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Testudoid and crocodiloid eggshells from the Upper Cretaceous Deccan Intertrappean Beds of Central India

Coquilles d'œufs de testudoïdés et de crocodiloïdés dans les lits inter-trappéens d'Inde centrale, Crétacé supérieur du Dekkan

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ABSTRACT

Chelonian and crocodilian eggs and eggshells are relatively rare in the fossil record as compared to those of dinosaurs and avians. In India, prior to the present report, turtle eggshells have been reported from the supposed Late Cretaceous infratrappean beds of Duddukuru, Andhra Pradesh. Likewise, crocodilian eggshells were described from the intertrappean beds of Bombay whose assignment to Maastrichtian age is not based on any age diagnostic fossils. Here we report the first definitive Late Cretaceous turtle and crocodilian eggshells from the intertrappean beds of Kisalpuri, Dindori District, Madhya Pradesh (Central India). The testudoid eggshells from Kisalpuri, though broadly comparable to those of Duddukuru, particularly in radial structure, differ from each other in finer details such as external surface ornamentation and the organization of crystallites in the radial section. The crocodiloid eggshells from Central India are distinct from known fossil eggshells in having non-interlocking wedge-like crystallites and ringed craters on the basal plate groups. Keeping in view the limited fossil specimens available for the present study, the testudoid and crocodiloid eggshells from the Late Cretaceous of Central India are referred to the oofamilies Testudoolithidae and Krokolithidae, respectively.

RÉSUMÉ

Les œufs et les coquilles d'œufs de chéloniens et de crocodiliens sont relativement rares dans le registre fossile, en comparaison de ceux des dinosaures et des aviens. Précédemment, en Inde, des œufs de tortue avaient été signalés dans les lits infratrappéens de Duddukuru, Andhra Pradesh, supposés Crétacé terminal. De même, des coquilles d'œufs de crocodiliens ont été décrits dans les lits inter-trappéens de Bombay, dont l'attribution au Maastrichtien ne repose sur aucun fossile diagnostique de cet âge. Ici, nous présentons les premières coquilles d'œufs de tortue et de crocodilien définitivement Crétacé supérieur, trouvées dans des lits inter-trappéens de Kisalpuri, Dindori District, Madhya Pradesh

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(Inde centrale). Les coquilles d'œufs de testudoïdé, bien que largement comparables à celles de Duddukuru, en particulier par leur structure radiale, en diffèrent par des détails plus fins, comme l'ornementation externe de surface et l'organisation de cristallites en section radiale. Les coquilles d'œufs de crocodiloïdé d'Inde centrale sont distinctes des coquilles d'œufs fossiles connues, par la présence de cristallites, en forme de coins non imbriqués et de cratères annulaires sur des groupes de plaquettes basales. Si l'on garde en mémoire le fait que les spécimens fossiles disponibles pour la présente étude sont limités, les coquilles d'œufs de testudoïdé et de crocolidoïdé du Crétacé supérieur d'Inde centrale sont attribués aux co-familles de Testudoolithidae et Krokolithidae respectivement.

1. Introduction

Chelonian eggshells are relatively rare in the fossil record as compared to avian and dinosaurian eggshells. This apparent rarity of fossil turtle eggs and eggshells has been attributed to the presence of small percentage of rigid chelonian eggshells in the original assemblage and also to low preservational potential of metastable aragonite (Hirsch, 1983). Even though the oldest record of chelonian eggshells is from the Upper Jurassic rocks of Portugal (Kohring, 1990a), there are very few chelonian eggshell reports from pre-Tertiary rocks. The Cretaceous and Tertiary records include those from England (Hirsch, 1983), France (Kohring, 1993; Masse, 1989), Spain (Kohring, 1990b; Moreno-Azanza et al., 2008), USA (Bray and Hirsch, 1998; Hirsch, 1996; Knell et al., 2011; Kohring, 1999; Tanaka et al., 2011 Zelenitsky et al., 2008), Mongolia (Mikhailov et al., 1994), Japan (Fukuda and Obata, 1991; Isaji et al., 2006), China (Fang et al., 2003; Jackson et al., 2008; Wang et al., 2013), Brazil (Azevedo et al., 2000), Venezuela (Winkler and Sánchez-Villagra, 2006), Greece (Mueller-Töwe et al., 2011), and India (Bajpai et al., 1997; Mohabey, 1998). Initially, most of the studies on turtle eggshells were based on megascopic features such as size and shape of the egg and shell texture (for example, Buckman, 1859; Hay, 1908), but later polarized microscopy and scanning electron microscopy were used by Hirsch (1983) to undertake a comparative study of fossil and recent chelonian eggshells. After comparing living and fossil chelonian eggshells, Hirsch (1983) observed that while modern chelonian eggshells vary from relatively flexible to rigid, the fossil record is limited to rigid eggshells only. Subsequently, Hirsch (1996) applied parataxonomic classification, earlier used for dinosaurs, to turtle eggshells as well. As all turtle eggs and eggshells share a basic shell organization such as having a single layer of spherulitic shell units composed of acicular radiating crystallites that originate from a nucleation center, Hirsch (1996) designated it as Testudoid basic type. Based on shell mineralization characteristics and arrangement of shell units, Hirsch (1996) suggested two morphotypes under Testudoid basic type: Spherurigidis and Spheruflexibilis and assigned them to the oofamilies Testudoolithidae with one genus and one species (*Testudoolithus rigidus* Hirsch, 1996) and Testudoflexoolithidae with one genus and two species (*Testudoflexoolithus agassizi* Hirsch, 1996 and *T. bathonicae* Hirsch, 1996), respectively. In the family Testudoflexoolithidae, the eggshell units are generally wider than high and loosely abutting. On the other hand, in the rigid eggshells of Testudoolithidae, eggshell units are higher than wide and adjacent units interlock with each other. Following this, the parataxonomic classification of Hirsch (1996) has been widely applied for the study of fossil turtle eggs and eggshells. More recently, in a comprehensive review of fossil turtle eggshells, eggs, embryos and nests, Lawver and Jackson (2014) discussed the skewed spatial distribution of fossil turtle eggs and eggshells towards Laurasian continents as a possible consequence of sampling biases, the limited utility of cladistics analysis of egg and eggshell characters in diagnosing turtle clades, and how pathological turtle eggshells can be used to understand the physiological or environmental stresses experienced by the gravid female. They further suggested that fossil eggs being integral parts of a developing organism be regarded as body fossils and there are only eight valid (two of Testudoflexoolithidae and six of Testudoolithidae) out of 15 named ootaxa.

As compared to extensive documentation of crocodylomorph body fossils, the record of fossil crocodiloid eggs is very limited and poorly understood, a gap partially attributed to their typically thin eggshell and the shell structure which is not tightly interlocking (Hirsch and Kohring, 1992) and because of the corrosion of external surface during incubation (Ferguson, 1982). As in the case of chelonian eggs and eggshells, crocodilian eggshells were initially described mainly by megascopic features (e.g., Erickson, 1978; Heller, 1931). Fossil crocodilian eggs were documented for the first time by Hirsch (1985) from the Eocene of the De Beque Formation of Colorado, USA. However, the oldest crocodilian eggshells are known from the Upper Jurassic of Portugal (Antunes et al., 1998). Though fossil eggs and eggshells have been documented from Jurassic, Cretaceous and Tertiary strata, all of them and modern crocodiles have more or less the same structural organization: i.e., eggshells with smooth to undulating external surface with irregularly spaced pores, radial section with discrete, irregular, inverted triangular, crystalline wedges arising from basal plate groups of the internal surface with pores randomly distributed between the shell units (Hirsch and Kohring, 1992). From Cretaceous rocks, crocodilian eggshells have been documented from the Early Cretaceous of Galve, Spain (Kohring, 1990b), the Lower Cretaceous (Albian) Glen Rose Formation, Texas, USA (Rogers, 2000), the Upper Cretaceous (Campanian) Two Medicine Formation of Montana (Jackson and Varricchio, 2010), the Upper Cretaceous (Campanian) Fruitland Formation, USA (Tanaka et al., 2011), the Late Cretaceous of France (Garcia, 2000. Kerourio, 1987) and the Late Cretaceous of Bolivia (Novas et al., 2009). Until recently, only the oogenus *Krokolithes* (oofamily Krokolithidae), represented by two oospecies (*K. wilsoni* Hirsch, 1985 and *K. helleri* Kohring and Hirsch, 1996), is known (Hirsch, 1985; Kohring and Hirsch, 1996). *K. wilsoni* was named on the basis of relatively small eggs and eggshells from the Eocene De Beque Formation, Colorado, USA (Hirsch, 1985) and was initially referred to the family Crocodylidae. Subsequent to this, six poorly preserved eggs from the Middle Eocene of Geiseltal, Germany were referred to a second species *K. helleri* (Kohring and Hirsch, 1996) and the name of the family was re-designated as Krokolithidae under the parataxonomic scheme of classification. In addition to these crocodilian eggs, eggshells have also been reported from the Middle Eocene Bridger Formation, Wyoming, USA (Hirsch and Kohring, 1992). A second oogenus *Bauruoolithus* with a type species *B. fragilis* Oliveira et al., 2011 has been described from the Upper Cretaceous Adamantina Formation (Bauru Group) of Brazil (Oliveira et al., 2011). In a comparative study of modern and fossil eggs and eggshells of crocodiles, Marzola et al. (2015) gave an over view of crocodilian eggshell characteristics in modern *Crocodylus mindorensis* Schmidt, 1935, *Alligator mississippiensis* (Daudin, 1802) and *Paleosuchus palpebrosus* (Cuvier, 1807). They identified two types of external surface ornamentation, rugosocavate and anastomotuberculate and an angusticanaliculate pore system in these taxa.

