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SCANNING ELECTRON MICROSCOPY OF EARLY DINOSAUR EGG SHELL  
STRUCTURE: A COMPARISON WITH OTHER RIGID SAUROPSID EGGS

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Abstract

Fossil eggs attributable to dinosaur (probably prosauropod) parentage that have been recovered from the early Jurassic Elliot Formation sediments at the Rooibdraai locality possess shells that are similar to those of birds and crocodylians, and distinctly unlike those of chelonians and gekkonids. The preserved shell is very thin, and distinct mammillary processes are lacking, although the inner surface displays an undulating contour. The absence of these processes may be attributable to the inner portion of the shell having been at least partially decalcified during incubation and not preserved in the fossil state. The shells appear to be composed of broadly wedge-shaped, albeit ill-defined calcareous units, and they are similar to those of birds and other dinosaurs in the pattern of cleavage shown by the tabular calcite crystals of the palisade layer, and in the absence of the dominant horizontal lamellae that characterize crocodylian shells. The differential resemblance of these early Jurassic shells to the eggs of other closely related sauropsid taxa may be pertinent to questions concerning the evolution of egg shell structure within this clade.

KEY WORDS: Egg shell, structure, avian, dinosaur, crocodylian, sauropsid, gekkonid, squamate, chelonian, fossils

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Introduction

Representative members of each of the principal sauropsid clades (i.e., chelonians, squamates, crocodylians and avians) lay eggs that possess a rigid calcareous shell. The structural configuration of the egg shell differs among chelonians, squamates and the taxa comprising the crocodylian-avian clade, and the possible evolutionary significance of these differences has yet to be explored to any degree.

The evolutionary development of the cleidoic amniote egg is generally held to have been of major significance in tetrapod history, inasmuch as it may have contributed in large measure to the successful colonization of terrestrial habitats by vertebrates. This type of egg, which constitutes a nearly self-contained life support system for the developing embryo, quite possibly evolved under climatic conditions of alternate flooding and drought, where its structural configuration would have enhanced survivability by obviating the necessity of a discrete larval stage of development (Romer 1966). The embryos of tetrapod taxa that were enclosed in this evolutionarily novel type of egg would have had the ability to continue viable development under conditions in which the external aquatic environment was lost during periods of climatic desiccation. As such, the development of the cleidoic amniote egg may well represent a developmental preadaptation, or exaptation (Gould and Vrba 1982) that permitted the eventual inhabitation of wholly non-aquatic habitats by tetrapod taxa.

Amongst extant amniotes (Fig. 1), while the marsupial and placental mammals and many of the squamates have evolved ovovivipary or vivipary, the majority of clades have retained the primitive condition of laying eggs. In forms such as monotremes and in many squamates and some chelonians, the egg is pliable, with the outer calcareous

shell layer being composed of thin, loosely packed units (Packard and Packard 1979; Packard 1980; Packard et al. 1982b, 1982c; Hirsch 1983; Packard and Hirsch 1986). Alternatively, as in crocodylians and birds as well as some chelonians and squamates, the egg may be rigid, where the calcium carbonate of the outer shell layer is in the form of tightly packed aragonitic or calcitic crystals (Wilbur and Simkiss 1968; Erben 1970; Becking 1975; Watabe and Dunkelberger 1979; Ferguson 1982; Packard et al. 1984; Packard and Hirsch 1986).

As aptly noted by Hirsch and Packard (1987), the structure of pliable amniote eggs makes it unlikely that they would be able to withstand intact the processes involved in fossilization; thus, they would have little chance of being recognized in the geological record. On the other hand, rigid egg shells possess a much greater intrinsic potential for being preserved, and recognized, as fossils.

With regard to fossil egg shells, there have been several reports on specimens attributable to chelonians, crocodylians and birds (Buckman 1860; Hay 1908; van Straelen 1928; Heller 1931; Dughi and Sirugue 1959; Erben 1970; Sauer 1972, 1976; Erikson 1978; Hirsch 1983, 1985; Hirsch and Packard 1987). By contrast, considerable attention has been paid to eggs that have been attributed to dinosaurs (van Straelen 1925, 1928; Jepsen 1931; Granger 1936; Swinton 1950; Chow 1954; Young 1954, 1959, 1965; de Lapparent 1957; Dughi and Sirugue 1957, 1966; Schwarz et al. 1962; Jensen 1966, 1970; Sochava 1969, 1971; Erben 1970; Erben et al. 1979; Zeng and Zhang 1979; Zhao 1979; Horner 1982; Williams et al. 1984; Hirsch and Packard 1987). Egg shells referable to dinosaurian taxa have been recorded from sediments of late Jurassic to late Cretaceous age in Asia, Europe, eastern Africa and the Americas. Two eggs in association with an incomplete juvenile skeleton of a dinosaur have been reported from the late Triassic of Argentina (Bonaparte and Vince 1979), but these have yet to be described.

