick section of eggshell was polished and examined with cathodoluminescence (CL) to assess potential diagenetic alteration. Photomicrographs were taken using a Nikon Digital Sight DS-5Mc camera, and microstructural features were measured with

the image analysis software ImageJ. Computed tomographic (CT) scans were performed with a GE Phoenix v|tome|x CT scanner at the Anthropologisches Institut der Universität Tübingen, Germany, with a resolution of $50\ \mu\text{m}$.

Institutional Abbreviations and Repatriation—ES, Earth Science Department, Montana State University, Bozeman, Montana, U.S.A. The specimens are given a provisional collection number of the laboratory collection of Paläontologisches Institut und Museum der Universität Zürich, Switzerland (PIMUZ lab). Under the guidance of Armand H. Rasoamiaramanana, the specimens will be incorporated into the paleontological collection of the Département de Paléontologie at the Université d'Antananarivo in Madagascar. Plaster casts of the eggs are housed at the Department of Earth Sciences, Montana State University, Bozeman, Montana, U.S.A., and accessioned under the collection number VP-0951.

SYSTEMATIC PALEONTOLOGY

OOFAMILY TESTUDOOLITHIDAE Hirsch, 1996
 OOGENUS *TESTUDOOLITHUS* Hirsch, 1996
TESTUDOOLITHUS oosp.

Material—PIMUZ lab#2012.IW30, complete egg; PIMUZ lab#2012.IW31 and PIMUZ lab#2012.IW32, natural casts of eggs.

Locality—Belo Region near the Tsiribinha River, Morondava Basin, Madagascar.

Description—Two of three spherical eggs, PIMUZ lab#2012.IW31 and PIMUZ lab#2012.IW32, lack eggshell and measure approximately 35.5 and $34.8\ \text{mm}$ in diameter, respectively. These eggs are natural casts resulting from sediment infill prior to surface erosion.

The third egg (PIMUZ lab#2012.IW30) measures approximately $33.5\ \text{mm}$ in diameter (including eggshell) with smooth eggshell preserved on half of the specimen (Fig. 2). In places where the eggshell is missing or removed for sampling, the underlying sediment exhibits impressions of small, circular features that measure approximately 250 – $500\ \mu\text{m}$ in diameter (Fig. 2b). These features likely represent the basal-most portions of the shell units that broke free while sampling the eggshell for thin-section, CL, and SEM analysis. This is evident by the fact that these features are made up of radiating crystals that originate from the impression left behind by the organic core. Additionally, the diameters of these circular features correspond to the diameters of the shell units within the eggshell.

The eggshell is $440\ \mu\text{m}$ thick with shell units that are tightly packed and have a height to width ratio of 2:1. Pores were not identified in any of the radial sections. The permineralized organic core at the inner shell surface measures $52\ \mu\text{m}$ in

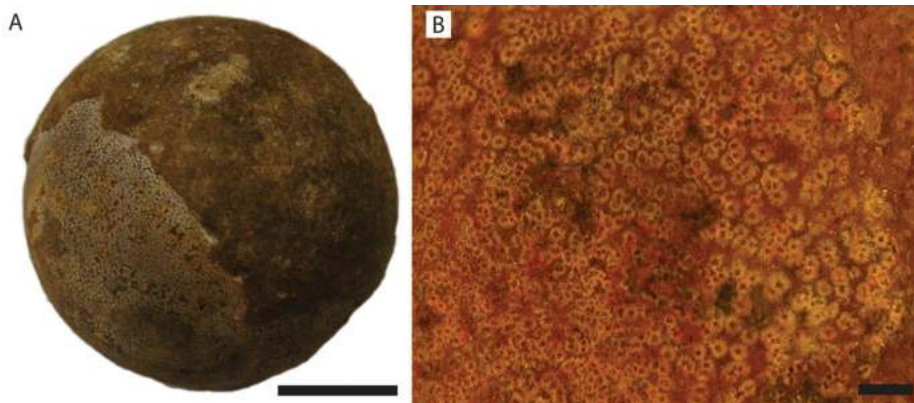


FIGURE 2. Fossil turtle egg (PIMUZ lab#2012.IW30). **A**, whole egg with eggshell preserved on approximately half of the specimen; **B**, close-up of underlying sediment with impression of shell units. Scale bars equal $1\ \text{cm}$ (**A**) and $1\ \text{mm}$ (**B**).

diameter. The lower two-thirds of the eggshell exhibits tight, interlocking acicular crystals that radiate from the organic core (Fig. 3). Under cross-polarized light, the eggshell displays a blocky extinction pattern (Fig. 4), and CL imaging reveals bright red to orange-red fluorescence over the entire sample (Fig. 3D).