In the Indian subcontinent, Sahni (1957) was the first to describe a fossil egg from the Cenomanian Karai Formation of Cauvery basin in association with marine invertebrates. Based on the similarities in size and external morphology to those of marine turtles, this egg was attributed to a chelonian. However, until now, no study of shell microstructure was carried out to confirm this. A second report of chelonian eggshells was made by Bajpai et al. (1997) from the Upper Cretaceous or Early Palaeocene infratrappean beds of Duddukuru, southeastern India. Crocodilian eggshells and egg have also been documented from the Upper Cretaceous or Early Palaeocene intertrappean beds of Bombay (Singh et al., 1998), Pliocene Saketi Formation (Upper Siwalik Subgroup), Himachal Pradesh (Patnaik and Schleich, 1993) and the Upper Miocene Chinji Formation of the Lower Siwalik Subgroup in the Potwar Plateau, Pakistan (Panadès et al., 2009).

More recently, the search for Cretaceous micromammal yielding horizons in the Deccan volcanic province led to the discovery of a fossiliferous intertrappean sedimentary sequence near Kisalpuri village in Dindori District, Madhya Pradesh in Central India (Khosla et al., 2004). This intertrappean section is highly fossiliferous yielding a vertebrate fauna consisting of fishes, amphibians, turtles, crocodiles, and mammals. Besides skeletal remains of these vertebrate groups, eggshell fragments with shell microstructure that compares very closely to those of chelonians and crocodiles are also recovered from this microvertebrate site. The main objective of this paper is to describe the newly discovered Late Cretaceous testudoid and crocodiloid eggshells from Central India.

2. Geological setting and locality information

The Deccan basaltic flows of the northeastern part of main Deccan volcanic province occur in a large, detached outcrop known as Mandla lobe. No well-established lava flow stratigraphy, magnetostratigraphy and geochronological dates are available for this belt of the Deccan Traps. The fossil eggshells described in this paper are derived from a sedimentary sequence occurring sandwiched between two volcanic flows of the Deccan Traps near Kisalpuri village in Dindori District, Madhya Pradesh. A highly fossiliferous intertrappean section is exposed on the right bank of Kharmer River, a tributary of Narmada River, about 1.5 km southwest of the village Kisalpuri (Fig. 1). Here the intertrappean sequence is 4.5 m thick and consists of soft green, red, yellow, chocolate brown clays, mudstones and brownish-green siltstone. The brownish-green colored siltstones are found to be rich in vertebrate microfossils. Surface prospecting of this horizon has led to the recovery of a few carapace fragments and postcranial bones of turtles, and dental and postcranial remains of crocodiles. In search of Cretaceous mammals, five tons of sediments from green siltstone horizon were screen-washed. The fauna recovered from the screen-washed residue includes fish: *Lepisosteus indicus* Woodward, 1908, Osteoglossidae indet., Pycnodontidae indet., *Igdabatis indicus* Prasad and Cappetta, 1993, *Rhombodus* sp.; anurans: Leptodactylidae indet. (Khosla et al., 2004; Verma, 2008); crocodiles: Dyrosauridae indet. (Khosla et al., 2009), Crocodilia indet., turtles: Bothremydidae indet. (De Lapparent de Broin et al., 2009), eggshell fragments; mammals: *Deccanolestes hislopi* Prasad and Sahni, 1988, *D. narmadensis* Prasad et al., 2010, *Bharattherium bonapartei* Prasad et al., 2007a, and *Kharmerungulatum vanvaleni* Prasad et al., 2007b. A Late Cretaceous (Maastrichtian) age was assigned to the intertrappean beds of Kisalpuri in view of the presence of *Igdabatis* and *Rhombodus* (Khosla et al., 2004). The occurrence of predominantly freshwater and terrestrial elements in association with batoid (*Igdabatis*, *Rhombodus*) and pycnodontid fishes in the microvertebrate assemblage of Kisalpuri point to deposition in a lacustrine basin proximal to the sea (Khosla et al., 2004).

3. Methods and materials

The specimens described here are primarily represented by isolated eggshell fragments. There are 10 specimens that are referable to chelonians and three to crocodilians. The eggshells were collected during a search for vertebrate microfossils from bulk screen-washed residue of the Kisalpuri intertrappean brownish-green siltstone.

The eggshell fragments were cleaned with an ultrasonic vibrator before subjecting to SEM study. After cleaning till free of dust, eggshells with internal and external surfaces and fractured radial sections were mounted on aluminum stubs and coated with gold-palladium for observation under Scanning Electron Microscope (SEM) at 20 kilovolts. External ornamentation, histostructural features of radial fractured surfaces, and internal surface were studied and photomicrographs were taken using Zeiss EVOMA10 SEM Model. A few thin sections are also

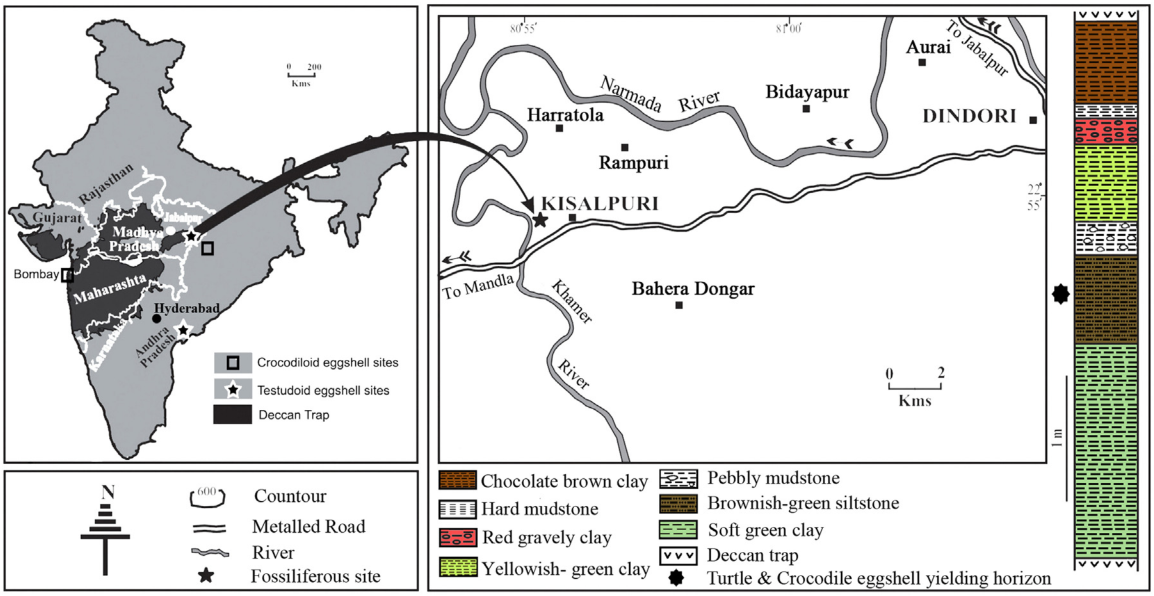

Fig. 1. Map of India showing the location and stratigraphic column of fossil eggshell yielding Kisalpuri intertrappean beds, Dindori District, Madhya Pradesh. Location of the measured lithocolumn is marked with a star on the map.

