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Preservation of Membrana Testacea in titanosaurid dinosaur eggshells from the Upper Cretaceous Deccan volcano-sedimentary strata of Central India

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Abstract

The calcitic eggshell units of amniote eggs are underlain by a soft organic layer, the Membrana Testacea (MT), which has a mesh-like texture consisting of fibrils of organic material. Because of its soft anatomy, the MT is rarely preserved in fossils and only a few fossil reports of MT are known so far. Here we report the preservation of a mineralized MT layer in titanosaur eggshells recovered from a marlstone facies interbedded with the Deccan lava flows exposed near Piplanarayanwar village of Chhindwara District, Madhya Pradesh state in Central India. The MT layer is mesh-like, resembling protein membranes of extant reptiles and the MT reported in titanosaurid eggshells of the Upper Cretaceous Anacleto Formation at Auca Mahuevo, Argentina. The presence of tendrils and fibres of calcite in the MT layer testifies to the fact that the calcium layer represents the original fibrous MT. It also supports the view that fossilization of soft tissues like MT is possible because of the inferred anaerobic conditions that prevailed during the deposition of Piplanarayanwar intertrappean sediments in lacustrine or paludal bodies in a coastal-plain setting.

1. Introduction

Reptilian eggs have a rigid mineralized external calcareous layer which is homogeneous as in Gekkonidae, has needle-like aragonite crystallites radiating from the inner core as in turtles, or consists of clearly defined cylindrical shell units arising from the outer surface of the shell membrane as in crocodiles and dinosaurs (Mikhailov, 1991). This assortment of ultrastructural units of eggshell is underlain by an organic shell membrane which consists of proteinaceous fibres and is known as Membrana Testacea (MT) (Grellet-Tinner, 2005; Schweitzer, 2011; Yang *et al.* 2018). In living reptiles, the MT is divided into two layers: the inner thin layer comprising organic fibres disposed in a sub-parallel fashion and the outer thick layer with interlacing fibres (Packard & DeMarco, 1995). The two layers of the MT are difficult to identify in fossil eggshells. The MT exists as a plane where zones of mineralized mammillae consisting of loosely assembled crystals are present in the centre (Cuif *et al.* 2010). These zones become nucleation points for the formation of eggshell units (Grellet-Tinner, 2005). The biological function of MT was considered as a filter for microorganisms (Krampitz & Graser, 1988). It has been observed that the MT does not bind Ca ions, hence it does not play any role in the initial phase of calcification of eggshells and its mesh-like structure supports calcium carbonate crystals (Krampitz & Graser, 1988).

While the outer rigid mineralized eggshell layer is generally found in fossils, the MT because of its soft anatomy is rarely preserved in fossils, specifically when exposed to oxidizing environments. However, there is evidence for the preservation of MT in the geological record. Some of the previous reports on preservation of MT in fossil state, such as the Pliocene turtle eggshells from the Canary Islands (Rothe & Klemmer, 1991) and the Upper Cretaceous dinosaur eggshells from Canada (Tazaki *et al.* 1994), were later rejected (Kohring, 1999). There are some undisputed records of fossilized MT. These include the Early Jurassic records in *Massospondylus* eggshells of Rooidraai locality in South Africa (Stein *et al.* 2019), *Lufengosaurus* eggs of China (Reisz *et al.* 2013) and *Mussasaurus* eggshells of Argentina (Reisz *et al.* 2013; Stein *et al.* 2019); the Late Cretaceous *Megaloolithus* eggshells from the Treppe Basin, Spain (Kohring, 1999; Sellés *et al.* 2013; Bravo & Gaete, 2015); the Late Cretaceous dinosaur eggshells of the Gobi desert (Sochava, 1969; Kolesnikov & Sochava, 1972); the Late Cretaceous *Triprismatoolithus* (probable alvarezsaurid) eggshells from Montana, USA (Yang *et al.* 2018); the eggshells of titanosaurid clutches with embryonic skeletons from the Late Cretaceous Auca Mahuevo site in Patagonia, Argentina (Grellet-Tinner *et al.* 2004; Grellet-Tinner, 2005); the Late Cretaceous *Megaloolithus siruguei* (Megaloolithidae) eggshells from

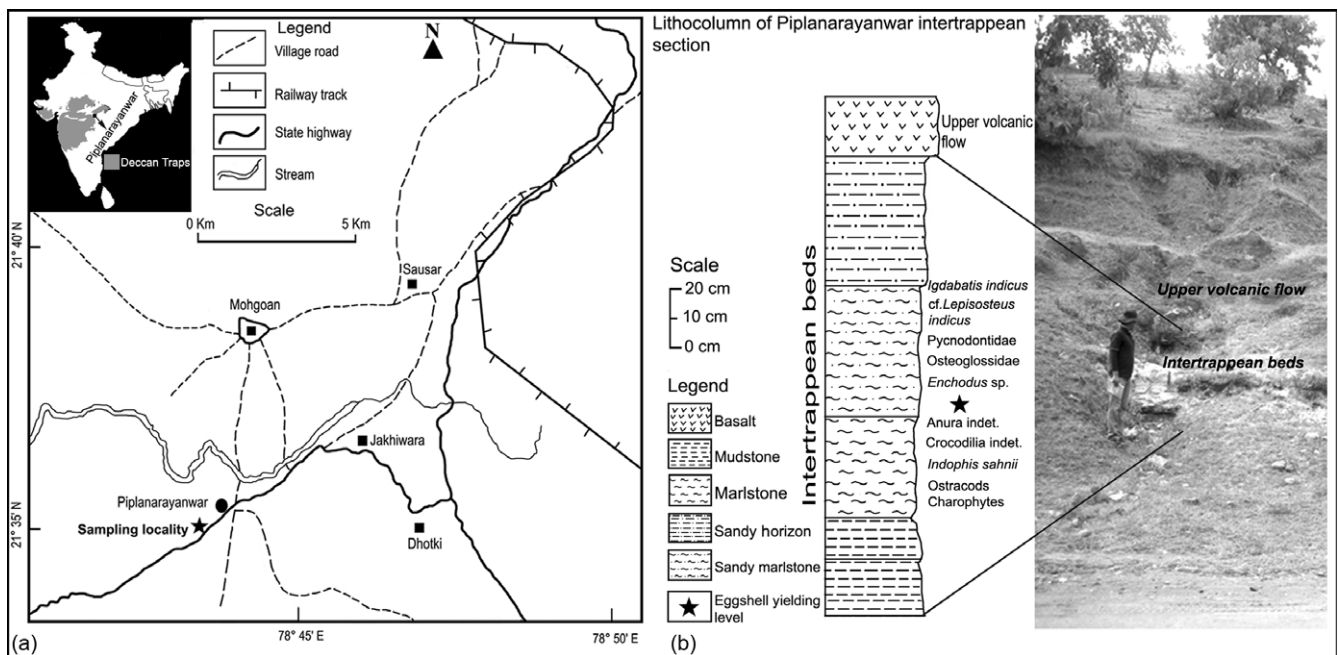


Fig. 1. Location map of the Deccan intertrappean section of Piplanarayanwar, Chhindwara District, Madhya Pradesh, India.

Hațeg Basin, Romania (Grigorescu & Oana-Claudia, 2017–18); crocodilian eggshells from the Eocene (Lutetian) of Geiseltal, Germany (*Krokolithes helleri* Kohring & Hirsch, 1996); Early Miocene avian eggshells from Dolnice, Czech Republic (Kohring, 1998); and avian eggshells from the Late Miocene of Nördlinger Ries, Germany (Kohring & Sachs, 1997).

The Late Cretaceous dinosaur fauna has been extensively documented from the Upper Cretaceous Lameta Formation or infra-trappean sedimentary beds that stratigraphically underlie the lava flows of the Deccan Traps in western and central India. The fauna comprises at least six species of abelisaurid theropod dinosaurs and about three taxa of titanosaurid sauropods (see Prasad, 2012; Prasad & Sahni, 2014; Khosla & Bajpai, 2021 for references). In addition to body fossils, widespread occurrence of clutches, eggs and eggshells of sauropod dinosaurs has also been reported from the Lameta outcrops of Madhya Pradesh, Gujarat and Maharashtra (Srivastava *et al.* 1986; Sahni *et al.* 1994; Khosla & Sahni, 1995; Mohabey, 1998; Srivastava & Mankar, 2015; H. Dhiman, unpub. PhD thesis, Delhi Univ., 2021; Dhiman *et al.* 2021). Additionally, some fragmentary dinosaur bones are also known from the Upper Cretaceous Kallamedu Formation (see Prasad *et al.* 2013) and the Upper Cretaceous Mahadek Formation of Meghalaya (Mishra & Sen, 2001). However, for the latest Cretaceous, dinosaur fauna from India is scarcely known and is represented by a few isolated occurrences of body fossils and fragmentary and isolated eggshells from the Upper Cretaceous (Late Maastrichtian) intertrappean beds that occur intercalated with the Deccan volcanic flows (see Prasad, 2012; Prasad & Sahni, 2014). No clutches or eggs have been reported so far from the Deccan intertrappean beds, and possibly the dinosaurs of India entered the waning phase by the time of their preservation in the intertrappean beds (Prasad & Sahni, 2014). Dinosaur eggshells were previously reported from the intertrappean beds of Asifabad, Nagpur (Sahni *et al.* 1984; Vianey-Liaud *et al.* 1987), Mohgaonkalan (Srinivasan, 1996), Kisalpuri (Khosla

et al. 2004) and Gujri (Kshetrimayum *et al.* 2021). Of these sites, Gujri and Kisalpuri intertrappean beds yield both sauropod and ornithoid eggshells.