DISCUSSION

The nearly spherical shape of the eggs suggests that embryos failed to hatch, but computer tomographic imaging of PIMUZ lab#2012.IW30 provides no evidence of embryonic remains inside the egg (Supplementary Data 1). This suggests that the eggs were either infertile or termination of embryonic development occurred prior to ossification of the skeleton.

With the exception of turtles, all other amniotes lay eggs composed of calcite, which has a more tabular, wedge-like microstructure (Mikhailov, 1991). The presence of tightly interlocking, acicular crystals in the lower two-thirds of the eggshell thickness (Fig. 3) is consistent with the aragonite microstructure of turtle eggshell. Therefore, the eggshell microstructure of the Malagasy eggs clearly suggests assignment to Testudines or their stem lineage.

Comparisons

Hirsch (1996) proposed a parataxonomic classification for fossil eggshells that recognized the oofamilies Testudoolithidae and Testudoflexoolithidae; these categories are primarily based on their rigid and flexible eggshell structure, respectively. The Malagasy eggs can be distinguished from the oofamily Testudoflexoolithidae based on their tightly packed shell units and a shell unit height to width ratio of 2:1 (Table 1). Among oospecies assigned to the Testudoolithidae, the Malagasy specimens differ from *Chelonoolithus braemi* Kohring, 1998, by a shell unit height to width ratio of 2:1. They differ from *Emydoolithus laiyangensis* Wang et al., 2013, in overall egg shape, but are similar in eggshell thickness and are within the lower range of height to width ratio of *E. laiyangensis*. They can be distinguished from *Haininchelys curiosa* Schleich et al., 1988, by their greater eggshell thickness. Conversely, the Malagasy eggs have thinner eggshell than the eggs of *Adocus* described by Zelenitsky et al. (2008). They differ from *Testudoolithus hirschi* Kohring, 1999, and *Testudoolithus jiangi* Jackson et al., 2008, by a smaller shell unit height to width ratio. Finally, the Malagasy eggs are similar to *Testudoolithus rigidus* Hirsch, 1996, by a shell unit height to width ratio of 2:1, but differ in the smaller egg size and thicker eggshell.

