



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

## 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.

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### R É S U M É

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 infratrapéens 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 testudoïd, 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 crocodiloïd 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 testudoïd et de crocodiloïd du Crétacé supérieur d'Inde centrale sont attribués aux co-familles de Testudoolithidae et Krokolithidae respectivement.

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## 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,

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