Fig. 1. Carte de l'Inde, montrant la localisation et la colonne stratigraphique des bancs inter-trappéens de Kisalpuri, district de Dindori, Madhya Pradesh, ayant fourni les coquilles d'œuf fossiles. La localisation de la lithocolonne inventoriée est marquée d'une étoile sur la carte.

made after embedding the eggshells in araldite for study under petrographic microscope. The terminology used for describing the eggshell morphotypes is that of Hirsch (1983) and Mikhailov (1997). The specimens used for this study are deposited in the Vertebrate Palaeontology Laboratory of Delhi University, India and bear the acronym DUGF/numbers (Department of Geology, Delhi University fossil catalogue numbers).

4. Systematic description of fossil eggshells

Oofamily Testudoolithidae Hirsch, 1996
Incertae sedis
(Fig. 2.1–2.2, Fig. 3.1–3.2)

4.1. Stratigraphic horizon and locality

Intertrappean beds of Kislapuri, Dindori District, Madhya Pradesh.

4.2. Age

Late Cretaceous (Maastrichtian).

4.3. Material

Ten isolated eggshell fragments (DUGF/70-79).

4.4. Description

The eggshell fragments are brown or amber in color. The external surface of the eggshells is either covered by sub-circular pits encircled by ridges as in a golf ball but not as closely placed (Fig. 2.2A, Fig. 3.1A) or a combination of sub-circular pits and elongated grooves bounded by longitudinal ridges (Fig. 2.1E). The individual pits range in diameter between 200–260 μm. Visible pore canals are generally absent, but some eggshell fragments display craters or pore canals filled with secondary deposits within the coarse sub-circular pits (Fig. 3.1A–C). These pores have a diameter of approximately 55 μm. The external surface of DUGF/75 is also rough and flaky in appearance (Fig. 3.1B–C). Fractured radial sections under Scanning Electron Microscope (SEM) exhibit a single layer of shell units, which are in the form of inverted triangles. The shell units are composed of acicular radiating crystallites that originate from nucleation centers at the inner surface and radiate outwards (Fig. 2.1D, 2.2B–C, Fig. 3.1G, 3.2). The acicular structure of the eggshell in radial section is suggestive of its aragonite composition. However, this needs to be confirmed by X-ray diffraction analysis. The shell units are tightly packed at the broad, outer zone and are separated from adjacent units at the inner one-third of the height and crystals of adjoining shell units are tightly interlocked. Because of this reason, no pore canals are visible in the radial section. Growth lines in the form of horizontal banding are visible in thin sections of these eggshell fragments (Fig. 3.2). The nucleation centres from which the acicular crystallites radiate are visible at the inner base of the fractured radial surface in the form of a depression (Fig. 2.2B–C). The shell thickness varies from 370–450 μm and is slightly variable in different eggshell fragments. The height and width of individual shell units range from 370–450 μm and 285–350 μm, respectively. The height to width ratio of the shell units is 1.28:1. The shell unit bases are tightly packed on the inner surface. The inner surface of these eggshells has nucleation centers or primary spherites in the form of spherical depressions

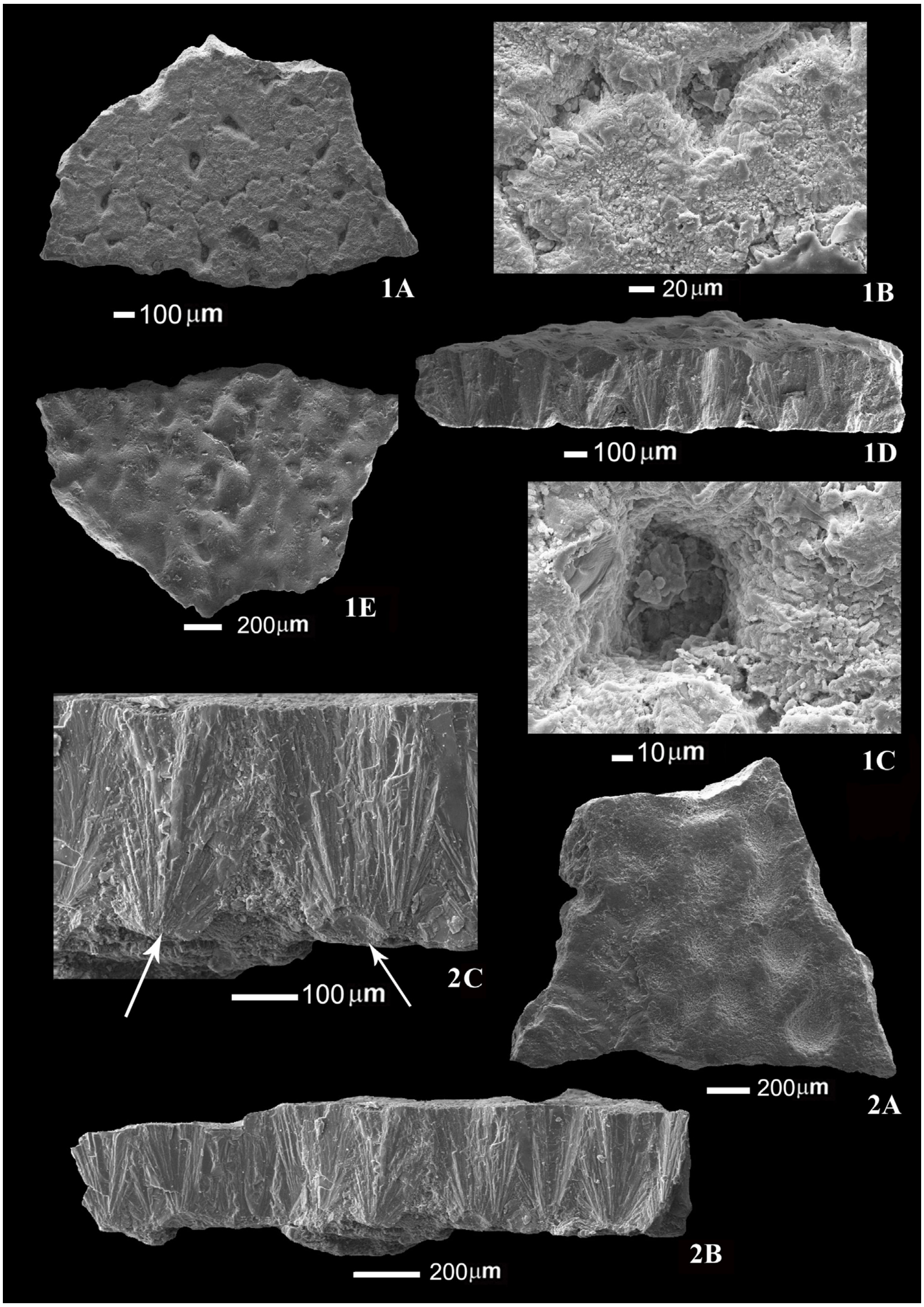

Fig. 2. 1–2. Eggshells of Testudoolithidae *incertae sedis* from the Upper Cretaceous intertrappean beds of Kisalpuri, Central India. 1A. Internal surface (DUGF/75). 1B. Internal surface showing small crystallites radiating outwards from a nucleation center (DUGF/75). 1C. Subcircular pore between adjacent nucleation centers (DUGF/75). 1D. Fractured radial surface (DUGF/75). 1E. External surface (DUGF/75). 2A. External surface with pits and ridges (DUGF/70). 2B. Fractured radial surface (DUGF/70). 2C. Enlarged view of 2B, arrows point to nucleation centers (DUGF/70).

Fig. 2. Coquilles d'œuf de Testudoolithidae *incertae sedis* en provenance des bancs inter-trappeéens de Kisalpuri, Inde centrale. 1A. Surface interne (DUDF/75). 1B. Surface interne montrant de petites cristallites rayonnant vers l'extérieur à partir d'un centre de nucléation (DUGF75). 1C. Pore subcirculaire entre des centres de nucléation contigus (DUGF75). 1D. Surface radiale fracturée (DUGF75). 1E. Surface externe (DUGF75). 2A. Surface externe avec crêtes et cavités (DUGF70). 2B. Surface radiale fracturée (DUGF70). 2C. Vue agrandie de 2B, les flèches pointant vers les centres de nucléation (DUGF/70).

