EGGSHELL MICROSTRUCTURE AND POROSITY OF THE NICOBAR SCRUBFOWL (*MEGAPODIUS NICOBARIENSIS,* GREAT NICOBAR ISLAND, INDIA)

by

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ABSTRACT

The eggshell of Nicobar scrubfowl (*Megapodius nicobariensis*) is described for the first time. Its egg porosity is calculated and discussed with data from several taxa (another megapode, some extant and fossil reptiles including a titanosaur group) in order to compare incubation types with eggshell structure. Eggshell microstructure reflects first phylogenetic traits and does not seem to have developed major adaptative features due to the incubation conditions, except for the pore canals.

RESUME

La coquille d'œuf du mégapode de Nicobar (*Megapodius nicobariensis*) est décrite pour la première fois. Sa porosité est calculée et discutée avec les données obtenues pour d'autres taxons (un autre mégapode, quelques reptiles actuels et fossiles dont un groupe de titanosaures), dans le but de comparer le type d'incubation et la structure de la coquille. Excepté pour les canaux aérifères, la microstructure de la coquille d'œuf reflète avant tout des traits phylogénétiques et ne semble pas avoir développé des caractères adaptatifs liés aux conditions d'incubation.

INTRODUCTION

Some birds differ fundamentally from all others by exploiting environmental heat rather than body heat to incubate their eggs. These birds, the megapodes (Megapodiidae), which constitute a monophyletic group within the Galliformes, are now represented only in the Nicobar and Australasian islands (Papua new Guinea, Bismarck Archipelago, Mollucas, Philippines) (Jones & Birks, 1992). The paleontological and archeological record indicate that their geographical repartition was wider than today (Steadman, 2006).

Megapodes were discovered over four centuries ago (Jones, 1989) but most interdisciplinary researches are recent. These studies deal particularly with their origin (Cracaft, 1973; Olson, 1985), their phylogeny (Sibley *et al.*, 1988), their biological / physiological adaptations (Seymour, 1985; Seymour *et al.*, 1987; Booth & Thompson, 1991) and the ecology of their environment (Jones, 1989). By making use of environmental heat, adult megapodes are almost emancipated from some usual constraints for reproductive success associated with parental care. The megapodes bury their eggs in burrows or mounds. As most of extant reptiles, incubation results from microbial decomposition, solar radiation and/or geothermal activity (Jones *et al.*, 1995). Such a reproductive strategy has been inferred from the studies of nesting environment and egg conductance, especially in some saurischian groups like titanosaurids and maniraptorans (Erben *et al.*, 1979; Seymour, 1979; Williams *et al.*, 1984; Sabath, 1991; Mohabey, 1996; Deeming, 2006).

Brooding and parenting care are regarded as modern bird features, therefore, megapodes are considered to have a primitive reptilian-like reproductive strategy (Clarck, 1964). Although both these two behaviours are common to the majority of birds, they do not necessarily represent avian synapomorphies (Varrichio & Jackson, 2003).

The main contribution of this paper is to describe for the first time the eggshell microstructural characteristics of a Nicobar scrubfowl, *Megapodius nicobariensis*. Additionally, we have calculated its egg porosity and compared it with derived data mainly from the literature in order to compare incubation type with eggshell structure.

GEOGRAPHICAL AND ECOLOGICAL CONTEXT

The Nicobar scrubfowl (*Megapodius nicobariensis*) is confined to the southernmost Indian territory of Great Nicobar Island. Though related to India's national bird peacock, it is considered to be the vulnerable species in the world (Jones & Everding, 1991, del Hoyo *et al.*, 1994). The habit and nature of the megapodes, represented by a solitary species in the Nicobar Islands and about 19 species from the Australasian region, are poorly known to specialists and laymen alike. The isolated distribution of a solitary species in the Nicobar Islands is somewhat problematic, as megapodes have not been found on the nearby islands of Java and Sumatra. Such a biogeographic distribution and endemic occurrence in the Nicobar Islands have important bearing on the recognition of the dispersal corridor of fauna and flora between post-Eocene emergent Nicobar and Australasian islands (Jones, 1989).