Here we report the exceptional preservation of a fossilized MT layer in titanosaurid dinosaur eggshells from the intertrappean beds of Piplanarayanwar in Chhindwara District, Madhya Pradesh (Fig. 1). The documentation of a MT layer from titanosaur eggshell adds to the few previously known reports and this is the first report of MT from the Mesozoic deposits of India. The discovery also helps us to understand possible environmental conditions that facilitated the preservation of the soft organic layer.

2. Geological context

The Deccan Traps, representing one of the largest continental flood basalts of the Earth, cover an area of *c.* 500 000 km² in central, western and south-central India. The Deccan lava flows in general occur unconformably over the Precambrian basement rocks or Gondwana sediments or at many places over the Upper Cretaceous sediments formally known as the Lameta Formation or informally as the infra-trappean beds. The Lameta Formation in the Lameta Ghat type section near Jabalpur attains a maximum thickness of 70 m and is composed of basal Green Sandstone, Lower Limestone, Mottled Nodular Bed and Upper Calcareous Sandstone (Tandon *et al.* 1995) in this order of superposition. Sedimentary beds are present not only below the Deccan lava flows, but also occur intercalated with the volcanic flows. Such sedimentary beds are relatively thin and are generally known as intertrappean beds, referring to their position sandwiched between the volcanic flows. Both the Lameta Formation and the intertrappean beds have been a great source of several vertebrate groups (see Khajuria *et al.* 1994; Prasad & Khajuria, 1995; Khosla & Sahni, 2003; Prasad, 2012; Prasad & Sahni, 2014). In the past, palaeontological evidence has been used to indicate that the Lameta Formation is Turonian in age (Sahni, 1972) and the intertrappean

beds range in age from Upper Cretaceous to Early Eocene (Sahni, 1934; Sastry & Lahiri, 1981; Bande *et al.* 1986) or even Oligocene (Mathur, 1968; Shivarudrappa, 1976–7). However, later studies have shown that the Lameta Formation is Maastrichtian in age based on fish remains, palynofossils and on comparison of dinosaur fauna with that of Madagascar (Courtillot *et al.* 1986; Buffetaut, 1987; Dogra *et al.* 1994; Khajuria *et al.* 1994). The intertrappean beds are now regarded as Latest Cretaceous to Early Palaeocene in age on the basis of vertebrate fossils, microfossils and palynofossils (Prasad, 1989; Raju *et al.* 1991; Jaiprakash *et al.* 1993; Khajuria *et al.* 1994; Prasad & Khajuria, 1995; Sahni *et al.* 1996; Singh *et al.* 2006; Keller *et al.* 2012; Samant *et al.* 2014).

The Deccan volcanic province of India is divided into four sub-provinces: Main Deccan Province, Malwa Plateau, Mandla Lobe and Saurashtra. The intertrappean sedimentary section under reference falling within the Mandla Lobe is exposed along a road 1.20 km SW of Piplanarayanwar village (21° 34' 45.50" N, 78° 42' 56.26" E) in Chhindwara District, Madhya Pradesh (Fig. 1a). The sedimentary sequence of this section consists of sandy marlstone, marlstone and mudstone (Fig. 1b) and measures 1.6 m in thickness. This intertrappean section preserves only the upper basaltic flow. However, the lower basaltic flow can be observed at the lower slopes of the hill along the road where the intertrappean beds are exposed. A total of 500 kg of bulk samples were collected from different sedimentary units of this intertrappean section and all the samples were screen-washed using microvertebrate fossil recovery techniques to recover vertebrate microfossils. A rich assemblage of vertebrate microfossils represented by *Igdabatis indicus* Prasad & Cappetta, 1993, ?*Rhombodus* sp., cf. *Lepisosteus indicus*, Pycnodontidae gen. et sp. indet., Osteoglossidae gen. et sp. indet., *Enchodus* sp., Anura indet., Crocodilia indet., *Indophis sahnii* Rage and Prasad (1992) (a nigerophiid snake), and dinosaur eggshell fragments was recovered from this intertrappean section. Eggshell fragments referred in this work were recovered from the marlstone beds. These beds also yielded ostracod fauna represented by *Paracyprretta jonesi* (Bhatia & Rana, 1984), *Cyclocypris amphibolos* (Whatley *et al.* 2002) and *Mongolianella cylindrica* (Sowerby, 1840) and a charophyte flora represented by *Chara* sp., *Platychara raoi* (Bhatia & Mannikeri, 1976) and *Dughiella obtusa* (Feist-Castel, 1975). The genus *Igdabatis* (*Igdabatis sigmodon*) was first reported from the Maastrichtian deposits of Niger (Cappetta, 1972). The second documentation of *Igdabatis* outside India was from the Campanian–Maastrichtian deposits of Spain (Soler-Gijón & López-Martínez, 1998; Kriwet *et al.* 2007). In India, until now, this genus has been described from the Upper Cretaceous (Maastrichtian) Lameta Formation of Pisdura in Maharashtra (Jain & Sahni, 1983), Jabalpur in Madhya Pradesh (Courtillot *et al.* 1986), Marepalli in Telengana (Prasad & Cappetta, 1993), and the Upper Cretaceous (Maastrichtian) intertrappean beds of Asifabad (Prasad & Sahni, 1987; Prasad & Cappetta, 1993) and Naskal in Telengana (Prasad & Khajuria, 1990), Nagpur in Maharashtra (Gayet *et al.* 1984), Lotkheri (Kapur *et al.* 2006) and Kisalपुरi in Madhya Pradesh (Khosla *et al.* 2004; Verma *et al.* 2016). So far, *Igdabatis* has not been reported from the Palaeocene strata of India. Though its alleged presence in the Upper Cretaceous – Palaeocene Fatehgarh Formation in Barmer Basin, Rajasthan, western India, was reported (Mathur *et al.* 2006), the batoid fish fauna of the Fatehgarh Formation is quite distinct from that of Deccan intertrappean beds and no form related to *Igdabatis* is present in the vertebrate fauna of this formation (GVRP pers. observ.). It can also be argued that the *Igdabatis*-

yielding intertrappean section of Piplanarayanwar is Campanian in age as this genus occurs in Campanian–Maastrichtian deposits of Spain (Soler-Gijón & López-Martínez, 1998). We do not subscribe to this argument as the oldest Deccan lava flows were dated at 67.4 ± 0.3 Ma (see Kale *et al.* (2019) for a synthesis of geochronology of the Deccan Traps) and the intertrappean sedimentary beds occur intercalated with the volcanic flows at younger stratigraphic levels than the oldest volcanic flows. Therefore, based on the presence of age-diagnostic myliobatid fish *Igdabatis indicus* (Prasad & Cappetta, 1993) and associated Maastrichtian ostracod fauna, the intertrappean beds of Piplanarayanwar are considered as Late Cretaceous (Maastrichtian) in age (Lourembam *et al.* 2017).

3. Materials and methods

Bulk screen-washing of 500 kg samples using the combined kerosene–water immersion technique led to the recovery of vertebrate microfossils and associated microfossils consisting of ostracods and charophytes from the Deccan intertrappean sediments of Piplanarayanwar. Following the sorting of screen-washed residue under a stereoscopic binocular microscope, only five eggshell fragments described here were recovered along with various other vertebrate microfossils. The specimens were cleaned with an ultrasonic vibrator before Scanning Electron Microscope (SEM) imaging was done. The chemical composition of different layers of the eggshells was measured using the Energy-Dispersive X-Ray (EDS) attachment to the SEM model Zeiss EVO MA10 at the Department of Entomology, Indian Agricultural Research Institute, New Delhi.

Institutional Abbreviation: DUGF stands for the fossil catalogue numbers of the Department of Geology, University of Delhi, Delhi.

4. Systematic palaeontology

Fusiolithidae Fernández and Khosla (2015)

Fusiolithus baghensis (Khosla & Sahni 1995) Fernández and Khosla (2015)

Referred material. DUGF/162–166

Stratigraphic horizon and locality. Intertrappean beds exposed 1.20 km NW of Piplanarayanwar village, Chhindwara District, Madhya Pradesh, India.

Age. Maastrichtian (Late Cretaceous).

Description. The external surface morphology of the eggshells is undulating, with moderately developed, coarse circular nodes (Fig. 2a, b, f). These nodes have a diameter ranging between 145 and 500 μm and coalesce to form linear, coarse ridges. The surface morphology is rough, and depressed areas are present between the ridges. Tubular pores with circular openings extending to the internal surface and measuring from 0.13 mm to 0.20 mm in diameter are observed on the external surface of the eggshell at the base of coarse and raised nodes or ridges (Fig. 2a, b, f). Elongated, cone-shaped pore canals are also observed in the radial section (Figs 2c–e, 3e).