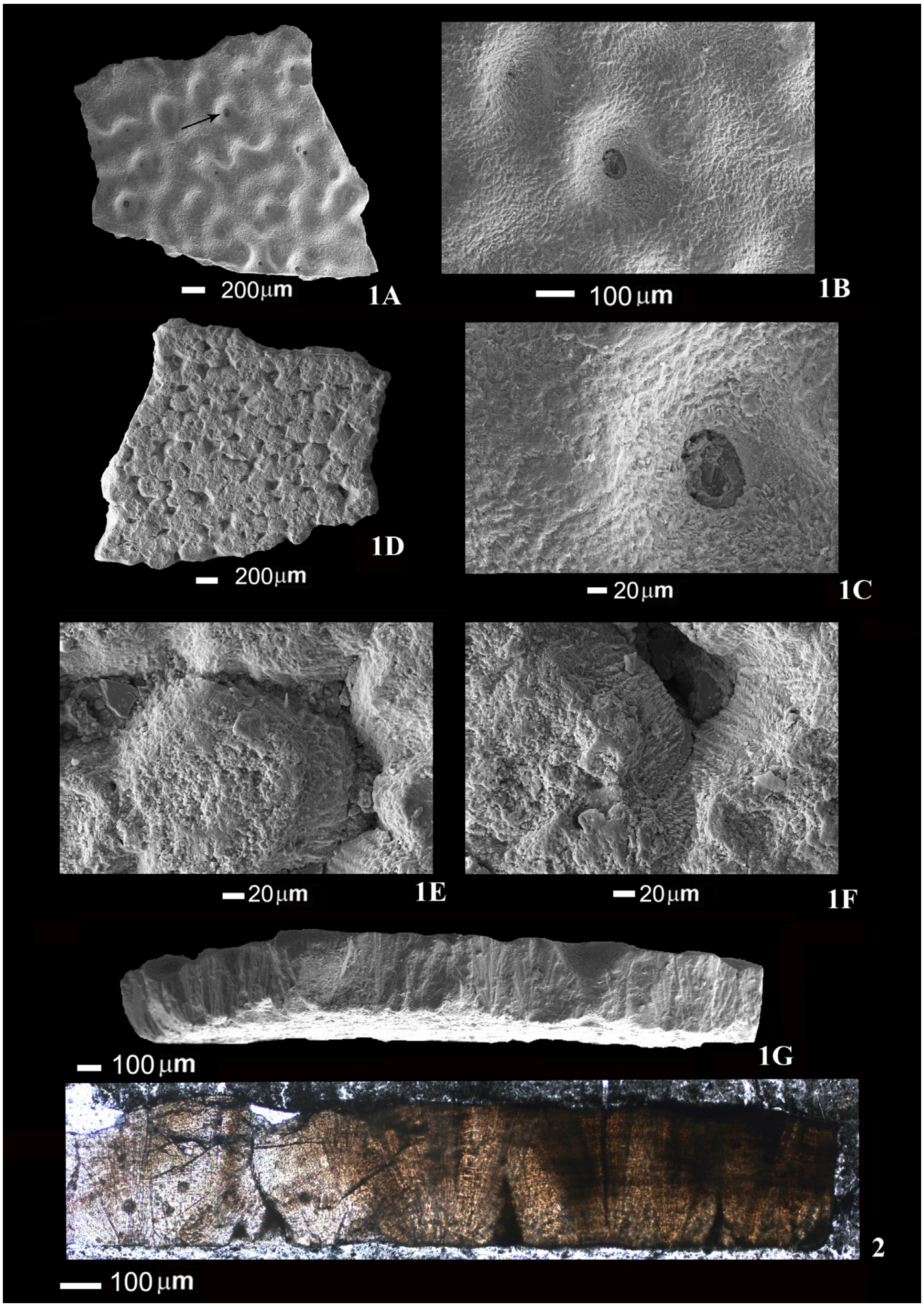

Fig. 3. 1–2. Eggshells of Testudoolithidae *incertae sedis* from the Upper Cretaceous intertrappean beds of Kisalpuri, Central India. 1A. External surface with many pits and ridges, arrow points to a pore within sub-circular pit (DUGF/76). 1B. Enlarged view of the pore marked by arrow in 1A (DUGF/76); 1C. Close-up view of the pore in 1B, shows rugose or flaky external surface (DUGF/76). 1D. Internal surface showing nucleation centers with irregular interstitial pores (DUGF/76). 1E. Enlarged view of a nucleation center with radiating crystals on the periphery (DUGF/76). 1F. Enlarged view of an irregular pore between nucleation centers. 1G. Fractured radial surface (DUGF/76). 2. Thin section of radial surface under plane polarized light displaying radiating striations and horizontal accretion lines (DUGF/77).

Fig. 3. Coquilles d'œuf de Testudoolithidae *incertae sedis*, en provenance des bancs inter-trappéens du Crétacé supérieur de Kisalpuri, Inde centrale. 1A. Surface externe avec nombreuses crêtes et cavités, la flèche pointant vers un pore au sein d'une cavité sub-circulaire (DUGF/76). 1B. Vue agrandie du pore marqué par la flèche en 1A (DUGF/76). 1C. Gros plan sur le pore en 1B, montrant une surface externe rugueuse ou écailleuse (DUGF/76). 1D. Surface interne montrant des centres de nucléation avec des pores interstitiels irréguliers (DUGF/76). 1E. Vue agrandie d'un centre de nucléation, avec des cristaux rayonnants à la périphérie (DUGF/76). 1F. Vue agrandie d'un pore irrégulier entre des centres de nucléation. 1G. Surface radiale fracturée (DUGF/76). 2. Section mince de surface radiale en lumière polarisée plane, montrant des striations rayonnantes et des lignes d'accrétion horizontales (DUGF/77).

(130–150 μm in diameter) with a central core and radiating crystals at the periphery (Fig. 2.1B, Fig. 3.1E–F). Many irregular pores occur at the junction of two or three such craters (Fig. 2.1C, Fig. 3.1E–F).

4.5. Comparisons

The Kisalpuri chelonian eggshells cannot be assigned to sea turtles because they have shell units that are wider than high, flexible and loosely arranged. They also cannot be assigned to chelydrid and emydid turtles because they lay eggs with flexible shell units with considerable space between them and are as high as wide. The presence of acicular radiating crystallites and primary spherites in the presently described eggshells point to their testudoid affinity. The presence of interdigitating crystallites of adjacent shell units without much gap between nucleation sites further suggests that these eggshell fragments belong to a rigid-shelled chelonian egg. The eggshells from Kisalpuri with interlocking shell units higher than wide and having acicular crystallites indicate these eggshell fragments belong to the oofamily Testudoolithidae.

In India, except for two reports, one each from the Lameta Formation (Mohabey, 1998) and intertrappean beds of Duddukuru (Bajpai et al., 1997), majority of fossil eggshell studies were of dinosaur eggshells. Mohabey (1998) referred a partial nest of elliptical egg and eggshell fragments from the Upper Cretaceous Lameta Formation of Pavna, in Chandrapur District, Maharashtra to a testudoid. The eggshells from Pavna have a thickness of 800 μm and a smooth external surface. Their height to width ratio is 3.5:1.0 The eggshells from Kisalpuri differ from those described by Mohabey (1998) in being very thin (370–450 μm) and having a pitted and ridged external surface ornamentation and a height/width ratio of 1.28:1. It has been pointed out that the thickness of the eggshell as measured from the figure of Mohabey (1998, fig. 10G) is only 500 μm (Jackson et al., 2008) and our measurements from Mohabay's (1998) figures confirm this. The highly diagenetically altered shell units obscuring acicular aragonitic structure and the observation of radiating mammillary layer on the inner surface have led to the conclusion that these Lameta eggshells are unlikely those of chelonians (Kohring, 1999; Jackson et al., 2008). From the figures of Mohabey (1998, fig. 10G–H), distinct inverted triangular shell units characteristic of testudoid basic type are not discernible. Rather, radial structure in the basal caps restricted to the lower one-fifth of the shell height and faint horizontal banding visible in rest of the shell unit are reminiscent of the radial structure of avian eggshells. Therefore, the testudoid identification of Pavna eggs and eggshells needs to be confirmed with additional well-preserved material.