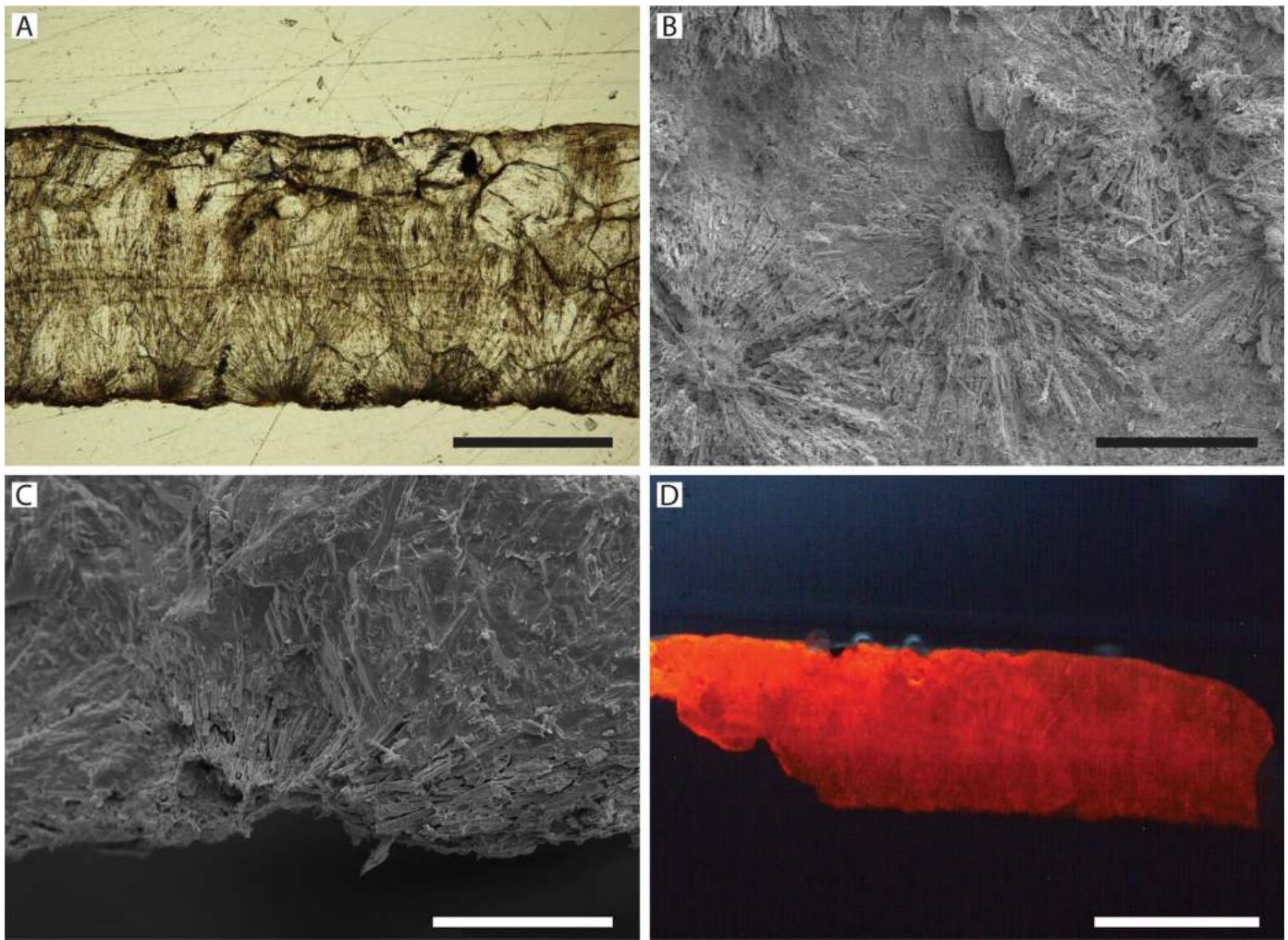


FIGURE 3. Photomicrographs of fossil eggshell (PIMUZ lab#2012.IW30). **A**, radial thin section showing original crystalline morphology on the lower two-thirds of the specimen; **B**, SEM image of the inner surface; **C**, SEM image in radial view; **D**, cathodoluminescence showing red to orange-red fluorescence suggesting calcite or dolomite replacement of the original aragonite composition. Scale bars equal 250 μm (**A**), 100 μm (**B**), 50 μm (**C**), and 150 μm (**D**).

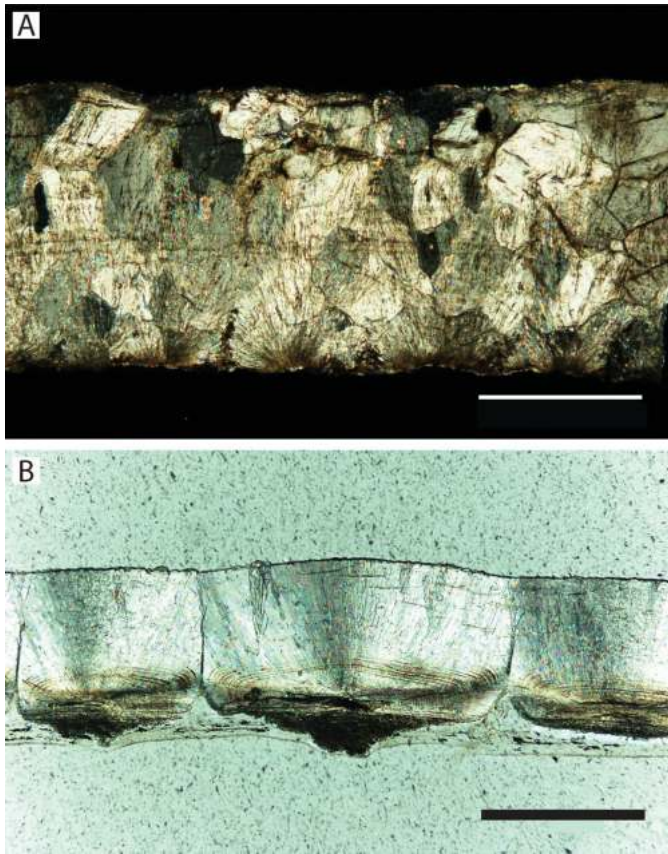


FIGURE 4. Polarized light microscopy of fossil and modern turtle eggshell. **A**, fossil eggshell (PIMUZ lab#2012.IW30) showing blocking extinction pattern; **B**, modern turtle eggshell (*Phrynops gibba*; ES 196) showing the typical sweeping extinction pattern of unaltered turtle eggshell. Scale bars equal 250 μm .