The height and width of individual shell units are c. 0.53 and 0.33 mm, respectively, with a height–width ratio of 1.60:1. The shell units are short, broad and fan-shaped, having flared out from both sides of the vertical axis of the nucleation centre. From one-third of their height, the lateral margins of shell units still flare out but to a lesser extent. This makes them appear parallel at this level. The concentric growth lines are not observed in SEM photographs. Numerous radial lines representing acicular calcite crystallites

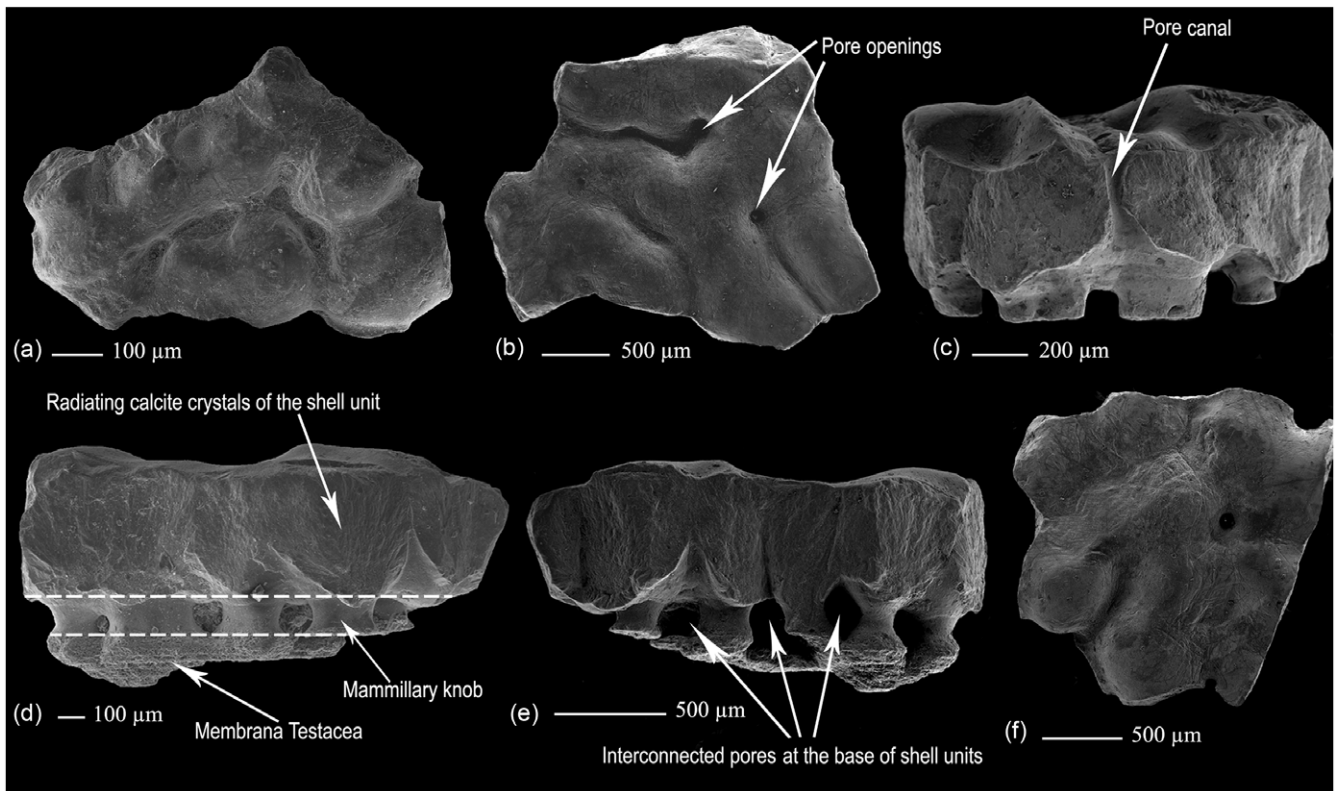


Fig. 2. SEM photomicrographs of the eggshell specimens of *Fusioolithus baghensis* (Khosla & Sahni, 1995; Fernández & Khosla, 2015) from the intertrappean beds of Piplanarayanwar. (a) External surface of DUGF/164 showing ridged and tuberculated morphology. (b) External surface of DUGF/163 showing undulating tubercles separated by depressed regions in between them and also exhibiting pore canal openings. (c) Radial section of DUGF/163 with broad shell units, pore canals and basal mammillary knobs. (d, e) Radial sections of DUGF/165 exhibiting the inner organic layer (Membrana Testacea), overlying mammillary knobs with interconnected pore canals, and outer shell units. (f) Tuberculated and undulating external surface of DUGF/162 with a pore opening.

commence from the calcium reserve body at the base of the shell units. A horizontal network of pore canals is seen at the base of shell units (Figs 2d, e, 3e). They seem to have formed at the intersection of mammillary knobs at the base of shell units.

The radial thin-section of the eggshells clearly shows shell units flaring upwards and fused with the adjacent shell units, resulting in arched and continuous growth lines (Fig. 4). The growth lines show concavity between adjacent shell units. The basal end knobs are also characteristically present (Fig. 4).

In the radial section of the eggshells, a thin (*c.* 245 µm) fibrous layer of compact calcite is present on the inner surface of the eggshell units (Figs 2d, e, 3e, f). SEM study of this part in DUGF/165 demonstrated the presence of disorganized, filament-like structures that measure 240–280 µm in length (Fig. 5a, b). We interpret this layer as the mineralized Membrana Testacea (MT). The MT proximal to the shell units is more compact than the one distal to them or occurring on the inner surface of the mammillary knobs. The change of MT's texture from more compact to somewhat aerated form has also been observed in the eggshells from egg-level 3 of Auca Mahuevo (Grellet-Tinner *et al.* 2004) which recalls the condition observed in modern non-avian reptiles and birds (Packard & DeMarco, 1995). Horizontally disposed parallel to oblique filamentous structures of calcite with specks of amorphous calcium carbonate on the surface (discernible at higher magnification) (Fig. 5b) and oriented perpendicular to the long axis of the shell units are present throughout the thickness of the MT layer (Figs. 3d–f, 5a, b). The individual strands are 4 to 5 µm in diameter.

The MT is succeeded externally by widely spaced cylindrical knobs representing the mammillary or basal knobs. The mammillary knobs, spherical or ridged in cross-section, have a diameter ranging between 180 and 370 µm and a height of *c.* 120 µm (Fig. 3a). The inner surface of the basal knobs is covered by long and criss-crossing or braided strands of calcite (Fig. 3d). Some of these knobs merge with each other (Fig. 3a). A few of them also exhibit central pits with radiating calcite crystals which may possibly represent the resorption craters (Fig. 3a–c). The distance between these knobs is variable. Above the basal knobs lie the individual fan-shaped, broad and short shell units which are set apart from each other by interstitial space or partially fused (Figs 2c–e, 3e).

Remarks: Fernández and Khosla (2015) erected a new oofamily Fusioolithidae in which the eggshells are characterized by dinosauroid–spherulitic basic type, tubospherulitic morphology, tubocanalicular pore system, compactituberculate ornamentation, growth lines crossing the boundary between shell units starting at the inner one-third of the eggshell thickness and sometimes continuing to the external surface, and fan-shaped eggshell units partially fused without clearly demarcated boundary lines. Many of the oospecies earlier described under the genus *Megaloolithus* were transferred to the new genus *Fusioolithus* (Fernández and Khosla, 2015). These authors synonymized *Megaloolithus baghensis* (Khosla & Sahni, 1995) and *Megaloolithus balasinorensis* (Mohabey, 1998) from India, *Megaloolithus pseudomamillare* from France (Vianey-Liaud *et al.* 1997), *Patagoolithus salitralensis* from Argentina (Simón, 2006) and *Megaloolithus cf. baghensis* (Sellés *et al.* 2013) from Spain with