The eggshells from Kisalpuri resemble the turtle eggshells described by Bajpai et al. (1997) from the intertrappean beds of Duddukuru, West Godavari District Andhra Pradesh in having shell units higher than wide (1.28:1.0), lacking intervening spaces between them and in the presence of sub-spherical depressed central cores with radiating needle-like crystals on the internal surface. However, the outer surface of the eggshells is smooth in those of Duddukuru as compared to the coarsely pitted or/and ridged ornamentation in Kisalpuri eggshells. Moreover, the small and fine crystallites present between adjacent shell units at their inner one-fifth of the shell unit height in Duddukuru eggshells are not very prominent in those of Kisalpuri. The Kisalpuri eggshells (370–450 μm) are also comparatively thicker than those of Duddukuru (190–260 μm). In this respect, they are more close to eggshells described from the Cretaceous of Mongolia under *Testudinovum* (Mikhailov, 1994, 1997; Mikhailov, 1991), which is now regarded as *nomen nudum* (Lawver and Jackson, 2014). In the Mongolian eggshells, the thickness ranges between 300–400 μm (Table 1). In shell thickness and height/width ratio, Kisalpuri eggshells though not very similar, are closer to those of an unidentified chelonian (400–430 μm) from the Early Cretaceous of Japan (Isaji et al., 2006), and the eggshells of *Emydoolithus laiyangensis* Wang et al., 2013 (400-500 μm) described from the Late Cretaceous of China (Wang et al., 2013) (Table 1). However, in all these taxa, the outer surface of the eggshells is either smooth or undulating as compared to the pitted and ridged ornamentation of Kisalpuri specimens. Other Cretaceous taxa, such as *Testudoolithus jiangi* (Fang et al., 2003) Jackson et al., 2008 from the Early Cretaceous of China and *Testudoolithus* sp. from Upper Cretaceous (Campanian) Fruitland Formation, USA (Tanaka et al., 2011) have thicker eggshells and greater height to width ratio than the present specimens. Eggs from a gravid turtle from Upper Cretaceous (Campanian) Kaiparowits Formation, USA (Knell et al., 2011) have shells thinner than those of the new Indian eggshells and have relatively greater height to width ratio. *Haininchelys curiosa* Schleich et al., 1988 from the Palaeocene of Belgium with a shell thickness of 250–300 μm and height to width ratio of 1.2:1–2.3:1 compares well with the present specimens. (Table 1). But unlike Kisalpuri eggshells, those of *Haininchelys* are characterized by funnel-like pores and rounded external surface of shell units.

Although the shell structure of present eggshells, compares well with that of the oogenus *Testudoolithus* Hirsch, 1996, all known rigid testudoid eggs and eggshells have smooth external surface as compared to coarsely pitted and ridged ornamentation in the eggshells of Kisalpuri. In this respect, they appear to represent a new genus or species, but we refrain from erecting a new taxon in view of limited number of specimens at our disposal.

Oofamily Krokolithidae Kohring and Hirsch, 1996
Incertae sedis
(Fig. 4.1A–G, Fig. 5.1–5.2)

4.6. Stratigraphic horizon and locality

Intertrappean Beds of Kisalpuri, Dindori District, Madhya Pradesh.

4.7. Age

Late Cretaceous (Maastrichtian).

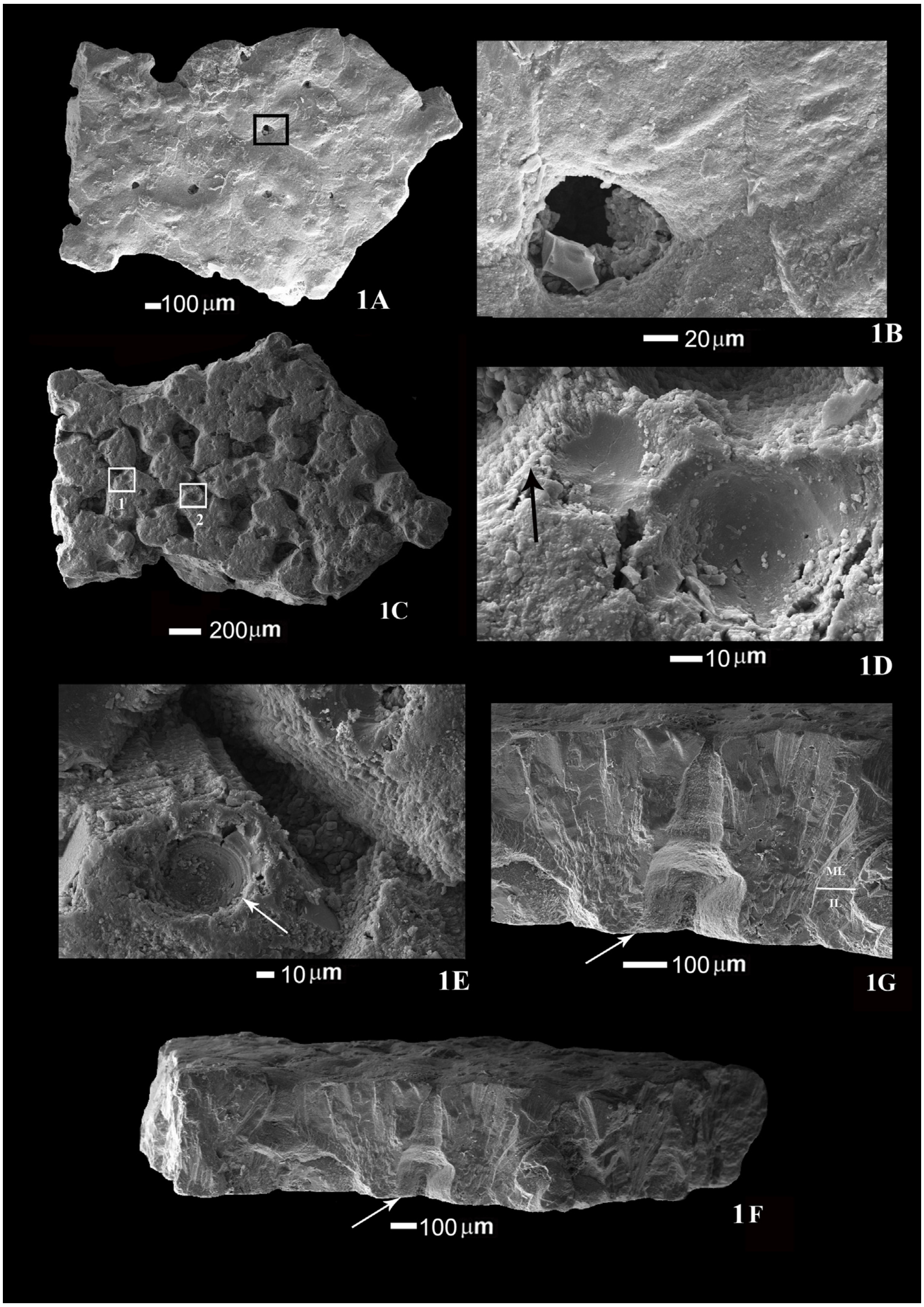

Fig. 4. 1. Eggshells of Krokolithidae *incertae sedis* from the Upper Cretaceous intertrappean beds of Kisalpuri, central India. 1A. External surface with many pore openings (DUGF/80); 1B. Enlarged view of a pore in the inset of 1A (DUGF/80). 1C. Internal surface showing coalescing basal knobs with many circular craters and interstitial pores (DUGF/80). 1D. Enlarged view of the twinned craters in the inset 1 of 1C (DUGF/80), black arrow points to inwardly directed microcrystals adjacent to the crater. 1E. Enlarged view of a ringed crater (white arrow points to the crater) in the inset 2 of 1C, horizontally placed tabular crystals can be seen beneath the crater (DUGF/80). 1F. Fractured radial surface (DUGF/80), white arrow points to inverted funnel-shaped pore canal (DUGF/80). 1G. Enlarged view shell units, white arrow points to the inverted funnel-like pore canal (DUGF/80).