The birds on Great Nicobar Island, comprising two subspecies *M. n. nicobariensis* and *M. n. abbotti*, inhabit the thick coastal jungles and lay eggs in sandy beach areas (Salim & Ripley, 1983). A low mound is built by several pairs of birds, (the so called "community mount building"). The eggs are covered with decaying vegetal matters (leaves, twigs) and then covered with sand. The site is so cleverly chosen that only filtered sunlight reaches the mound during the day. When the heat of vegetal decay together with that generated by solar radiation reaches approximately 33° C, the female lays on average 4 eggs (in a season) in the pits. The eggs of megapodes and particularly those of *M. nicobariensis* are exceptionally large (wt. 120 g) compared to the size of an adult female (wt. 550-950 g; pers. comm. Mr K. Sivakumar, Coimbatore). A remarkably constant temperature of 34° C +/- 1° C is maintained by periodic digging and ventilation or covering with sand (pers. comm. Mr K. Sivakumar). The incubation period lasts about 10-12 weeks and, when hatched the offspring are well equipped with fully developed feathered legs to dig their way upwards and fly on their own. These large-footed birds skilfully exploit the thermal sensitivity of their face and mouthparts, (especially tongue) to maintain constant temperature during incubation (Seymour, 1985; Jones, 1989). Mound building in hot tropical regions is then an efficient device to maintain constant temperature during the incubation of eggs, chiefly by the selection of mound site and use of decaying vegetal matter by these birds.

MATERIAL AND METHODS

The eggshells are collected from one incubation mound situated in the southernmost part of Great Nicobar Island by one of us (S. A. Jafar) during April 1997. We used a scanning electron microscope (SEM) for studying radial sections. The eggshells were mounted on the aluminium stubs with double sticky tape. The stubs with the mounted specimens were then sputtered with gold in a JEOL FC-110 Ion Sputtering Device. Descriptive terminology follows Mikhailov (1997).

The eggshell permeability (water vapour and gases), represented by the conductance rate (GH_2O), vary with the nest environments. This rate is determined with the formula given by Ar *et al.* (1974) and Seymour (1979): $GH_2O = 23.42 \times Ap \times L^{-1}$ where the water vapour conductance is water in mg per Torr per day, and 23.42 is a conversion constant based on the diffusion of water vapour in air. Ap refers to the pore area (estimated from the number of pores per cm^2 x the surface area of egg) and L is the average length of the pore canal. Data on water vapour conductance and morphology eggshells were collected directly from new specimens (8-25 analysed shell fragments, Table) and from the literature (Packard *et al.*, 1979; Garcia, 1998 and Vianey-Liaud & Garcia, 2000). The eggshells, obtained for the analysis were acquired from museum (Muséum National d'Histoire Naturelle de Paris) and universities (Montpellier II and Poitiers).

SYSTEMATICS

Taxonomy

Parataxonomy eggshell
GALLIFORMES

Basic type Ornithoid
MEGAPODIIDAE
Megapodius nicobariensis Blyth 1846

Material: fragmentary eggshells (VLP/SAJ 5000-5007 and housed at Vertebrate Paleontology Laboratory, Panjab University, Chandigarh).

Referred material: VLP/SAJ 5000-5002

Description

These fragments are extremely thin compared to the ratite eggshells (ostrich), with thickness ranges between 0.25 and 0.30 mm. The outer surface is generally smooth (Pl. a). Microstructurally, the eggshell reveals compact shell units with a trilaminate arrangement of calcite crystals (Pl. b).

Mammillary layer

Its lower part is well preserved and varies in thickness from 1/4 to 1/6 part of the total shell thickness. It is composed of the variable sub-circular mammillae (diameter 0.02 to 0.04 mm) which are tightly packed (Pl. c) and vertically extended. The bases of the mammillae show fine radiating calcite crystals (the edges) characterized by a tabular ultrastructure (parallel striations) from central cores and broadening towards their distal ends (Pl. c). Some fragments (Pl. d) have distinct craters in the centre of the mammillae cores, indicating possible reabsorption of calcite by the growing embryo (Booth & Thompson, 1991) or weathering.

Spongy layer

It is exceptionally preserved in all studied samples and its thickness varies from 0.185 to 0.20 mm, approximately 67 % of the total shell thickness. In broken sections, a squamatic pattern is clearly observed (Pl. 1, d). The boundary between the mammillary and prismatic layers is not abrupt.