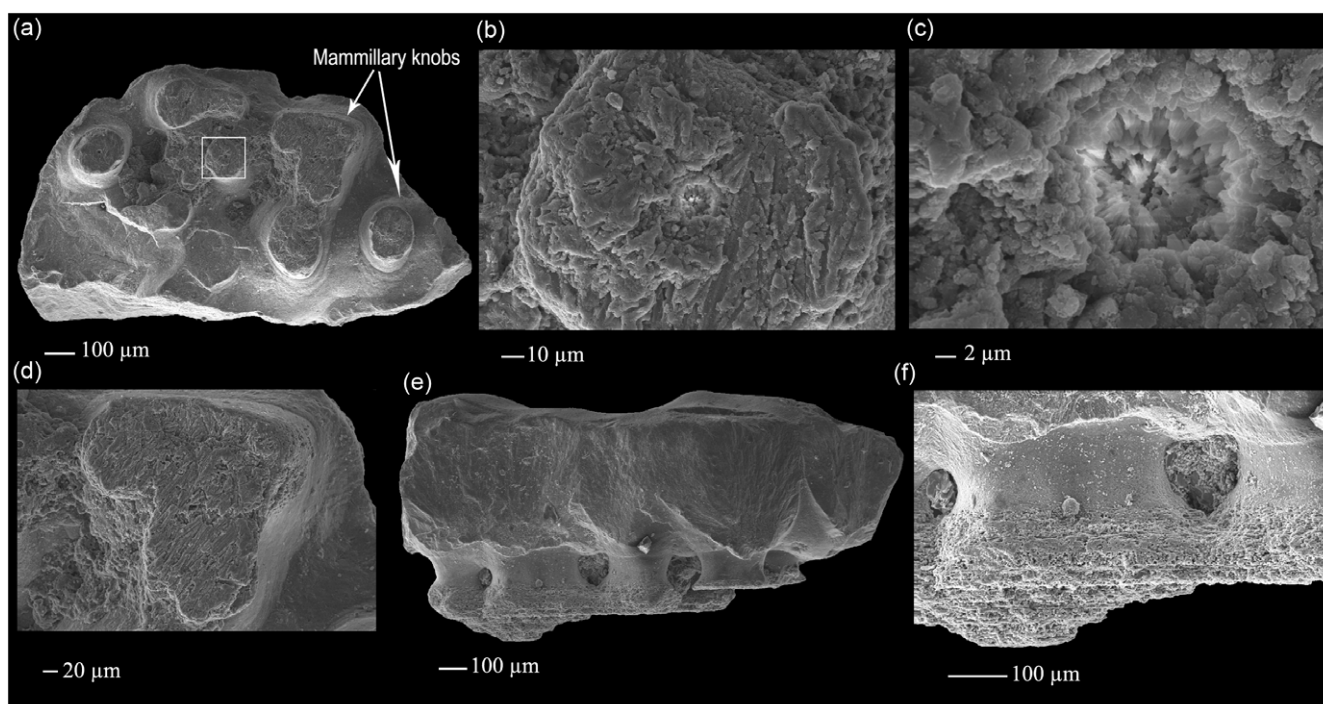


Fig. 3. SEM photomicrographs of the eggshell specimens of *Fusioolithus baghensis* (Khosla & Sahni, 1995; Fernández & Khosla, 2015) from the intertrapean beds of Piplanarayanwar. (a) Internal surface of DUGF/166 consisting of circular knobs that are connected to each other at some places and are composed of criss-crossing calcite strands. (b, c) Enlarged views of a resorption crater (squared area in (a)) showing calcite crystals radiating from the centre. (d) Enlarged view of one of the basal knobs displaying calcite strands oriented perpendicular to the long axis of the shell units. (e) Radial section of DUGF/165. The shell units are wider than tall at places separated by cone-shaped pore canals and show acicular lines radiating from an organic core and well-developed basal knobs underlain by a layer of Membrana Testacea. (f) Enlarged view of Membrana Testacea (DUGF/165).

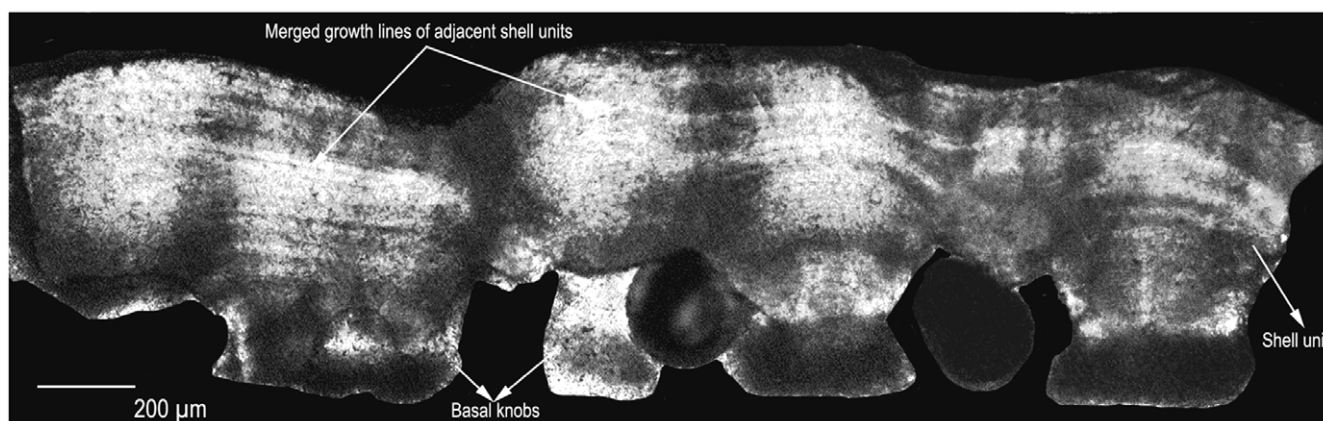


Fig. 4. Thin-section of *Fusioolithus baghensis* eggshell (DUGF/162) showing broad, short and partially fused shell units with well-developed basal knobs. The growth lines of adjacent shell units merge with each other, forming concave surfaces where they merge with their counterparts on the adjacent shell unit.

Fusioolithus baghensis (Khosla & Sahni, 1995), the type species for the genus *Fusioolithus*.

Eggshells from egg-level 3 of the Upper Cretaceous Auca Mahuevo site, Argentina, were initially referred to the oofamily Megaloolithidae (Chiappe *et al.* 1998). Grellet-Tinner *et al.* (2004) referred them to *Megaloolithus patagonicus*, an oospecies previously described from the Upper Cretaceous rocks of Neuquén Basin, Argentina, by Calvo *et al.* (1997). However, Fernández *et al.* (2022) observed that the Auca Mahuevo eggshells are indistinguishable from those of *Patagoolithus salitralensis* (Simón, 2006) known from the Salitral Moreno area in Argentina. The latter is quite distinct from *M. patagonicus* in

eggshell microstructure and ultrastructure. Fernández *et al.* (2022) assigned Auca Mahuevo eggshells from egg-level 3 along with *P. salitralensis* to *F. baghensis*.

Fusioolithus includes two oospecies *F. baghensis* and *F. berthelii* (Khosla & Sahni, 1995). The latter differs from the former in having thicker eggshells (2.4–2.9 mm) and greater height–width ratio (3.27:1). The microstructural and ultrastructural features of Piplanarayanwar eggshells clearly indicate that these eggshell fragments belong to the dinosauroid–spherulithic type with tubocanalliculate pore system. The radial thin-section of the eggshells shows fan-shaped shell units flaring upwards and partially fused with the adjacent shell units, resulting in arched and continuous growth

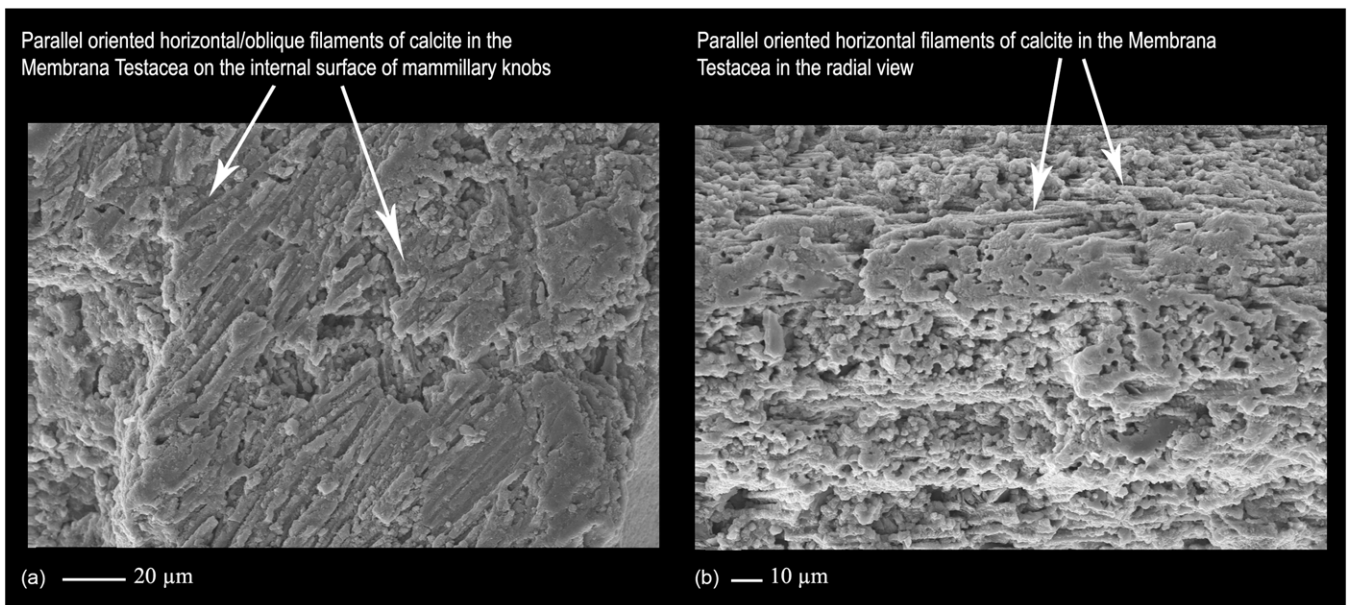


Fig. 5. (a) Enlarged view of basal knobs showing parallel or obliquely oriented calcite filaments on the internal surface (DUGF/166). (b) Enlarged view of parallel calcite filaments in the MT layer oriented perpendicular to the long axis of the shell units (DUGF/165). Specks of amorphous calcium carbonate can be seen on the surface of these filaments at higher magnification.

lines (Fig. 4). The growth lines showing concavity in between two shell units and basal end knobs are also characteristically present. Such fused shell units, merged growth lines and swollen basal-end caps strongly support the assignment of *Piplanarayanwar* eggshells to the oospecies *Fusioolithus baghensis*.

In general morphology of having fibrous bundles perpendicular to the long axis of the shell units and on comparison with the earlier reports of MT in dinosaur eggshells (Kohring, 1999; Grellet-Tinner *et al.* 2004; Sellés *et al.* 2013; Bravo & Gaete, 2015), the calcitic layer at the base of shell units is identified as an MT layer. However, these eggshell fragments are clearly different from other *Megaloolithus* and *Fusioolithus* oospecies of Khosla and Sahni (1995), Mohabey (1998) and Fernández and Khosla (2015) in being thin and lacking more pronounced cylindrical shell units and highly nodose external surface ornamentation. Though the wide shell units resemble those of the eggshell of turtles, the presence of basal knobs and the horizontal network of pore canals identify them as sauropod eggshells (Grellet-Tinner *et al.* 2004; Dhiman *et al.* 2019).