Fig. 4. 1. Coquilles d'œuf de Crocolithidae *incertae sedis* en provenance des bancs inter-trappéens de Kisalpuri du Crétacé supérieur, Inde centrale. 1A. Surface externe avec nombreuses ouvertures de pores (DUGF/80). 1B. Vue élargie d'un pore dans l'encart de 1A (DUGF/80). 1C. Surface interne montrant des bosses basales coalescentes avec de nombreux cratères circulaires et pores interstitiels (DUGF/80). 1D. Vue agrandie de cratères jumelés dans l'encart de 1C (DUGF/80), la flèche noire pointant vers des microcristaux adjacents au cratère, dirigés vers l'intérieur. 1E. Vue agrandie d'un cratère annulaire (la flèche blanche pointe vers le cratère) dans l'encart 2 d'1C, des cristaux tabulaires placés horizontalement pouvant être observés sous le cratère (DUGF/80). 1F. Surface radiale fracturée (DUGF/80), la flèche blanche pointant vers un canal de pore en forme d'entonnoir retourné (DUGF/80). 1G. Vue agrandie de morceaux de coquille, la flèche blanche pointant vers un canal de pore retourné (DUGF/80).

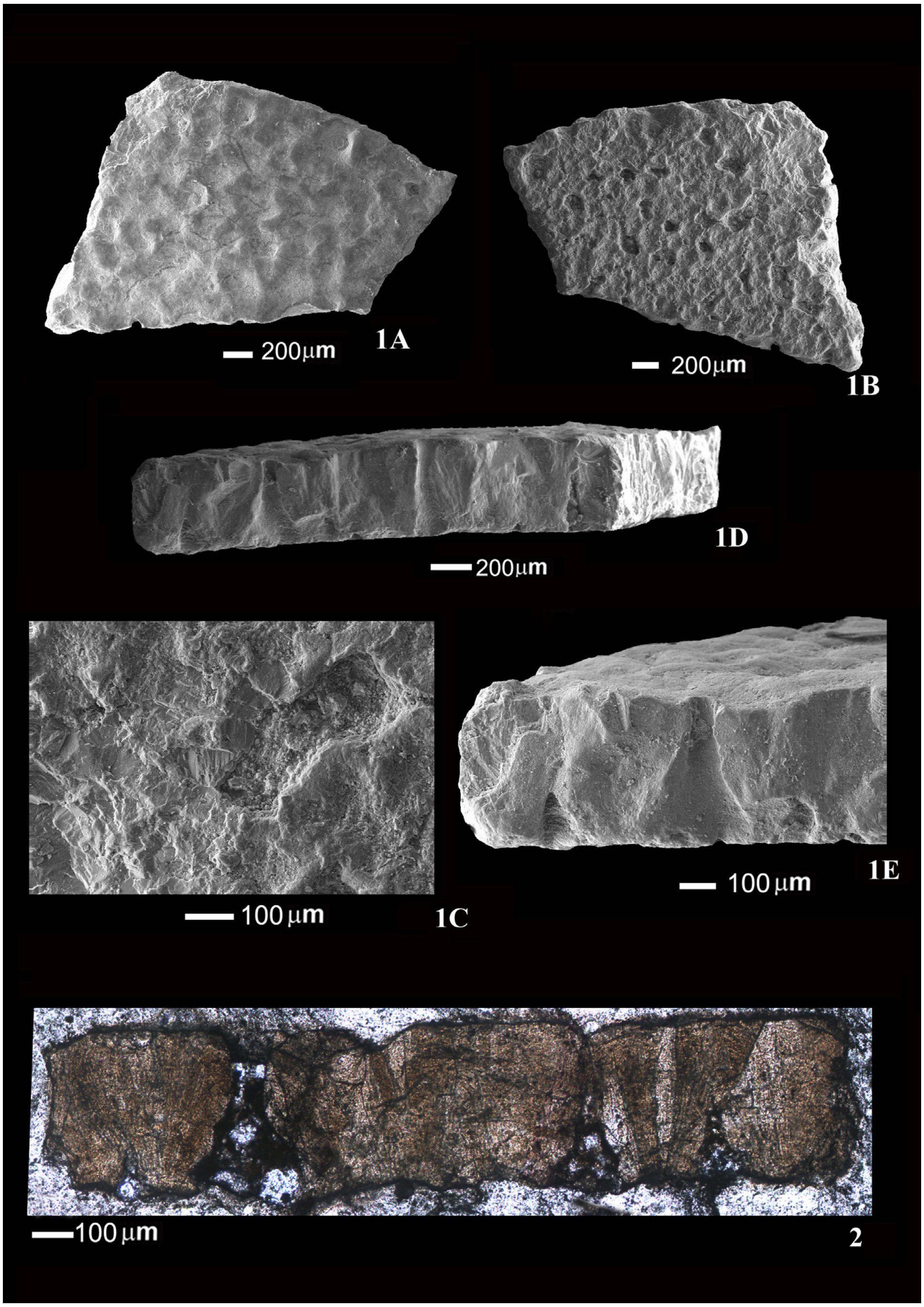

Fig. 5. 1–2. Eggshells of Krokolithidae *incertae sedis* from the Upper Cretaceous intertrappean beds of Kisalpuri, central India. 1A. External surface with many coarse pits (DUGF/81). 1B. Internal surface with irregular interstitial pits (DUGF/81). 1C. Enlarged view of internal surface showing irregular pits. 1D. Fractured radial surface (DUGF/81). 1E. Enlarged view of fractured radial surface showing trapezoidal shell units and intervening inverted funnel-shaped pore canals (DUGF/81). 2. Thin section of radial surface in plane polarized light showing basal knobs and wedged shell units (DUGF/82).

Fig. 5. 1–2. Coquilles d'œuf de Crocolithidae *incertae sedis*, en provenance des bancs inter-trappéens du Crétacé supérieur de Kisalpuri, Inde centrale. 1A. Surface externe avec de nombreuses cavités grossières (DUGF/81). 1B. Surface interne avec des cavités interstitielles irrégulières (DUGF/81). 1C. Vue agrandie de la surface interne montrant des cavités irrégulières. 1D. Surface radiale fracturée (DUFG/81). 1E. Vue agrandie de la surface radiale fracturée, montrant des fragments de coquille trapézoïdaux et des canaux de pores en forme d'entonnoirs retorunés (DUGF/81); 2. Section mince de surface radiale en lumière polarisée plane, montrant des bosses basales et des fragments de coquille en biseau (DUGF/82).

Table 1
Comparison of present eggshells with well known rigid turtle ootaxa.
Tableau 1
Comparaison de coquilles d'œuf actuelles avec l'ootaxa rigide bien connu de tortue.

Name of ootaxon	Shell thickness (μm)	Shell height/width ratio	Age	References
Unnamed	110–180	?	Jurassic	1
Chelonoolithus braemi	200	1:1	Jurassic	2
MOR710	680	?	Cretaceous	3
Emydoolithus laiyangensis	400–500	2:1–5:1	Cretaceous	4
Unnamed	220–250/400–430	1.34:1–2.02:1	Cretaceous	5
Testudoolithus hirshi	150	3:1	Jurassic	6
Testudoolithus jiangi	700–1000	2.5:1–3.0:1	Cretaceous	7
Testudoolithus rigidus	220–240	2:1	Cretaceous–Pliocene	8
Testudinovum (egg containing embryo)	180(1991) 300–400(1994	?	Cretaceous	9, 10
Unamed gravid *Adocus*	500–600	2.5–3.5:1	Cretaceous	11
Testudoolithus sp.	240–280	2.5:1	Cretaceous	12
Testudoolithus sp.	400–1004	3.5:1–4.2:1	Cretaceous	13
Unnamed (egg containing embryo)	676	2:1	Cretaceous	14
Haininchelys curiosa	250–300	1.2:1 –2.3:1	Palaeocene	15
Unnamed	190–260	1.7:1	Cretaceous/Palaeocene	16
127/CRP/89	800	3:5:1	Cretaceous	17
Unnamed	370–450	1.28:1	Cretaceous	This work

Modified after Jackson et al., 2008; Knell et al., 2011 and Wang et al., 2013.
References: 1) Bray and Hirsch, 1998; 2) Kohring, 1998; 3) Jackson and Schmitt, 2008; 4) Wang et al., 2013; 5) Isaji et al., 2006; 6) Kohring, 1999; 7) Jackson et al., 2008; 8) Hirsch, 1996; 9) Mikhailov, 1991; 10) Mikhailov et al., 1994; 11) Zelenitsky et al., 2008; 12) Knell et al., 2011; 13) Tanaka et al., 2011; 14) Jackson et al., 2008; 15) Schleich et al., 1988; 16) Bajpai et al., 1997b; 17) Mohabey, 1998.