We refer the Malagasy eggs to the oofamily Testudoolithidae and to oogenus *Testudoolithus* oosp. However, classification at the oospecies level is difficult due to extensive alteration of the specimens. Thin-section analysis of the eggshell shows substantial recrystallization, characterized by blocky extinction under

cross-polarized light microscopy. This differs from the sweeping extinction pattern characteristic of modern and unaltered fossil turtle eggshell. Cathodoluminescence also reveals bright red to orange-red fluorescence suggesting calcite or dolomite replacement of the original aragonite, which prohibits assessment of pore density and gas conductance in these specimens due to recrystallization. Despite this replacement, pseudomorphs of the needle-like aragonite crystals are clearly preserved. Additionally, Hirsch (1983) and Masse (1989) demonstrate that, despite substantial alteration of aragonite to calcite, the structure of fossil turtle eggs can be identifiable when comparing the microstructure of altered specimens with avian and crocodylian eggshell under polarized light and scanning electron microscopy.

Malagasy Turtles

Late Cretaceous Malagasy turtle taxa are only known from the Maevarano Formation within the Mahajanga Basin of northern Madagascar. To date, no cryptodires have been discovered from the Mesozoic of Madagascar. In contrast, pleurodires are represented by the podocnemideran *Sokatra antiitra* Gaffney and Krause, 2011, *Kinkonychelys* sp., and *K. rogersi* Gaffney et al., 2009, cf. *Erymnochelys* sp., and an indeterminate bothremydid (Gaffney and Forster, 2003), all of which belong to Panpodocnemidae (sensu Joyce et al., 2004). However, all specimens are Maastrichtian in age and therefore geologically younger than the Campanian Morondava eggs.

The origin of crown chelonioids is controversial. Hirayama (1998) describes *Santachelys gaffneyi* from the Lower Cretaceous of Brazil as the oldest sea turtle (Chelonioidea). However, others dispute this identification and suggest that Chelonioidea did not appear until the Late Cretaceous (Joyce, 2007; Sterli, 2010; Anquetin, 2012). Additionally, molecular divergence analysis places the origin of Chelonioidea at the latest Cretaceous (Joyce et al., 2013). Despite this, no skeletal material of chelonioids has been documented from the Mesozoic of Madagascar. However, this does not suggest that sea turtles were not laying their eggs on the beaches of Madagascar during the Late Cretaceous. Because these specimens were discovered in marine rocks, it could be tempting to identify them as sea turtle eggs; however, the poorly mineralized eggshell of extant sea turtles consists of loosely organized shell units that differ significantly from the rigid eggshell of the Malagasy eggs (Hirsch, 1996). Despite this, it is not known if stem chelonoid turtles laid rigid or pliable-shelled eggs.

TABLE 1. Turtle ootaxa and diagnostic features.

Oospecies	Type specimen	Material	Egg shape	Length \times Width (mm)	Eggshell thickness (mm)	Shell unit (height:width)	References
<i>Testudoflexoolithus agassizi</i>	MCZ 2810/HEC 49	Eggshell fragments	—	—	0.06–0.1	1:1 or 2:3	Hirsch, 1996
<i>Testudoflexoolithus bathonicae</i>	BMNH 37983/HEC 186	An egg imbedded in matrix	Ellipsoidal	48 \times 26	0.2–0.25	1:1	Hirsch, 1996
<i>Chelonoolithus braemi</i>	Guimarota 98-2	Eggshell fragments	—	—	0.2	1:1	Kohring, 1998
<i>Emydoolithus laiyangensis</i>	IVPP V18544	A nearly complete egg	Elongate	91 \times 22	0.4–0.5	2:1–5:1	Wang et al., 2013
<i>Haininchelys curiosa</i>	—	Eggshell fragments	—	—	0.25–0.3	1.2:1–2.3:1	Schleich et al., 1988
<i>Testudoolithus hirschi</i>	—	Eggshell fragments	—	—	0.15	3:1	Kohring, 1999
<i>Testudoolithus jiangi</i>	ZMNH M8713	A clutch of 23 eggs	Spherical	35–52	0.7–1.0	2.5:1–3:1	Jackson et al., 2008
<i>Testudoolithus rigidus</i>	UCM 55806/HEC 425	Half of an egg	Spheroidal	42 \times 47	0.22–0.24	2:1	Hirsch, 1996
<i>Adocus</i> eggs	—	Gravid females and clutch with embryos	Spherical	40 \times 42	0.73–0.81	2.5:1–3.5:1	Zelenitsky et al., 2008
Malagasy eggs	—	Three eggs	Spherical	33.5–35.5	0.44	2:1	This paper

Modified from Lawver and Jackson (2014).