Outer layer

A structural change with an indistinct boundary defines the base of the third and external layer which varies in thickness from 5 to 10 µm (Pl. 1, b and d). It is composed of vertical prisms that are structurally continuous.

Pores and pore canals

No pore openings are visible on the outer surface but we were able to distinguish in longitudinal sections (Pl. 1, a and c) numerous narrow orifices. In broken sections, pore canals are rarely seen but wherever present, they originate in the middle of a spongy layer. The pore canals are sub-vertical (angusticanaliculate type) and slightly inclined in shape (Pl. 1, b and d). The maximum length of the pore canal studied is 0.06 mm, well less that the entire thickness of eggshell.

TAXA EGGS	**Egg mass** (g)	**System of pore canals**	**Ap: estimated pore area** (cm^2)	**L: Shell thickness** (mm)	**Conductance value** (mg $Torr^{-1}$ day^{-1})
Megapodes					
Megapodius nicobariensis	125	complex	1.11	0.27	3384
Lepoia ocellata	200	complex	2.17	0.15	2790
Our observations n= 8 measurements					
Reptiles (Packard *et al.*, 1979)					
Trionyx spiniferus	10	simple	1.14	0.20	810
Alligator mississipiensis	72	simple	8.16	0.387	2903
From Litterature					
Sauropod eggshells : Megaloolithidae (Garcia, 1998; Vianey-Liaud & Garcia, 2000)	(estimated)				
Megaloolithus mamillare	5283	complex	19.26	1.76	3723
Cairanoolithus dughii	3057	complex	7.06	2.10	2586
Our observations n= 8 measurements					

Table: Data on the shell characteristics of the studied taxa eggs

RESULTS AND DISCUSSION

Eggshell microstructure

Eggshell micro- and ultra-structures of *Megapodius nicobariensis* are identical to those of *Lepoia ocellata* (our observations), and consist of the usual three structural zones (mammillary, squamatic and external layers). The boundary between these layers is not abrupt as in modern ratite eggshell. They share several characteristics with the neognathes (recent avian), and particularly with the Galliformes (comparisons with taxa belonging to the Phasianidae: *Gallus*, *Alectoris*, *Coturnix*): layers arranged in the same proportions (ratio between structural strata), smooth outer surface and similar pore canal system. We have not specified in this study the morphotype of the scrubfowl eggshells, which characterizes also the neognath birds, according to the concept of egg parataxonomy. This morphotype [first defined as Prismatic "neognathe" by Mikhaılov *et al.* (1996) and by Hirsch *et al.* (1997)] has been almost abandoned since the eggshell is examined from a phylogenetic perspective (Zelenitsky & Modesto, 2003; Grellet-Tinner & Makovicky, 2006; Zelenitsky, 2006)

Conductance (gas and water vapour data) and its calculation

The conductance values for all taxonomic eggs are relatively high. The lowest conductance (810 mg/Torr/day) is for a trionychid egg, which shows a value consistent with that of an equivalent-sized avian egg. The others values range between 2903 and 3723 (Table), up to 20 times larger than predicted for avian eggs of the same initial mass.

The conductance value of an eggshell has been used like a tool to indicate or precise the nesting environmental of egg-layers and particularly for dinosaurs (Seymour, 1979; Williams *et al.*, 1984; Sabath, 1991; Grigorescu *et al.*, 1994; Mikhailov *et al.*, 1994; Garcia 1998; Deeming, 2006, Jackson *et al.*, 2008). The calculated high conductances in this study confirm the previous results and would indicate the same incubation strategy between all of these taxa (Alligatoridae, Megapodiidae and probably sauropod dinosaurs with the Megaloolithidae eggs). The alligators, as caimans and some crocodiles construct low mounds of vegetation and dirt (Coombs, 1989; Varrichio *et al.*, 1999). Also, the megapodes bury their eggs in burrows or mounds composed both of vegetable matter and sand. Concerning the interpretation of sauropod reproductive biology, several studies on nest structures of european megaloolithid eggs (Kerourio, 1981; Garcia, 1998; Cousin & Breton, 2000; Garcia *et al.*, 2003) have suggested a burial mode of incubation including probably vegetation. The eggs are often packed in mudstone layers (bank deposits) and regrouped in some close small « structures ».