4.8. Material

Three isolated eggshell fragments (DUGF/80-82).

4.9. Description

The height and width of an individual shell unit vary from 425–480 μm and 400–420 μm, respectively. The height to width ratio is 1.06–1.14:1.0. The external surface of the eggshells differs in its appearance in different crocodilian species. It is known to vary from fairly smooth to dimpled, coarse or heavily eroded and flaky (Hirsch, 1985). In the described specimens, the external surface is either roughly undulating with sub-circular to oval pits, some of which may represent dissolution pits (Fig. 4.1A) or with coarse sub-circular pits bounded by ridges (Fig. 5.1A). Under SEM, fractured radial section reveals discrete, inverted triangular, radiating crystalline wedges that form a tabulate layer, with pores between the shell units (Fig. 4.1F–G, Fig. 5.1D–E). Inverted funnel-like pore openings extending from the base to outer surface of the shell unit are visible in the radial section (Fig. 4.1F–G, Fig. 5.1D–E). The pore openings have an average diameter of 185 μm. The pore canals are continuous from the internal to external surface (Fig. 4.1F–G, Fig. 5.1D–E) and hence interlocking between adjacent shell units is weak. These wedged shell units rise from basal plate groups beneath them, which are loose aggregates of platy, calcitic crystallites (Fig. 4.1F–G, Fig. 5.1D–E, 5.2). Radial striations are observed rising from the basal plate groups and passing through the upper end of the shell units (Fig. 4.1F, Fig. 5.2). The interstices between the crystalline wedges form an acute-angled triangle. The basal plate groups are surrounded by large irregular interstices (Fig. 4.1C). On the inner surface, the coalescing basal plate groups are separated by elongated depressions some of which may represent pore openings. The basal plate groups bear a number of circular, crater-like depressions with ring-like or stepped layers (Fig. 4.1E). Sometimes these craters-like depressions occur in twins and are surrounded by inwardly directed microcrystals (Fig. 4.1D). Beneath these craters, the basal plate groups exhibit horizontally laid crystals oriented parallel to the outer surface (Fig. 4.1E). The basal plate groups are separated by a distance of about 130–160 μm. The three structural layers identified in crocodilian eggshells (Ferguson, 1982; Moreno-Azanza et al., 2014), viz., the inner layer (IL) or the basal plate groups, the middle layer (ML) growing parallel to the shell surface like a book-like tabular structure, and the densely calcified outer layer (OL) are not always identifiable in fossil crocodiloid eggshells (Moreno-Azanza et al., 2014). In the present specimens, IL is evident, but it is difficult to distinguish between ML and OL as prominent accretion lines with tabular book-like structure extending from the top of basal plate groups to the outer surface are not visible.

4.10. Comparisons

Crocodilian eggshells are easily distinguished from those of turtles, which are generally diagnosed by their spherulitic shell units consisting of needle-like radiating aragonitic crystals. The typical radial section of the Kisalpuri eggshells clearly demonstrates that these specimens belong to the crocodiloid type of basic eggshell organization (Mikhailov, 1997). The external surface of these eggshells exhibits the same general ornamentation of other crocodiloid eggs such as in *K. wilsoni*, *K. helleri*

Table 2
Comparison of shell thickness of some modern and fossil crocodilian eggshells.
Tableau 2
Comparaison de l'épaisseur de la coque de quelques coquilles d'œuf crocodiliennes modernes et fossiles.

Egg laying Taxon	Eggshell thickness in mm	Age	References
Crocodylus acutus	0.45	Modern	Hirsch and Kohring, 1992
Crocodylus niloticus	0.53	Modern	Hirsch, 1983
Crocodylus porosus	0.53	Modern	Hirsch and Kohring, 1992
Crocodylus johnstoni	0.40	Modern	Hirsch and Kohring, 1992
Crocodylus mindorensis	0.43	Modern	Marzola et al., 2015
Alligator mississippiensis	0.53	Modern	Hirsch and Kohring, 1992
Paleosuchus palpebrosus	0.41	Modern	Marzola et al., 2015
Gavialis gangeticus	0.30–0.59	Modern	Panadès et al., 2009
Caiman latirostris	0.36–0.72	Modern	Fernández et al., 2013
Fossil crocodiloid eggs			
Pai Mogo eggs	0.20–0.35	Jurassic	Antunes et al., 1998
Unnamed eggshells (Galve Type)	0.50–0.70	Cretaceous	Kohring, 1990b
Araçatuba Formation eggs (*Mariliasuchus amarali*?)	0.24–0.36	Cretaceous	Magalhães-Ribeiro et al., 2006
Cajones Formation eggs (*Yacarerani boliviensis*?)	0.20	Cretaceous	Novas et al., 2009
Bauruoolithus fragilis	0.15–0.25	Cretaceous	Oliveira et al., 2011
Glen Rose Formation	0.60–0.70	Cretaceous	Rogers, 2000
Two Medicine Formation	0.65	Cretaceous	Jackson and Varricchio, 2010
Fruitland Formation	0.51–0.64	Cretaceous	Tanaka et al., 2011
Intertrappean beds of Bombay	0.35	? Cretaceous	Singh et al., 1998
Intertrappean Beds of Kisalpuri	0.42–0.48	Cretaceous	This work
De Beque Formation *Krokolithes wilsoni*	0.25–0.45	Eocene	Hirsch, 1985
Geiseltal *Krokolithes helleri*	0.36–0.45	Eocene	Kohring and Hirsch, 1996
Bridger Formation eggs	0.60–0.70	Eocene	Hirsch and Kohring, 1992
Chinji Formation	0.18–0.76	Miocene	Panadès et al., 2009
Saketi Formation	1.9–6.6	Pliocene	Patnaik and Schleich, 1993

Modified after Oliveira et al., 2011 [Table 1].

and *Bauruoolithus fragilis* and in extant *Crocodylus johnstoni* Krefft, 1873 and *C. porosus* Schneider, 1801, and has trapezoidal eggshell units and basal knobs. In shell thickness, the Kisalpuri eggshells fall within the range of variation for fossil crocodiloid eggshells (290 μm–700 μm) and eggshells of extant crocodiles (400 μm–530 μm) (Hirsch, 1983) (Table 2). Though DUGF/81 with coarse pitted external surface ornamentation appears distinct from DUGF/80, in which the outer surface is undulating, in fractured radial section both have similar looking shell units separated by inverted funnel-shaped pore canals.

Ferguson (1982) identified five layers, viz., the inner membrane layer, the mammillary layer, the organic layer, the honeycomb layer, and the outer calcified layer in the eggshells of *Alligator mississippiensis*. However, the single-layered eggshell structure corresponding to crocodiloid basic type of Mikhailov (1997) has been widely followed in describing fossil eggshells until now. More recently, Moreno-Azanza et al. (2014) revisited the taxonomic status of eggshell fragments from the Uppermost Cretaceous of Pyrenees, Spain attributed to Megaloolithidae (López-Martínez, 2003) and classified them as Krokolithidae indet. In this work, the authors confirmed that the microstructure and ultrastructure of crocodylomorph eggshell contains several structural layers as was envisaged by Ferguson (1982). According to Moreno-Azanza et al. (2014), the calcified part of crocodiloid eggshell consists at least of three layers, namely the inner layer (IL) with basal knobs made up of poorly ordered aggregates of calcite microcrystals and protein fibers (basal plate groups of Hirsch, 1985), the middle layer comprising an aggregate of prismatic calcite crystals interwoven with protein fibers and growing parallel to the shell surface like a book-like tabular structure (corresponding to organic and honeycomb layers of Ferguson, 1982), and the densely calcified outer layer lacking organic matter and reminiscent of tabular ultrastructure of theropod eggshells. As discussed above, it is not easy to identify all these structural layers in fossil crocodiloid eggshells. Only the inner layer (IL) is identifiable in the studied sample and as the horizontal accretion lines are not preserved, the distinction between the middle and outer layers is not possible.