Investigation of chelonioid outgroups of other americhelydian turtles may provide information on the microstructure of stem chelonioid eggs. The eggs of chelydrids are spherical and semipliable, whereas *Dermatemys mawii* and kinosternids lay rigid-shelled eggs with an elongate shape (Ernst and Barbour, 1989). Tracing these characters on to a simplified tree of americhelydian turtle demonstrates that stem chelonioids likely laid spherical eggs, but whether these eggs were pliable or rigid is equivocal. Furthermore, turtle eggs of the oospes species *Testudoflexoolithus bathonicae* from the Middle Jurassic (Bathonian) of England have flexible eggshell and closely resemble those of crown chelonioids (Hirsch, 1996), and may have been laid by a stem chelonioid, although eggs of *T. bathonicae* differ from those of crown chelonioid eggs in having an elongate shape. With this in mind, we suggest that it is plausible that a stem chelonioid turtle may have laid the Malagasy specimens.

Other taxa that may have laid their eggs in a near-shore environment are large terrestrial turtles, protostegids, bothremydids, or podocnemidids. Neither protostegids nor large terrestrial turtles have been documented from the Mesozoic of Madagascar and, therefore, can be preliminarily ruled out. Additionally, definitive eggs from bothremydids have not yet been documented, but the close phylogenetic relationship between bothremydids and podocnemidids may indicate that they had similar eggs. Podocnemidid eggs are typically rigid-shelled and elongate. *Podocnemis expansa*, however, lays pliable, spherical eggs that are similar to extant sea turtles (Ernst and Barbour, 1989). Therefore, we suggest that it is plausible that the Malagasy eggs were laid by either a bothremydid or podocnemidid turtle. In fact, this may be more likely than the stem chelonioid hypothesis because only panpodocnemidid turtles are known from the Mesozoic of Madagascar. Definitive taxonomic identification requires the preservation of embryos or preservation of a gravid female.

Finally, evidence for thinning of the eggshell and rounded edges (Oser and Jackson, 2014), as well as the association of these eggs with scaphite ammonites and the heteromorph ammonite *Bostrichoceras* in marine rocks, suggests that the eggs were subject to transport from the paleo-nesting environment or reworking during their taphonomic history (Evans, 2012, and references therein).

Jackson et al. (2008) and Zelenitsky et al. (2008) use egg shape and clutch size to estimate the adult body size of the female turtles that laid their specimens. Therefore, comparisons of the Malagasy eggs with those of extant turtles may also provide useful paleoecological data. Extant turtles lay eggs that range in shape from spherical in large-bodied taxa to elongate in small-bodied taxa (Ewert, 1979; Elgar and Heaphy, 1989; Iverson and Ewert, 1991). Spherical eggs, which pack into the uterus more efficiently, are either associated with taxa that lay large clutches (12 or more eggs) or with reduced surface area, thereby reducing water loss during incubation (Iverson and Ewert, 1991). Additionally, thicker eggshell reduces water vapor conductance. This suggests that the spherical Malagasy eggs with thick eggshell are from a taxon that would have laid a large clutch in a relatively arid incubation environment, similar to that of other Late Cretaceous turtle eggs (Jackson et al., 2008; Zelenitsky et al., 2008). Adult body size cannot be calculated for the individual that laid the Malagasy eggs due to the incomplete preservation of the clutch.

The Malagasy eggs are only the fifth documented occurrence of Mesozoic turtle eggs from Gondwanan continents, following two specimens from Brazil (Azevedo et al., 2000; Marsola et al., 2014) and two from India (Sahni, 1957; Mohabey, 1998). The specimens described by Azevedo et al. (2000) and Sahni (1957) were identified only by gross morphology, however, and microstructural analysis was not performed. Additionally, many have questioned a turtle origin for the specimens described by

Mohabey (1998) because of low-quality figures and the identification of a mammillary layer at the basal-most portion of the eggshell (Kohring, 1999; Jackson et al., 2008; Knell et al., 2011). This feature is characteristic of only avian and non-avian theropod eggshell. Therefore, additional microstructural analysis is needed to clarify the identity of these specimens.

CONCLUSIONS

Although recent paleontological interest in the Mesozoic of Madagascar has documented a great diversity of vertebrates from the Late Cretaceous, no fossil eggs have been documented to date in this area. Despite significant diagenetic alteration the eggs described here can be identified confidently to Testudines because of their distinctive microstructure of radiating, acicular crystals. Additionally, they can be identified as rigid-shelled turtle eggs by tightly interlocking shell units with a shell unit height to width ratio of 2:1. The lack of associated skeletal remains, however, precludes taxonomic assignment of the specimens. Future discovery of turtle eggs associated with skeletal remains of embryos or gravid females may elucidate the taxonomic identification of these eggs.

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