In the late 1970's, one of us (J.W.K.) recovered a 'clutch' of six fossil eggs from the Rooidraai locality in the Golden Gate Highlands National Park, northern Orange Free State (Fig. 2). The specimens, which are embedded in a block of sandy mudstone, derive from the Elliot Formation (Red Bed Stage) some 3 to 4 metres below the contact between this and the overlying Clarens Formation (Kitching 1979). The sediments of the Elliot Formation at this locality have yielded numerous specimens of the cynodont, *Tritylodon*,

together with the bones of a small thecodont, *Clarencea gracilis*, and the prosauropod dinosaur, *Massospondylus*. Based on these faunal associations, the egg shells can be accorded an early Jurassic age (Kermack 1982; Olsen and Galton 1984; Kitching and Raath 1984).

Three of the eggs preserve skeletal remains, including a partially exposed cranium. As noted by Kitching (1979), the morphology of the cranium is comparable to that possessed by dinosaurs. The eggs themselves, which measure on average some 65 mm by 55 mm (Kitching 1979), are too large to have been laid by *Clarencea*. Thus, there is considerable likelihood that these eggs are of dinosaur origin, and given the composition of the fauna preserved at Rooidraai, it is probable that these eggs are referable to the prosauropod, *Massospondylus*. Being of early Jurassic age, these specimens, together with those from Argentina that have been attributed also to a prosauropod, are among the oldest dinosaurian eggs yet recorded. Indeed, with Hirsch's (1979) dismissal of a reputed Permian egg, the Rooidraai specimens would appear to constitute one of the earliest undisputed occurrences of amniote eggs.

Despite their size, the preserved shells of the Rooidraai eggs are very thin. While initial estimates suggested that they were on the order of 0.5 mm thick (Kitching 1979), closer inspection has revealed that the shells have a preserved thickness of only some 0.2 mm to 0.3 mm. Moreover, whereas the gross external appearance of the eggs suggested that they may have been 'leathery' and pliable (Kitching 1979), microscopic examination has shown that the shells possess a manifestly rigid structure.

In an attempt to elucidate the structure shown by the Rooidraai egg shells, specimens of these together with representative rigid-shelled eggs of various extant sauropsids were examined by scanning electron microscopy (SEM).

#### Materials and Methods

In order to examine the structure of the Rooidraai eggs, several pieces of shell together with adhering matrix were cut from two of the specimens. These pieces were then cut into smaller blocks such that a total of thirteen specimens were available for SEM examination. Four of these preserved naturally fractured radial surfaces, and in another four the cut radial faces were polished with fine grade water paper. Two of the remaining pieces of shell were polished from the outer surface so as to produce a tangential face below the level of the external surface. Two

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of the naturally fractured and two of the polished radial faces, as well as one of the polished tangential surfaces were etched in 10% HCl for periods of between 20 and 60 seconds in an attempt to further accentuate any structural details. All specimens were thoroughly washed in distilled water, allowed to air dry and mounted on aluminium stubs with Glyptal cement. The specimens were then ringed with colloidal graphite and 'sputter' coated with  $25 \pm 5$  nm of a combination of 60% gold and 40% palladium.

The comparative sample comprised dried museum specimens of incubated and/or hatched eggs from three avian taxa, one squamate species, one chelonian species and one crocodilian species. The avian shells examined were from the domestic black australorps chicken (*Gallus domesticus*), the Japanese quail (*Coturnix coturnix*) and the ostrich (*Struthio camelus*). The chelonian eggs studied derived from the leopard tortoise (*Testudo (= Geochelone) pardalis*), and the rigid-shelled squamate eggs were those of the African gecko (*Hemidactylus mabouia*). The crocodilian eggs were represented by the Nile crocodile (*Crocodylus niloticus*). For each of these extant sauropsid taxa, shells from two eggs were examined.