The calculations of gas conductance assume the porosity take place across the shell by a simple geometrical system, the pore canal. But, the eggshell is a multi-complex network of organic and crystalline material (Mikhailov, 1997). The predicted GH2O values, measured from the classic formula (Ar *et al.*, 1974; Seymour, 1979; Ar & Rahn, 1985) could be questionable because most of parameters are not really apprehended. The conductance and the flux rates are directly proportional to the number of pores (Rahn *et al.*, 1987). The shape of pores plays also a dominant role in total conductance (Sibly & Simkiss, 1987), particularly in their narrow part (Toien *et al.*, 1988). Besides, the nodular ornamentation in outer surface could facilitate gas exchanges through the pore openings located around or at the base of each node (Garcia, 1998; Grellet Tinner *et al.*; 2004; Grellet Tinner *et al.*, 2006).

The eggshells are composed of structural layers [2 to 3 organized differently according to phylogeny, (Mikhaılov *et al.*, 1996)] from nucleation poles fixed in the shell membrane, crisscrossed by a network of pore canals, often very complicated. To calculate the pore area (Ap), the pore canal is always compared to a straight tube which is always functional and which passes through to the outer surface to one circular shape opening. The pore canals, in modern bird and dinosaur eggshell are organized in systems more complex with ramifications and differences in the canal length (Board & Scott, 1980; Vianey-Liaud & Garcia, 2000).

Physiologically important eggshell soft tissues like membranes and pore plugs (Board, 1982; Board *et al.*, 1982; Kern & Ferguson, 1997) are preserved only in part (particularly for fossils), further complicating functional interpretations. In a bird egg, gas exchange is not possible through all pores (Board & Scott, 1980) which may be partially or completely blocked by organic or inorganic material. It would be necessary in further investigations on conductance studies to integrate all these parameters in order to approach the real values of the shells *in vivo*.

Eggshell structure and incubation type

Mound nesting is a reproductive strategy which might have been adopted by different reptilian and avian groups to balance the poor contribution in the parental care (Varrichio *et al.*, 1997**.** It does not represent the primitive condition in birds, but an independently-evolved autapomorphy of the Megapodiidae (Jones *et al.*, 1995) in accordance with the results of reproduction phylogenetic distributions in the bird ancestors (Tullberg *et al.*, 2002). This strategy of incubation is thus appeared at different times in a phylogeny of major amniote lineages, probably independently to the shell structure and its elaboration process.

Eggshells of scrubfowl are derived rigid type composed of three structural layers, very different in organisation with these of extant reptiles (squamates, turtles and crocodiles) and some dinosaurs (for example sauropods and hadrosaurs). These shell microstructures, which express distinct reproductive behaviours have very diverse phylogenetic histories and do not seem to have developed major adaptative features due to the incubation conditions, except the number and the shape of pore canals (Table). The only other eggshell adaptation to the incubation constraints seem be the thinning of shell thickness. This feature greatly facilitates (despite stressful levels of CO2 and O2), the moisture loss necessary for development of the embryo. For megapode eggs, the shells are on average 30% thinner than those of other Galliforms (Booth & Thompson, 1991). It could possibly be the same for French titanosaurid eggs and generally for sauropod dinosaurs (Garcia *et al.*, 2006).

CONCLUSION

Eggshells of *Megapodius nicobariensis*, by their general morphology, microstructure (composed of 3 layers orderly in the same proportions) and thickness, are similar to the Galliforms. Their water conductance values, although overestimated by a classic theory, reflect the peculiar incubation strategy, which has been well studied by ornithologists from field observations. The megapodes, as other reptiles had developed a reproductive behaviour which could have appeared several times in the archosaurian evolutionary history, from crocodiles to modern birds. The oological observations show, except for the pore canals, that eggshell microstructure, reflects first phylogenetic features and does not seem to have developed major adaptative features due to the incubation conditions.

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PLATE 1

a. Smooth outer surface. Scale bar 1 cm = 27 µm.

b (x 200) and d (x 600). Eggshell ultrastructure of *Megapodius nicobariensis* showing an outer prismatic layer (PL), a spongy layer (SL), a mammillary layer (ML) and a well defined pore canal (Cn) straight and narrow.

c. Inner surface. Mammillae are closely spaced and appear cratered due to hatching and (or) weathering. Scale bar 1.9 cm = 50 µm.

PLATE 1