The present eggshells, particularly DUGF/80, differ from most of the known crocodiloid eggs and eggshells in which wedges were found to be interlocked in a continuous layer. In contrast, the crystalline wedges of Kisalpuri eggshells do not show interlocking. The eggshells from the intertrappean beds show crystalline wedges without interlocking from the base to near the external surface, in which it differs from almost all the described fossil taxa and may warrant their placement in a new oogenus. However, Mikhailov et al. (1996) suggested that oogenera should be based on egg shape and differences in structural morphotypes, outer surface ornamentation and pore system. Moreover, we cannot rule out the possibility that the lack of interlocking shell units may be an artifact of dissolution causing enlargement of pore canals as the available sample size is too small.

A few Cretaceous records of crocodiloid eggs and eggshells are known from the Upper Cretaceous (Campanian) Fruitland Formation (Tanaka et al., 2011), the Two Medicine Formation (Jackson and Varricchio, 2010), the Lower Cretaceous Glen Rose Formation (Rogers, 2000) and the Upper Cretaceous Adamantina Formation, Brazil (Oliveira et al., 2011). The crocodiloid eggshells from the Glen Rose Formation and the Two Medicine Formation have relatively thicker shells than those of Kisalpuri. Moreover, the eggshells from the Two Medicine Formation have smooth outer surfaces and lack pore canals both in radial section and on the exposed shell surface. In Krokolithidae eggshells from the Fruitland Formation, the lower end of eggshell thickness range (450–800 μm) is comparable to those described here. However, they differ in having reticulate to nodose surface ornamentation, horizontal accretionary lines and a step-like erosional pattern. The new eggshells from central India also differ from *Bauruoolithus fragilis* from the Upper Cretaceous of Brazil, as the shell is much thinner (150–250 μm), shell units are broader, and the interstices between the crystalline wedges are proportionately smaller, forming an obtuse angle in the Brazilian oospecies. Among all known fossil crocodilian eggshells, those of *Krokolithes wilsoni* from the Eocene De Beque Formation, Colorado, USA (Hirsch, 1985) have a shell thickness (0.36–0.45) which is the closest to that of the Kisalpuri eggshells (Table 2). But in the former, the external surface is heavily degraded and bears stepped erosion craters.

In the Indian subcontinent, there are two reports of fossil crocodilian eggshells from the Siwalik deposits and one from the intertrappean beds of Bombay (Singh et al., 1998). The eggshells from Kisalpuri are slightly thicker (480–420 μm) than those described from the intertrappean beds of Bombay (350 μm). However, Singh et al. (1998) mentioned the presence of discrete mammillae on the internal surface, which are not generally observed in crocodiloid eggshells. They also mentioned that the average thickness of individual shell units is only 75 μm, which is smaller than that of the Kisalpuri eggshells. Moreover, the inverted triangular wedge-like crystallites are not very clear from the photomicrographs of Singh et al. (1998; Plate 2a-c); rather they appear as cylindrical spheroliths. In view of these morphological inconsistencies, we consider them doubtful crocodiloid type eggshells. Patnaik and Schleich (1993) described smooth crocodiloid eggshell fragments from the Pliocene Saketi Formation, near Moginand, in Himachal Pradesh, which are comparatively thicker than those of Kisalpuri with a thickness range of 1.9–6.6 mm. These eggshells were assigned to *Gavialis* cf. *G. gangeticus* Gmelin, 1789 and *Crocodylus* cf. *C. palustris* Lesson, 1831 just based on the thickness range of eggshells. The lone egg reported from the Upper Miocene Chinji Formation in Pakistan has a shell thickness ranging from 180–760 μm (Panadès et al., 2009). No pore canals are present in the radial section of Chinji eggshells as in the present specimens but have well developed accretion lines. In these characters, it differs from the eggshells from Kisalpuri referred to Krokolithidae. Based on the size dimensions of the egg and shell thickness range, the Chinji egg has been compared with those of *Gavialis* cf. *G. gangeticus.*

5. Discussion

Though dinosaur eggs, eggshells and nesting sites from the Cretaceous rocks of India have been well studied in the last three decades, we know very little about the eggshells of other reptilian groups such as geckonid lizards, turtles and crocodilians. Therefore, any new oological discoveries of these groups will improve our knowledge of these groups immensely. The present study assumes great significance in this context. The isolated eggshell fragments from the intertrappean beds of Kisalpuri in central India are identified with testudoid and crocodiloid types based on their shell structure. The new testudoid eggshells from central India are distinct from all known fossil turtle eggshells in the presence of coarse pits and linear depressions surrounded by ridges on the outer surface. But shell units with acicular crystals radiating outwards from inner cores or nucleation centres and interlocking with adjacent shell units favour their assignment to Testudoolithidae. Prior to the present finds, testudoid eggshells have been reported from the infratrappean beds of Duddukuru (Bajpai et al., 1997). These infratrappean beds have been assigned a Late Cretaceous (Maastrichtian) age as the overlying, younger intertrappean beds in subsurface sections were dated as Danian (Bajpai et al., 1997). However, Bhalla (1966) based on foraminifera suggested shallow marine (inner neritic) environment of deposition and a Palaeocene age for the infratrappean outcrops in the vicinity of Duddukuru. Therefore, the Maastrichtian age for the infratrappean beds of Duddukuru needs to be confirmed. In this respect, the turtle eggshells described in this paper represent a definitive Cretaceous record of turtle eggshells from the continental rocks of India.

Similarly, Singh et al. (1998) documented crocodilian eggshells from the intertrappean beds of Bombay that were originally dated as Early Eocene (Chiplonkar, 1940; Verma, 1965). But later Singh and Sahni (1996) considered the intertrappean beds of Bombay as Maastrichtian in age based on ostracod fauna recovered from these beds which compares well with that of Maastrichtian intertrappean beds of Anjar and Nagpur (Bajpai and Whatley, 2001) and the Lameta Formation of Jabalpur and Nand-Dongargaon (Khosla et al., 2005). However, the recent discovery of similar ostracod assemblages from the Lower Palaeocene (Danian) intertrappean beds of Jhilmili and Papro (Sharma and Khosla, 2009) renders the utility of intertrappean ostracod fauna as age markers less reliable. In the absence of any other distinctive Late Cretaceous marker fossils, distinctiveness of the fauna from that of other Upper Cretaceous intertrappean beds, and the proximity of Bombay intertrappean beds to the youngest flows, these intertrappean beds may actually range into the Palaeocene. Therefore, if the intertrappean beds of Bombay are conclusively interpreted as Palaeocene, the crocodilian eggshells from the intertrappean beds of Kisalpuri described here may turn out to be the oldest record of crocodile eggshells from India.

An interesting finding of the present study is the occurrence of small circular crater-like depressions on basal knobs of the crocodiloid eggshells with concentric rings and downwardly pointing microcrystals adjacent to the craters. Kohring and Hirsch (1996) had observed somewhat similar circular craters on the inner surface of crocodilian eggshells from the Middle Eocene of Geiseltal, Germany (Hirsch, 1996; fig. 4G). They interpreted these crater-like depressions as possible sites from where organic fiber has been dissolved. A similar interpretation can be made for the craters observed on the basal knobs of DUGF/80 (Fig. 4.1C–E). In addition to this structural feature, the book-like arrangement of horizontal crystals from the basal knobs towards outer surface may actually indicate the presence of tabular middle layer in these Indian specimens.

The intertrappean vertebrate fauna of Kisalpuri includes both turtle and crocodilian skeletal elements. The turtle remains are represented by carapace fragments and postcranial bones which have been tentatively assigned to Bothremydidae gen. et sp. indet. (De Lapparent de Broin et al., 2009). However, the present eggshells cannot be confidently assigned to this group of turtles as the fossil eggshell record of turtles is poorly understood at present. Similarly, crocodiles are represented by at least two groups in the vertebrate fauna of Kislapuri; one represented by the Dyrosauridae family and the second one by an indeterminate group. The family Dyrosauridae is known by partially preserved mandible, frontal, cervical and dorsal vertebrae (Khosla et al., 2009). The indeterminate crocodiles are represented by isolated teeth only and these are represented by anterior conical teeth, triangular intermediate, labiolingually compressed anterior most posterior, and globular to sub-globular posterior teeth (Khosla et al., 2004; Verma, 2008). The crown ornamentation of these teeth point to false ziphodont crocodile teeth of Prasad and de Lapparent de Broin (2002). As in the case of turtle eggshells, it is not possible to identify the crocodilian eggshells of Kislapuri with any of these two groups as the variation in shell morphology and ultrastructure of various groups of crocodiles are not currently well understood.

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