Following the practice employed in the preparation of the Rooidraai shells, naturally fractured as well as cut and polished radial surfaces were produced. Several pieces of shell of each species were treated with 10% HCl for periods ranging from 3 to 10 seconds to remove calcified portions of the shell, whilst others were treated by boiling in 2.5% NaOH for up to 5 minutes in order to remove the internal shell membranes. Several specimens of each species were not subjected to either of these preparative regimens.

All comparative specimens were thoroughly washed in distilled water, allowed to air dry, mounted on aluminium stubs with colloidal graphite and 'sputter' coated with  $25 \pm 5$  nm of a combination of 60% gold and 40% palladium.

The fossil and recent shells were examined using either a Cambridge S-4 Stereoscan or an AMR 1400 scanning electron microscope at accelerating voltages of between 10 and 30 kV in the secondary electron mode.

Comparative Structure of Rigid-shelled Sauropsid Eggs

Avian egg shell structure

The structure of the egg shells of extant avian species has been rather extensively documented, especially by comparison with the amount of attention

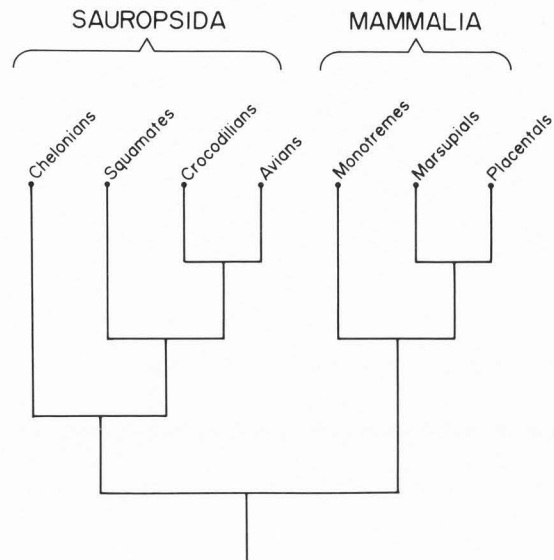


Fig. 1. Phylogenetic relationships of extant amniote clades.

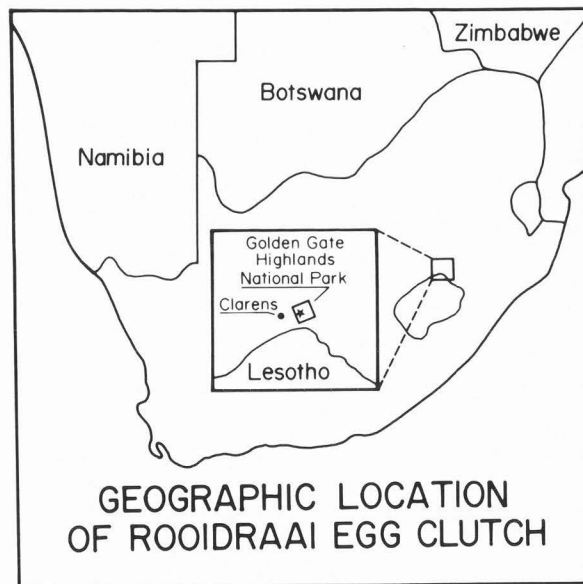


Fig. 2. Map of southern Africa showing geographic position of the Rooidraai locality (star).

that has been paid to the structural configurations exhibited by the egg shells of other amniotes. Because of the emphasis that has been placed on bird eggs, the terminology that is widely employed in the description of shell structure, however seemingly confused it may appear, has been developed (and modified) in large measure with reference to the avian egg.

The avian egg consists of two principal external layers: a membrane

layer that surrounds the albumen, and the calcified shell (Fig. 3). Immediately external to the chorioallantoic membrane are two fibrous layers: the fibers of the inner shell membrane are smaller in diameter than those of the outer shell membrane, and the inner membrane is commonly less than half the thickness of the outer (Bellairs and Boyde 1969; Becking 1975). The fibrous layers form concentric rings around the albumen as the fibers do not cross between layers.

The calcified part of the shell is commonly regarded as being divisible into two portions (Fig. 3). The inner portion, composed of the mammillary processes, is partially embedded in and attached to the most external fibers of the outer shell membrane (Figs 4 and 5). The mammillary processes have been referred to also as the cone layer or as basal cones, with the term basal cap having been applied to the part embedded in the shell membrane fibers (Schmidt 1962a, 1962b; Tyler 1964a; Erben 1970; Becking 1975).