5. Elemental composition of the eggshell layers using Energy-Dispersive X-Ray Spectroscopy

Elemental analysis by Energy-Dispersive Spectroscopy (EDS) was performed at the top and base of the eggshell units and below mammillary knobs where the Membrana Testacea is preserved. The EDS analysis showed that the mineralogical composition of the top and bottom levels of the eggshell units are essentially the same, consisting of carbon (C), calcium (Ca), oxygen (O) and silicon (Si) as the main components, in addition to small quantities of sodium (Na), magnesium (Mg), potassium (K) and chlorine (Cl) (Fig. 6a, b) which are characteristic of fossil amniote eggshells. EDS elemental analysis of the MT showed closely similar elemental values except for some minor variations (Fig. 6c). Although the more common elements such as Ca, O and C occur in more or less similar proportions

throughout the preserved eggshell, as compared to the eggshell proper the MT layer has slightly reduced amounts of Ca and Na and slightly increased levels of Si. Additionally, it is observed that aluminium (Al) and iron (Fe) are also present, but Cl and K are absent in this layer. The slightly increased levels of Si and Al might have been introduced by clay minerals from the siliclastic rocks in which the eggs were buried. Decreased Ca content, increased Si content and the introduction of Fe indicated that limited diagenetic replacement of calcium carbonate has taken place in the MT layer during the process of fossilization. Increased Si values in the MT layer may also point to the fact that organic matter may have formed a template for early silicification (Folk & Lynch, 2001) as was observed in the MT layer of Auca Mahuevo dinosaur eggs from Argentina (Grellet-Tinner, 2005).

6. Discussion

6.a. Membrana Testacea

Though Rothe and Klemmer (1991) reported the presence of MT in diagenetically altered chelonian eggshells from the Pliocene of the Canary Islands, based on the occurrence of the same material in the pore canals, on the edge of the shell fragments and in the supposed MT, Kohring (1999) interpreted the porous structure below the shell units as diagenetically altered sediment attached to the shell. Similarly, Kohring (1999) suggested that the putative MT identified on the inner surface of dinosaur eggshell from the Upper Cretaceous of Canada by Tazaki *et al.* (1994) might be hyphae of fungi and, hence, a modern contamination. Later, Grellet-Tinner (2005) documented the presence of MT on the inner surface of the calcareous eggshells of megaloolithid dinosaurs recovered from the Campanian Anacleto Formation, Auca Mahuevo, Patagonia, Argentina. The eggshells described here are isolated in occurrence and no clutches were found. Hence their identification is essentially based on comparison to other known

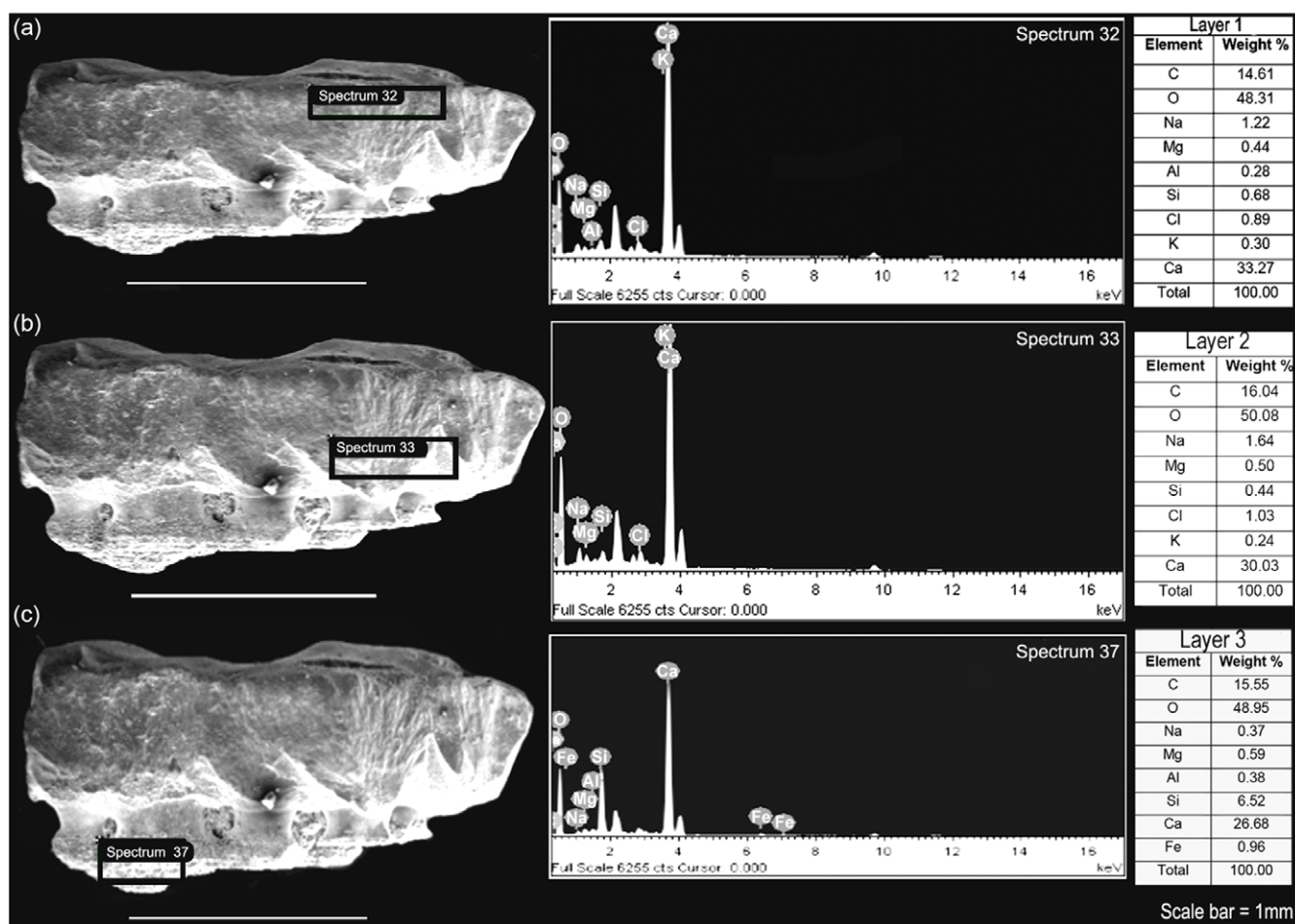


Fig. 6. Elemental profiles of *Fusioolithus baghensis* eggshell (DUGF/165) from the intertrappean beds of Piplanarayanwar in the Energy Dispersive X-ray Spectroscopy (EDS) spectra. EDS spectra from the top (a) and base (b) of the eggshell units and the Membrana Testacea (c).

and undisputed titanosaurid eggs having embryonic bones such as Auca Mahuevo, Argentina (Grellet-Tinner *et al.* 2004). Gross morphological features and comparison with known MT layers in previously reported dinosaur eggshells (Kohring, 1999; Grellet-Tinner, 2005) favour the identification of the calcareous layer on the inner surface of dinosaur eggshells from the intertrappean beds of Piplanarayanwar, Chhindwara District, Madhya Pradesh, as the MT. The MT layer of Piplanarayanwar eggshells exhibits a mesh-like texture, and the ultrastructure exhibits fine tendrils and fibres of calcitic material that replicate the soft membrane, similar to those of previous reports (Kohring, 1999; Grellet-Tinner, 2005). In the presence of external nodes and nodes coalescing into ridges, a similar pore diameter and horizontal pore canal network at the base of inner knobs of shell units, partially fused eggshell units, and the merging of growth lines of adjacent shell units starting from the inner one-third of the shell thickness, the Piplanarayanwar eggshells are somewhat comparable to the eggshells of the Auca Mahuevo site (Grellet-Tinner *et al.* 2004; Grellet-Tinner, 2005). However, the eggshell dimensions of Piplanarayanwar and Auca Mahuevo do not match, as the eggshells of the Indian site have imperfectly preserved outer shell surface. The thickness of the MT layer is c. 245 µm in the Indian eggshells, which is intermediate between the values reported for the MT layer of the dinosaur eggshells from egg-level 3 of Auca Mahuevo, Argentina (281 µm; Grellet-Tinner *et al.* 2004), and

Tremp Basin, Spain (300 µm; Sellés *et al.* 2013). In height–width ratio, the Piplanarayanwar eggshells (1.60:1) are closer to those of Tremp Basin (1.88:1) than to those of Auca Mahuevo (>2.0:1). On the other hand, the diameters of pore openings of Piplanarayanwar eggshells (0.13 to 0.20 mm) are within the range of Auca Mahuevo eggshell pore openings (0.15 to 0.29 mm).