Within each mammillary process, at a level adjacent to the outer shell membrane, is a small center of crystallization (the mammillary core) that has been shown to consist of organic matrix (Simkiss 1958). The crystals that grow outward from these cores initially form well-shaped (idiomorphic) structures comprising the mammillary processes. These crystals in the mature (i.e., laid) egg shell are calcite, as are those that form the outer shell thickness (Heyn 1963). Although Erben (1970) has indicated that the crystals of the avian mammillary processes are aragonitic, the existence of this polymorph of calcium carbonate has not been observed by other workers in any of the taxa examined by them (Sauer et al. 1975; Quintana and Sandoz 1978; Pooley 1979).

The outer portion of the shell, referred to here as the palisade layer (Fig. 3), forms approximately 65 to 70% of the shell thickness in diverse avian species (Becking 1975). This portion of the shell has been referred to also as the column or spongy layer (Tyler 1964a, 1969; Erben 1970; Watabe and Dunkelberger 1979). The transition from the mammillary processes to the palisade layer involves a gradual change in the pattern of calcite crystal packing. While Young (1950) and Dughi and Sirugue (1962) were of the opinion that the crystals of the palisade layer are not continuous with those of the mammillary processes, and that the outer portion of the shell must therefore be formed separately, Schmidt (1962a, 1962b), Tyler (1964a, 1969), Becking (1975) and Pooley (1979), amongst others, have

demonstrated that the palisade layer is structurally (i.e. crystallographically) continuous with the mammillary processes. Thus, the demarcation between these two portions of the calcified avian shell is not represented by a distinct boundary; rather, it involves a gradual alteration in crystal alignment.

External to the mammillary processes, the shell possesses an increasingly tabular arrangement of large crystals. While some of these tabular lamellae may run approximately parallel to the outer surface, others run at angles to these, especially in the outer portion of the palisade layer, resulting in what Schmidt (1964) termed the 'Fischgrätenmuster' (herring-bone pattern) zone. This structural configuration, as observed on naturally fractured surfaces (Fig. 6), is produced by the rhombic cleavage pattern of the calcite crystals (Heyn 1963; Schmidt 1964; Wilbur and Simkiss 1968; Becking 1975).

The outermost aspect of the palisade layer commonly consists of small crystals with their c axes orientated perpendicular to the external surface (Fig. 6). The alignment of these crystals, however, may vary across the surface of the shell (Tyler 1964a, 1969; Wilbur and Simkiss 1968; Becking 1975).

Comparative studies of the shells of diverse avian taxa have shown that they conform rather uniformly to the structure described above (Tyler 1964b, 1965, 1966; Becking 1975; Pooley 1979). Notwithstanding differences between some taxa in the composition of the covering cuticle and the presence in some (e.g. some Sphenisciformes) of a calcified matrix external to the cuticle, the basic structure of the shell between the outer shell membrane and the cuticle is similar in all birds examined to date. Apart from differences that may be attributable to egg size, such as the thickness of the outermost crystal layer, the shells of *Coturnix*, *Gallus* and *Struthio* examined here were found to possess the same structural arrangement (Fig. 7).

The principal differences encountered amongst the shells of extinct and extant avian species relates to the configuration of the respiratory pores. This, however, may be related also to shell size and thickness. In smaller eggs the pores consist of single, narrow canals, whilst in the larger eggs the pores exhibit dendritic and reticulate branching as they pass from the inner to the outer surface (Tyler and Simkiss 1959; Tyler 1964b, 1965, 1966; Becking 1975; Board et al. 1977).

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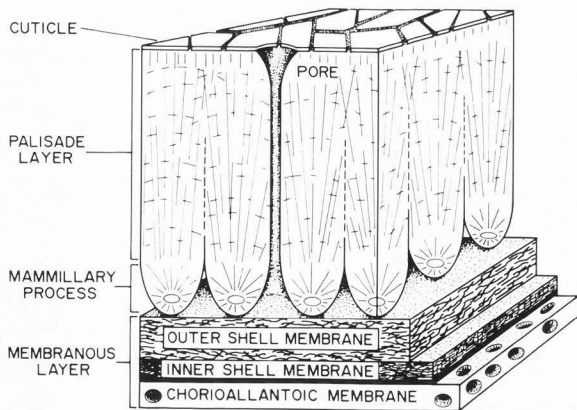


Fig. 3. Schematic diagram of a generalized avian egg showing the principal constituents of the shell.

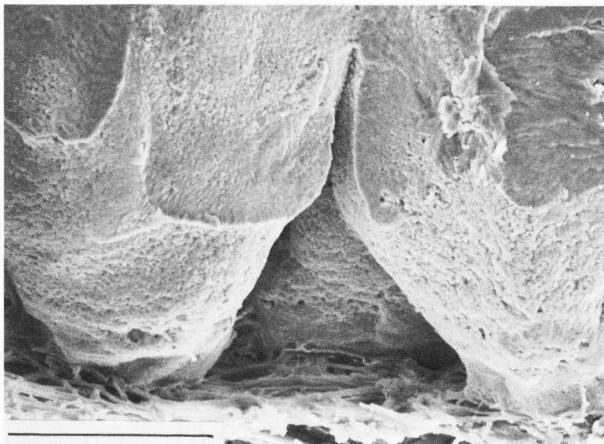


Fig. 4. Relationship of the mammillary processes to the fibers of the outer shell membrane in *Gallus domesticus*. Bar = 50  $\mu$ m.

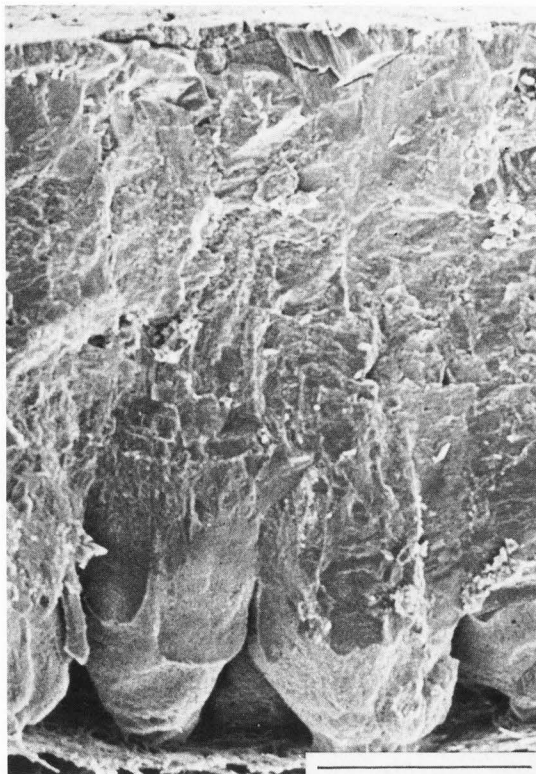


Fig. 6. Naturally fractured radial section of *Gallus domesticus* egg shell. Bar = 100  $\mu$ m.

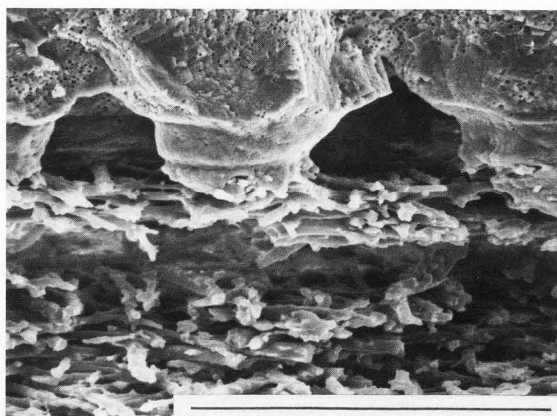
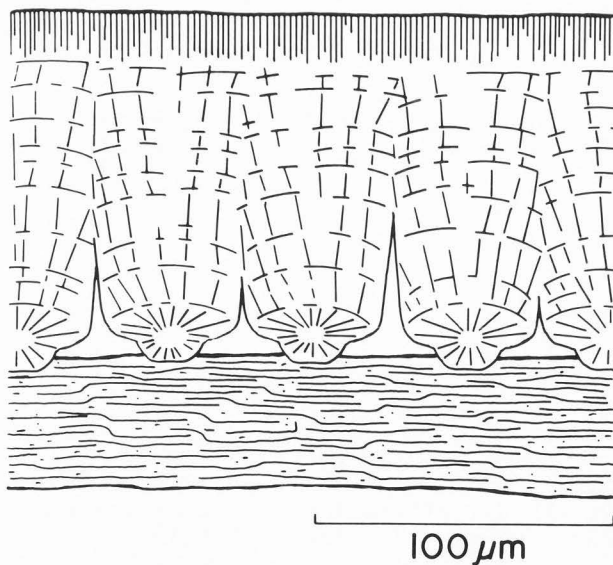


Fig. 5. Relationship of the mammillary processes to the fibers of the outer shell membrane in *Coturnix coturnix*. The basal cap is clearly delineated. Note the numerous vesicles (gas inclusions) in the lower part of the palisade layer. Bar = 50  $\mu$ m.