6.b. Conditions of preservation

Preservation of micron-sized fibres of MT is not common in the fossil record and such rare preservations are possibly the result of some favourable conditions for preservation such as anoxic depositional environments and the metabolic activities of associated microbes (Bottjer *et al.* 2002). Based on the study of Cretaceous sauropod dinosaur eggshells from Spain, Eocene crocodylian eggshells from Germany, Miocene avian eggshells from the Czech Republic and Germany, and modern bird eggshells, Kohring (1999) concluded that the preservation of MT in these eggshells was due to the aerobic decay of the internal tissue prior to burial that allowed the formation of calcium-rich gel within the MT. An analysis of modern avian eggs showed resistance of MT to early stage of diagenesis and formation of gel composed of calcium and sulphur in between the organic fibrils of the MT (Kohring, 1999). However, later studies have shown that aerobic decay prior to burial is not necessary for bacterial mediation of the calcium

carbonate precipitation onto the MT strands (Reid *et al.* 2000; Visscher *et al.* 2000). Subaerial exposure would result in the desiccation and removal of the MT from the eggshell (Hayward *et al.* 2000). Soft tissue like the MT can be preserved as fossil only when it undergoes rapid replication by mineral precipitation, such as calcium carbonate (Allison, 1988). As soft tissues get destroyed by their own enzymes such as those released by lysosomes under aerobic conditions, their preservation necessitates an anaerobic environment in which the bacteria replicate the original soft tissue structure in exquisite cellular detail before its destruction and then stimulate biomineralization of the replica (Raff *et al.* 2008). Grellet-Tinner (2005) suggested that lack of energy and no exposure to subaerial conditions are more important for the preservation of MT. As observed in the lithification of microbial mats such as stromatolites (Reid *et al.* 2000; Visscher *et al.*, 2000), in an anaerobic depositional environment, sulphate- or sulphur-reducing bacteria would transform the inorganic and organic compounds of the eggshells into an energy source that leads to alkaline conditions congenial for the precipitation of calcium carbonate (Grellet-Tinner, 2005).

The MT-bearing eggshells of the present study have been retrieved from the marlstone facies of the intertrappean unit that was deposited in a coastal-plain palaeoenvironment (Lourembam *et al.* 2017). The Piplanarayanwar intertrappean biota is represented predominantly by freshwater and terrestrial elements such as *Lepisosteus*, Osteoglossidae gen. et sp. indet., Siluriformes indet., indeterminate anurans, aquatic snake *Indophis sahnii*, crocodiles (Crocodylia indet.), sauropod dinosaur eggshells, coprolites, freshwater ostracods and charophytes, as compared to limited marine/brackish water elements like *Igdabatis indicus*, *?Rhombodus* sp., Pycnodontidae gen. et sp. indet. and *Enchodus* sp. Composition-wise, the biota of these intertrappean beds constitute 40 % actinopterygians, 8 % chondrichthyans, 4 % amphibians, 16 % reptiles, 12 % ostracods and 20 % charophytes. The predominance of freshwater elements over brackish-water/marine forms suggests that the freshwater forms occupied a permanent body such as a lake or pond close to the sea coast intermittently connected with a river system and the marine/brackish water taxa were introduced into the lake when they moved upstream of the river (Sahni, 1983; Díez-Canseco *et al.* 2014; Verma *et al.* 2016; Lourembam *et al.* 2017; Prasad *et al.* 2018). Fossils from these intertrappean beds are very well preserved, with intact tooth enamel, and do not show any evidence of long-distance transport with respect to other intertrappean beds of the Deccan Volcanic Province such as those of Naskal and Asifabad in south-central India, which were either subjected to surficial etching or long-distance transport. In the absence of well-preserved clutches in the studied intertrappean beds we can only speculate on the possible preservation medium that facilitated permineralization of the MT layer. Preservation of the MT in a permineralized condition at the base of the mammillary knobs of the dinosaur eggshells suggests that the palaeoenvironment was conducive for the replacement of the organic layer with calcium carbonate before its decomposition. Stagnant brackish water body might have inhibited the decomposition or large-scale diagenetic recrystallization. These eggshells might have been derived from eggs deposited close to the banks of a lacustrine system or transported into the water body from a nearby terrestrial clutch site soon after hatching and before the decomposition of organic material. The presence of well-preserved pore canals without sediment or mineral infilling, as evident from the circular pore openings at the base of external nodes of the shell (Fig. 2b, f) and from radial sections (Fig. 2c–e), point to the sufficiently

porous nature of the eggshell that permitted the exchange of gases and vapour with the external environment. In the case of Piplanarayanwar eggshells, shielding of eggshells from the aerobic conditions through rapid burial by fine sediments possibly occurred soon after hatching of the eggs. As in the case of the titanosaurid eggs of Auca Mahuevo, Argentina (Grellet-Tinner, 2005), and Hațeg Basin, Romania (Grigorescu & Oana-Claudia, 2017–18), we believe that the preservation of the MT layer in the dinosaur eggshells of the Piplanarayanwar intertrappean beds was facilitated by bacterially mediated precipitation of calcium carbonate. Whether the permineralization or replacement of the MT by calcium carbonate took place before the segregation of eggshells from the clutch or after their burial by fine sediment is difficult to interpret in our current state of knowledge. However, neither the eggshells nor the associated fossils provide any evidence for long-distance transport to the depositional milieu.

7. Summary

Here we document for the first time the preservation of fossil Membrana Testacea, the organic layer that underlies the mammillary knobs of eggshells, from the Mesozoic rocks of India. The eggshells with preserved MT come from a marlstone facies of the Upper Cretaceous intertrappean beds of Piplanarayanwar in central India, and their microstructure places them within the titanosaurid oospecies *Fusioolithus baghensis*. The MT layer occurring on the internal surface of the eggshells is characterized by parallel strands of calcium carbonate oriented perpendicular to the long axis of the eggshell units. The preservation of soft organic layer such as MT in fossil state is rarely known and mostly restricted to fossil sites of exceptional preservation. Circumstantial evidence from associated fossils, the fine marly sediments in which the eggshells were preserved, and the state of preservation of pore canals and the MT layer all point to rapid burial in a humid environment under anaerobic conditions and calcium carbonate mineralization of the MT layer by bacterial mediation as was interpreted for eggshells of the Auca Mahuevo (Argentina) (Grellet-Tinner, 2005) and Hațeg Basin (Romania) (Grigorescu & Oana-Claudia, 2017–18) sites. The fossils of the Piplanarayanwar intertrappean beds represented by a higher number of freshwater than brackish/marine taxa point to the presence of lacustrine bodies in a coastal setting with intermittent connections to the sea, the banks of which were the possible clutch sites of dinosaurs. The stagnant brackish water bodies where the eggshells were deposited could have prevented early decomposition of the soft MT.

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Conflict of interest. None.

References

- Allison PA (1988) The role of anoxia in the decay and mineralization of proteinaceous microfossils. *Paleobiology* **14**, 139–54.
- Bande MB, Chandra A, Venkatachala, BS and Mehrotra RC (1986) Deccan intertrappean floristics and its stratigraphic implications. In *Proceedings of*