*Coturnix coturnix*

Fig. 7. Diagrammatic representation of a radial section through an avian egg shell.

Cretaceous dinosaur egg shell structure

As noted above, amongst sauropsids, the eggs of dinosaurs - or, at least those attributed to dinosaurs - have received perhaps the greatest attention next to those of their closest relatives, the birds. Apart from reports of 'pathological' or aberrant shells (e.g. van Straelen 1925; Erben et al. 1979), studies of Cretaceous dinosaur eggs have shown them to be essentially similar in form to those of birds (van Straelen 1928; Dughi and Sirugue 1957; Schwarz et al. 1962; Sochava 1969; Erben 1969, 1970). That is, they possess well-developed mammillary processes, the palisade layer is basically columnar in form, and the tabular structure of the calcite crystals of the palisade layer conforms to the pattern displayed by avian shells. The essential similarity of dinosaur and avian egg shell structure is perhaps noteworthy in respect to recent arguments over the closeness of the phylogenetic relationship between these sauropsid groups.

Although studies by different workers (e.g., Dughi and Sirugue 1966; Sochava 1969, 1971; Erben et al. 1979; Williams et al. 1984) have resulted in the recognition of various 'types' of Cretaceous shells, many of the differences appear to be related primarily to the configuration of the respiratory pores and the sculpture of the external surface. Whilst differences in the microstructure of various Cretaceous egg shells have been noted in these studies, it has not been demonstrated conclusively that those shells that evince a non-avian structure are, indeed, dinosaurian.

Crocodylian egg shell structure

Dinosaurs aside, there is general agreement amongst zoologists that crocodylians represent the closest living relative of birds (Walker 1972). Crocodylian shells have been described by Schmidt and Schoenwetter (1943) and by Hirsch (1985) using polarizing light microscopy, and by Erben (1970), Erben and Newseley (1972), Ferguson (1981, 1982) and Hirsch (1985) with scanning electron microscopy.

Erben (1970) reported that mammillary processes are lacking in the shells of crocodylians (e.g., Crocodylus cataphractus and Melanosuchus niger), where the shells are composed entirely of tabular aggregates of calcite crystals, while Hirsch (1985) has argued that apart from the presence of 'basal knobs' by which the shell is attached to the membrane layer, the entire shell thickness in crocodylians (referred to as the 'wedge layer' by him) corresponds to the mammillary processes of the avian shell. These findings and suggested

homologies, however, are not supported by the results of Ferguson's (1982) examination of Alligator mississippiensis eggs. Nor are they supported by the results of the present investigation of Crocodylus niloticus shell structure.

In both A. mississippiensis and C. niloticus the innermost portion of the shell consists of mammillary processes that are tightly packed (Figs. 8 and 9), although these processes may be less pronounced at the non-opaque ends of crocodylian eggs (Ferguson 1982). The crystals of the mammillary processes radiate outwards from a basal core (Figs. 9 and 10). Rather than continue vertically through the palisade layer as in avian shells, however, the crystals arising from the mammillary core become gradually extinguished by tabular crystal lamellae (Fig. 10). The palisade layer, then, is composed almost entirely of tabular aggregates with the lamellae running parallel to the outer surface (Fig. 11). The horizontal stacking of these crystal lamellae is notably more marked in crocodylian than in avian shells, with the result that, compared to the shells of birds, it is extremely difficult to identify individual shells units in crocodylian eggs (Ferguson 1982).

In his analysis of Alligator mississippiensis eggs, Ferguson (1982) reported the presence of an organic layer between the mammillary processes and the palisade layer, and he equated this to the crystal discontinuity that has been suggested to exist in avian shells (see above). It was suggested by him that the crystal discontinuity in these shells is responsible for the observed tendency for the mammillary processes to cleave from the palisade layer when the shell is fractured. However, just as this purported discontinuity has been shown to be non-existent in avian shells, so, too, in crocodylian shells do the crystals of the mammillary processes appear to be continuous with some of those of the palisade layer. The observed tendency for shells to cleave between the palisade and mammillary layers may be related to the zone where the crystals undergo a change in orientation from the radial configuration of the mammillary processes to the more horizontal packing of the palisade layer.

As in avian shells, the outermost portion of crocodylian shells is composed of crystals with their c axes orientated perpendicular to the outer surface. Ferguson (1982) reported this outer layer to attain a thickness of between 100 and 200  $\mu\text{m}$  in Alligator mississippiensis; it was observed to be some 20 to 50  $\mu\text{m}$  thick in the Crocodylus

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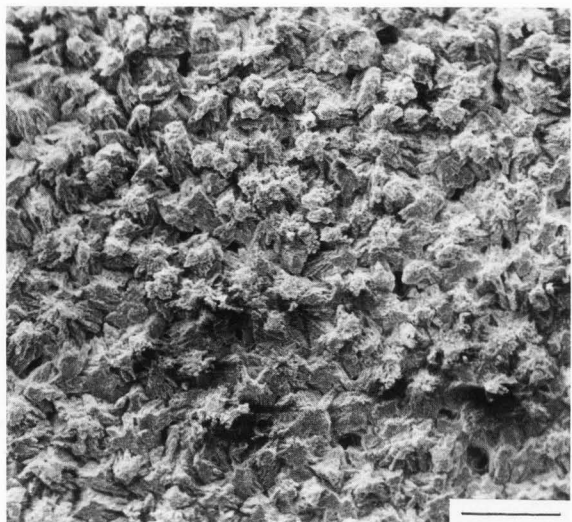


Fig. 8. Internal surface of Crocodylus niloticus egg shell showing the dense packing of the mammillary processes. Membranous layer removed by NaOH. Bar = 50  $\mu$ m.

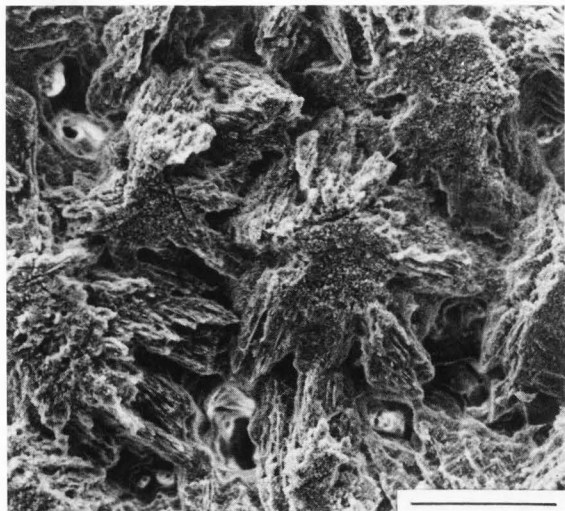


Fig. 9. Internal surface of Crocodylus niloticus egg shell showing surface crystal configuration of the mammillary processes. Bar = 100  $\mu$ m.

niloticus shells examined in the present study. This same layer has been reported to range between 1 and 20  $\mu$ m in avian shells (Tyler 1964b, 1965, 1966, 1969; Becking 1975).

One apparently unique feature of crocodilian egg shells pertains to the development of extrinsic erosion craters with characteristically stepped concentric rings on the outer surface. This phenomenon was first reported for the eggs of Alligator mississippiensis (Ferguson 1981), and they were observed also on the Crocodylus niloticus shells

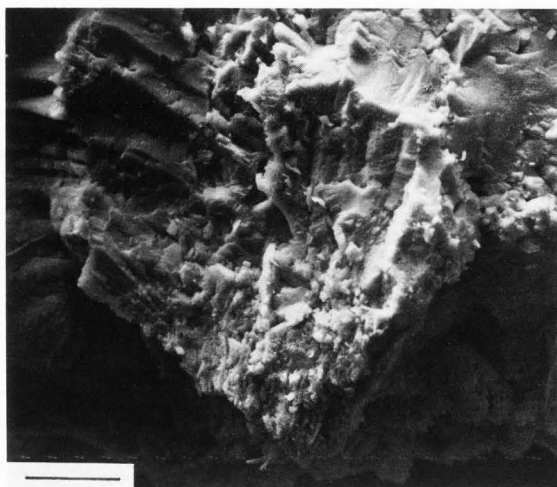


Fig. 10. Natural radial fracture through the mammillary process of Crocodylus niloticus egg shell. Bar = 50  $\mu$ m.