- the *Symposium on Paleocene of India: Limits and Subdivisions* (ed. BS Venkatachala), pp. 83–123. Lucknow: Birbal Sahni Institute of Palaeobotany.
- Bhatia SB and Mannikeri MS** (1976) Some charophytes from the Deccan intertrappean beds near Nagpur, Central India. *Geophytology* **6**, 75–81.
- Bhatia SB and Rana RS** (1984) Palaeogeographic implications of the Charophyta and Ostracoda of the intertrappean beds of peninsular India. *Memoirs of the Geological Society of France* **147**, 29–35.
- Bottjer DJ, Etter W, Hagadorn JW and Tang CM** (2002) Fossil-Lagerstätten: jewels of the fossil record. In *Exceptional Fossil Preservation: A Unique View on the Evolution of Marine Life* (eds DJ Bottjer, W Etter, JW Hagadorn and CM Tang), pp. 1–10. New York: Columbia University Press.
- Bravo AM and Gaete R** (2015) Titanosaur eggshells from the Tremp Formation (Upper Cretaceous, Southern Pyrenees, Spain). *Historical Biology* **27**, 1079–89.
- Buffetaut E** (1987) On the age of the dinosaur fauna from the Lameta Formation (Upper Cretaceous of Central India). *Newsletters on Stratigraphy* **18**, 1–6.
- Calvo JO, Engelland S, Heredia SE and Salgado L** (1997) First record of dinosaur eggshells (?Sauropoda–Megaloolithidae) from Neuquén, Patagonia, Argentina. *Gaia* **14**, 23–32.
- Cappetta H** (1972) Les poissons crétacés et tertiaires du bassin des Iullemeden (République du Niger). *Palaeovertebrata* **5**, 179–251.
- Chiappe LM, Coria RA, Dingus L, Jackson F, Chinsamy A and Fox M** (1998) Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* **396**, 258–61.
- Courtillot V, Besse J, Vandamme DM, Montigny, R, Jaeger JJ and Cappetta H** (1986) Deccan flood basalts at the Cretaceous/Tertiary boundary? *Earth and Planetary Science Letters* **80**, 361–74.
- Cuif JP, Dauphin Y and Sorauf JE** (2010) *Biominerals and Fossils through Time*. Cambridge: Cambridge University Press, 490 pp.
- Dhiman H, Dutta S, Kumar S, Verma V and Prasad GVR** (2021) Discovery of proteinaceous moieties in Late Cretaceous dinosaur eggshell. *Palaeontology* **64**, 585–95.
- Dhiman H, Prasad GVR and Goswami A** (2019) Parataxonomy and palaeobiogeographic significance of dinosaur eggshell fragments from the Upper Cretaceous strata of the Cauvery Basin, South India. *Historical Biology* **31**, 1310–22.
- Diez-Canseco D, Arz JA, Benito MI, Díaz-Molina M and Arenillas I** (2014) Tidal influence in redbeds: a palaeoenvironmental and biochronostratigraphic reconstruction of the Lower Tremp Formation (South-Central Pyrenees, Spain) around the Cretaceous/Paleogene boundary. *Sedimentary Geology* **312**, 31–49.
- Dogra NN, Singh RY and Kulshrestha SK** (1994) Palynostratigraphy of infra-trappean Jabalpur and Lameta formations (Lower and Upper Cretaceous) in Madhya Pradesh, India. *Cretaceous Research* **15**, 205–15.
- Feist-Castel M** (1975) Répartition des Charophytes dans le Paléocène et l'Éocène du bassin d'Aix-en-Provence. *Bulletin de la Société géologique de France (ser. 7)* **17**, 88–97.
- Fernández MS and Khosla A** (2015) Parataxonomic review of the Upper Cretaceous dinosaur eggshells belonging to the oofamily Megaloolithidae from India and Argentina. *Historical Biology* **27**, 158–80.
- Fernández MS, Vila B and Moreno-Azanza M** (2022) Eggs, nests, reproductive biology of sauropodomorph dinosaurs from South America. In *South American Sauropodomorph Dinosaurs* (eds A Otero, JL Carballido and P Diego), pp. 393–41. Cham: Springer Earth System Sciences, Springer. doi: [10.1007/978-3-030-95959-3_11](https://doi.org/10.1007/978-3-030-95959-3_11).
- Folk RL and Lynch FL** (2001) Organic matter, putative nanobacteria and the formation of ooids and hardgrounds. *Sedimentology* **48**, 215–29.
- Gayet M, Rage JC and Rana RS** (1984) Nouvelles ichthyofaune et herpétofaune de Gitti Khadan, le plus ancien gisement connu du Deccan (Crétacé/Paléocène) à microvertébrés. Implications paléogéographiques. *Mémoires de la Société géologique de France* **147**, 55–65.
- Grellet-Tinner G** (2005) Membrana testacea of titanosaurid dinosaur eggs from Auca Mahuevo (Argentina): implications for exceptional preservation of soft tissue in Lagerstätten. *Journal of Vertebrate Paleontology* **25**(1), 99–106.
- Grellet-Tinner G, Chiappe LM and Coria R** (2004) Eggs of titanosaurid sauropods from the Upper Cretaceous of Auca Mahuevo (Argentina). *Canadian Journal of Earth Sciences* **41**, 949–60.
- Grigorescu D and Oana-Claudia B** (2017–18) Comparative analysis of the eggshell biomineralization in modern birds and megaloolithid eggs from the Maastrichtian of the Hațeg Basin: abnormal shell units linked to diagenesis in the fossil eggshells. *Revue Roumaine de Géologie* **61–62**, 45–65.
- Hayward JM, Zelenitsky DK, Smith DL, Zaft DM and Clayburn JK** (2000) Eggshell taphonomy at modern gull colonies and a dinosaur clutch site. *Palaios* **15**, 343–55.
- Jain SL and Sahni A** (1983) Some Upper Cretaceous vertebrates from Central India and their palaeogeographical implications. In *Cretaceous of India* (ed HK Maheshwari), pp. 66–83. Indian Association of Palynostratigraphers Symposium, Lucknow: Birbal Sahni Institute of Palaeobotany.
- Jaiprakash BC, Singh J and Raju DSN** (1993) Foraminiferal events across K/T boundary and age of Deccan volcanism in Palakollu area, Krishna-Godavari basin, India. *Journal of the Geological Society of India* **41**, 105–17.
- Kale VS, Dole G, Shandilya P and Pande K** (2019) Stratigraphy and correlations in Deccan volcanic province, India: quo vadis? *GSA Bulletin* **132**, 588–607.
- Kapur VV, Bajpai S, Saravanan N and Das DP** (2006) Vertebrate fauna from the Deccan intertrappean beds of Bhanpura, Mandasaur District, Madhya Pradesh. *Gondwana Geological Magazine* **21**, 43–6.
- Keller G, Adatte T, Bhowmick PK, Upadhyay H, Dave A, Reddy AN and Jaiprakash BC** (2012) Nature and timing of extinctions in Cretaceous-Tertiary planktic foraminifera preserved in Deccan intertrappean sediments of the Krishna-Godavari basin, India. *Earth and Planetary Science Letters* **341–344**, 211–21.
- Khajuria CK, Prasad GVR and Manhas BK** (1994) Palaeontological constraints on the age of Deccan Traps. *Newsletters on Stratigraphy* **31**, 21–32.
- Khosla A and Bajpai S** (2021) Dinosaur fossil records from India and their palaeobiogeographic implications: an overview. *Journal of Palaeosciences* **70**, 193–212.
- Khosla A, Prasad GVR, Verma O, Jain AK and Sahni A** (2004) Discovery of a micromammal-yielding Deccan intertrappean site near Kisalpur, Dindori District, Madhya Pradesh. *Current Science* **87**, 380–3.
- Khosla A and Sahni A** (1995) Parataxonomic classification of Late Cretaceous dinosaur eggshells from India. *Journal of the Palaeontological Society of India* **40**, 87–102.
- Khosla A and Sahni A** (2003) Biodiversity during the Deccan volcanic eruptive episode. *Journal of Asian Earth Sciences* **21**, 895–908.
- Kohring R** (1998) Schildkriter- und Vogeleischalen aus dem Untermiozän (MN4b) von Dolnice (Tschechien). *Documenta naturae* **122**, 49–57.
- Kohring R and Hirsch KE** (1996) Crocodylian and avian eggs and egg-shells from the Eocene of the Geiselal. *Journal of Vertebrate Paleontology* **16**, 67–80.
- Kohring R and Sachs O** (1997) Erhaltungsbedingungen und Diagenese fossiler Vogeleischalen aus dem Nördlinger Ries (Miozän, MN6). *Archaeopteryx* **15**, 73–96.
- Kohring RR** (1999) Calcified shell membranes in fossil vertebrate eggshell: evidence for preburial diagenesis. *Journal of Vertebrate Paleontology* **19**, 723–7.
- Kolesnikov CM and Sochava AV** (1972) A paleobiochemical study of the Cretaceous dinosaur eggshell from the Gobi. *Paleontological Journal* **2**, 235–45.
- Krampitz G and Graser G** (1988) Molecular mechanisms of biomineralization in the formation of calcified shells. *Angewandte Chemie International Edition in English* **27**, 1145–56.
- Kriwet J, Soler-Gijón R, López-Martínez N** (2007) Neoselachians from the upper Campanian and lower Maastrichtian (Upper Cretaceous) of the Southern Pyrenees, Northern Spain. *Palaeontology* **50**, 1051–71.
- Kshetrimayum DS, Parmar V, Lourembam RS and Prasad GVR** (2021) A diversified Ostracoda (Crustacea) assemblage from the Upper Cretaceous intertrappean beds of Gujri, Dhar District, Madhya Pradesh, India. *Cretaceous Research* **124**. doi: [10.1016/j.cretres.2021.104784](https://doi.org/10.1016/j.cretres.2021.104784).
- Lourembam RS, Prasad GVR and Grover P** (2017) Ichthyofauna (Chondrichthyes, Osteichthyes) from the Upper Cretaceous intertrappean beds of Piplanarayanwar, Chhindwara District, Madhya Pradesh, India. *Island Arc* **26**, e12200, doi: [10.1111/iar.12200](https://doi.org/10.1111/iar.12200).

- Mathur SK, Mathur SC and Loyal RS** (2006) First microvertebrate assemblage from the Fatehgarh Formation (Cretaceous), Barmer District, Western Rajasthan. *Journal of the Geological Society of India* **67**, 759–69.
- Mathur UB** (1968) Record of fossil *Scylla serrata* and its bearing on the origin of intertrappeans of Bombay. *Geological Society of India Bulletin* **5**, 88–90.
- Mikhailov KE** (1991) Classification of fossil eggshells of amniotic vertebrates. *Acta Palaeontologica Polonica* **36**, 193–238.
- Mishra UK and Sen S** (2001) Dinosaur bones from Meghalaya. *Current Science* **80**, 1053–6.
- Mohabey DM** (1998) Systematics of Indian Upper Cretaceous dinosaur and chelonian eggshells. *Journal of Vertebrate Paleontology* **18**, 348–62.
- Packard MJ and DeMarco VG** (1995) Shell structure and formation in eggs of oviparous reptiles. In *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles* (eds CD Deeming and MWJ Ferguson), pp. 53–70. Cambridge: Cambridge University Press.
- Prasad GVR** (1989) Vertebrate fauna from the infra- and intertrappean beds of Andhra Pradesh: age implications. *Journal of the Geological Society of India* **34**, 161–73.
- Prasad GVR** (2012) Vertebrate biodiversity of the Deccan volcanic province of India: a review. *Bulletin de la Société géologique de France* **183**, 597–610.
- Prasad GVR and Cappetta H** (1993) Late Cretaceous selachians from India and the age of Deccan Traps. *Palaeontology* **36**, 231–48.
- Prasad GVR and Khajuria CK** (1990) A record of microvertebrate fauna from the intertrappean beds of Naskal, Andhra Pradesh. *Journal of the Palaeontological Society of India* **35**, 151–61.
- Prasad GVR and Khajuria CK** (1995) Implications of the infra- and intertrappean biota from the Deccan, India, for the role of volcanism in Cretaceous-Tertiary boundary extinctions. *Journal of the Geological Society of London* **150**, 289–96.
- Prasad GVR and Sahni A** (1987) A coastal-plain microvertebrate assemblage from the terminal Cretaceous of Asifabad, Andhra Pradesh. *Journal of the Palaeontological Society of India* **32**, 5–19.
- Prasad GVR and Sahni A** (2014) Vertebrate fauna from the Deccan volcanic province: response to volcanic activity. *Geological Society of America Special Papers* **505**, 193–211.
- Prasad GVR, Verma O, Flynn JJ and Goswami A** (2013) A new Late Cretaceous vertebrate fauna from the Cauvery Basin, South India: implications for Gondwanan paleobiogeography. *Journal of Vertebrate Paleontology* **33**, 1260–8.
- Prasad V, Farooqui A, Murthy S, Sarate OS and Bajpai S** (2018) Palynological assemblage from the Deccan Volcanic Province, central India: insights into early history of angiosperms and the terminal Cretaceous paleogeography of peninsular India. *Cretaceous Research* **86**, 186–98.
- Raff CE, Schollaerta KL, Nelsona DE, Donoghue PCJ, Ceri-Wyn T, Turnera FR, Stein BD, Dong X, Bengtson S, Hultgren T, Stambanoni M, Chongyui Y and Raff RA** (2008) Embryo fossilization is a biological process mediated by microbial biofilms. *Proceedings of the National Academy of Sciences* **105**, 19360–5.
- Rage JC and Prasad GVR** (1992) New snakes from the Late Cretaceous (Maastrichtian) of Naskal, India. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **187**, 83–97.
- Raju DSN, Ravichandran CN, Dave A, Jaiprakash BC and Singh J** (1991) K/T boundary events in the Cauvery and Krishna-Godavari basins and age of Deccan volcanics. *Geoscience Journal* **12**, 177–90.
- Reid RP, Visscher PT, Decho AW, Stolz JF, Bebout BM, Dupraz C, Macyntyre IG, Paerl HW, Pinckney JL, Prufert-Bebout L, Steppe TF and Des Marais DJ** (2000) The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. *Nature* **406**, 989–92.
- Reisz RR, Huang TD, Roberts EM, Peng S, Sullivan C, Stein K, LeBlanc AR, Shieh D, Chang R, Chiang C and Yang C** (2013) Embryology of Early Jurassic dinosaur from China with evidence of preserved organic remains. *Nature* **496**, 210–4.
- Rothe P and Klemmer K** (1991) Fossil eggs of terrestrial tortoises (Family Testudinidae) from Pliocene calcarenites of Fuerteventura (Canary Islands, Spain). *Senckenbergiana Lethaea* **71**, 307–17.
- Sahni A** (1972) Paleoecology of Lameta Formation at Jabalpur (M. P.). *Current Science* **41**, 652.
- Sahni A** (1983) Upper Cretaceous palaeobiogeography of Peninsular India and the Cretaceous–Paleocene transition: the vertebrate evidence. In *Cretaceous of India* (ed HK Maheshwari), pp. 128–40. Indian Association of Palynostratigraphers Symposium. Lucknow: Birbal Sahni Institute of Palaeobotany. .
- Sahni A, Rana RS and Prasad GVR** (1984) SEM studies of thin eggshell fragments from the intertrappeans (Cretaceous-Tertiary transition) of Nagpur and Asifabad, peninsular India. *Journal of the Palaeontological Society of India* **29**, 26–33.
- Sahni A, Tandon SK, Jolly A, Bajpai S, Sood A and Srinivasan S** (1994) Upper Cretaceous dinosaur eggs and nesting sites from the Deccan volcano-sedimentary province of peninsular India. In *Dinosaur Eggs and Babies* (eds K Carpenter, KF Hirsch and JR Horner), pp. 204–26. Cambridge: Cambridge University Press.
- Sahni A, Venkatachala BS, Kar RK, Rajnikanth A, Prakash T, Prasad, GVR and Singh RY** (1996) New paleontological data from the intertrappean beds: implications for the latest record of dinosaurs and synchronous initiation of volcanic activity in India. *Memoirs of the Geological Society of India* **37**, 267–83.
- Sahni B** (1934) The Deccan Traps: are they Cretaceous or Tertiary? *Current Science* **3**, 134–6.
- Samant B, Mohabey DM, Srivastava P and Thakre D** (2014) Palynology and clay mineralogy of the Deccan volcanic associated sediments of Saurashtra, Gujarat: age and paleoenvironment. *Journal of Earth System Science* **123**, 219–32.
- Sastry MVA and Lahiri TC** (1981) Life during Deccan Trap episode. *Geological Society of India Memoirs* **3**, 279–86.
- Schweitzer MH** (2011) Soft tissue preservation in terrestrial Mesozoic vertebrates. *Annual Review of Earth and Planetary Sciences* **39**, 187–216.
- Sellés AG, Bravo AM, Delclòs X, Colombo F, Martí X, Ortega-Blanco J, Parellada C and Galobart À** (2013) Dinosaur eggs in the Upper Cretaceous of the Coll de Nargò area, Lleida Province, south-central Pyrenees, Spain: oodiversity, biostratigraphy and their implications. *Cretaceous Research* **40**, 10–20.
- Shivarudrappa TV** (1976–7) Discovery of fossil reproductive organs of Chara from intertrappeans of Gurmatkal, Gulbarga District, Karnataka. *Journal of Mysore University, Section B – Science* **27**, 104–10.
- Simón ME** (2006) Cáscaras de huevos de dinosaurios de la Formación Allen (Campaniano-Maastrichtiano), en Salitral Moreno, provincia de Río Negro, Argentina. *Ameghiniana* **43**, 513–28.
- Singh RS, Kar R and Prasad GVR** (2006) Palynological constraints on the age of mammal yielding Deccan intertrappean beds of Naskal, Rangareddi District, Andhra Pradesh. *Current Science* **90**, 1281–5.
- Sochava AV** (1969) Dinosaur eggs from the Upper Cretaceous of the Gobi Desert. *Paleontological Journal* **3**, 517–27.
- Soler-Gijón R and López-Martínez N** (1998) Sharks and rays (chondrichthyes) from the Upper Cretaceous red beds of the south-central Pyrenees (Lleida, Spain): indices of an India-Eurasia connection. *Palaeogeography, Palaeoclimatology, Palaeoecology* **141**, 1–12.
- Sowerby de JC** (1840) On the fossils of the eastern portion of the great basaltic district of India. *Transactions of the Geological Society of London* **5**, 537–75.
- Srinivasan S** (1996) Late Cretaceous eggshells from the Deccan volcano-sedimentary sequences of central India. *Memoirs of the Geological Society of India* **37**, 321–36.
- Srivastava AK and Mankar RS** (2015) *Megaloolithus* dinosaur nest from the Lameta Formation of Salbardi area, districts Amravati, Maharashtra and Betul, Madhya Pradesh. *Journal of the Geological Society of India* **85**, 457–462. <https://doi.org/10.1007/s12594-015-0237-0>
- Srivastava S, Mohabey DM, Sahni A and Pant SC** (1986) Upper Cretaceous dinosaur egg clutches from Kheda District (Gujarat, India), their distribution, shell ultrastructure and palaeoecology. *Palaeontographica, Abteilung A, Paläozoologie, Stratigraphie* **193**, 219–33.
- Stein K, Prondvai E, Huang T, Baele JM, Sander PM and Reisz R** (2019) Structure and evolutionary implications of the earliest (Sinemurian, Early Jurassic) dinosaur eggs and eggshells. *Scientific Reports* **9**, 1–9.

- Tandon SK, Sood A, Andrews JE and Dennis PF** (1995) Palaeoenvironments of the dinosaur-bearing Lameta beds (Maastrichtian), Narmada valley, central India. *Palaeogeography, Palaeoclimatology, Palaeoecology* **117**, 153–84.
- Tazaki K, Aratani M, Noda S, Currie PJ and Fyfe WS** (1994) Microstructure and chemical composition of duckbilled dinosaur eggshell. *Scientific Reports of the Kanazawa University* **39**, 17–37.
- Verma O, Khosla A, Kaur J and Prashanth M** (2016) Myliobatid and pycnodontid fish from the Late Cretaceous of Central India and their paleobiogeographic implications. *Historical Biology* **29**, 253–65.
- Vianey-Liaud M, Jain SL and Sahni A** (1987) Dinosaur eggshells (Saurischia) from the Late Cretaceous intertrappean and Lameta formations (Deccan, India). *Journal of Vertebrate Paleontology* **7**, 408–424.
- Vianey-Liaud M, Hirsch K, Sahni A and Sigé B** (1997) Late Cretaceous Peruvian eggshells and their relationships with Laurasian and eastern Gondwanian material. *Geobios* **30**, 75–90.
- Visscher PT, Reid RP and Bebout BM** (2000) Microscale observation of sulfate reduction: correlation of microbial activity with lithified micritic laminae in modern marine stromatolites. *Geology* **28**, 919–22.
- Whatley R, Bajpai S and Srinivasan S** (2002) Upper Cretaceous nonmarine Ostracoda from intertrappean horizons in Gulbarga District, Karnataka State, South India. *Revista Española de Micropaleontología* **34**, 163–86.
- Yang TR, Chen YH, Wiemann J, Spiering B and Sander PM** (2018) Fossil eggshell cuticle elucidates dinosaur nesting ecology. *PeerJ* **6**, e5144.