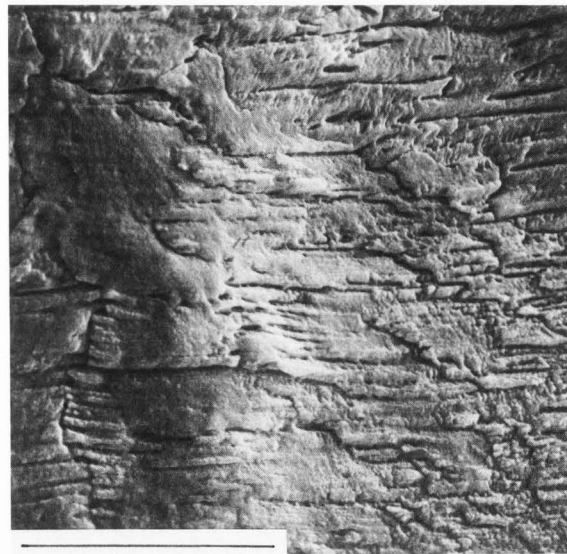


Fig. 11. Radial section through the palisade layer of Crocodylus niloticus egg shell showing the distinctive lamellate stacking of calcite crystals. Outer surface above. Bar = 50  $\mu$ m.

examined here (Fig. 12).

Thus, the crocodilian egg shell (Fig. 13) is comparable in its general configuration to that of the avian shell (Fig. 7), insofar as both possess the same structural components. That is, in both, the shell consists of mammillary processes in which the calcite crystals radiate outward from a central core, a palisade layer in which the radial structure of the mammillary processes is lost, and an outermost zone in which the crystals tend to be orientated perpendicular to the external surface.



Crocodylian shells differ from their avian counterparts, however, in that the crystals arising from the mammillary cores become extinguished by tabular crystal lamellae that run parallel to the outer surface. The lamellar configuration evinced by crocodylian shells is much better developed than in avian shells, with the result that it is extremely difficult to identify individual shell units. Crocodylian shells also appear to be unique in the development of external erosion craters with characteristically stepped concentric rings.

#### Squamate egg shell structure

Amongst the numerous extant squamates, only the geckos have been observed to lay rigid-shelled eggs. Gecko eggs (e.g. those of *Gekko* and *Hemidactylus*) are structurally very distinct from those of crocodylian, avian and dinosaurian taxa. Like the eggs of these other sauropsids, gecko shells are composed of calcite (Erben and Newesely 1972; Krampitz et al. 1972; Packard et al. 1982a). Gekkonid shells, however, consist of jagged crystal columns apparently without mammillary processes (Fig. 14).

In juxtaposition to the outermost fibers of the membranous layer, the calcified shell consists of small crystals that are orientated perpendicular to the inner surface. The vertical crystal arrangement exhibited by the inner portion of the shell is gradually masked by a lamellar configuration, such that the columnar structure becomes progressively less evident towards the external surface of the shell. Examination of radially fractured surfaces of both etched and unetched specimens (Fig. 14) suggests that the outer two-fifths of the shell may be less densely calcified than the inner three-fifths.

While the structure of the gecko egg shell bears a superficial resemblance to the pliable eggs of some other squamates (e.g., *Sphenodon*) (Packard et al. 1982b), it is readily distinguishable from the rigid shells of crocodylians and avians. The entire thickness of the gekkonid shell (Fig. 15) appears to be composed of what would be referred to as the palisade layer in crocodylian and avian eggs, inasmuch as the mammillary processes that comprise the initial calcific stage in the latter appear to be lacking.

#### Chelonian egg shell structure

While the calcareous shell of all other oviposited sauropsid eggs occurs in the form of calcite, extant chelonian eggs are made up of aragonite (Watabe and Dunkelberger 1979; Packard et al. 1982a, 1984; Hirsch 1983). Although the presence of calcite has been observed in

the shells of farm-reared *Chelydra mydas* (Baird and Solomon 1979), this has not been recorded in wild populations of any of the chelonian taxa examined. Moreover, whilst the meta-stable aragonite of chelonian shells may be converted to calcite through the diagenetic processes of fossilization (Hall and Kennedy 1967), Hirsch (1983) has demonstrated that completely altered fossil specimens of chelonian shell can be readily distinguished from other sauropsid shells because of their unique structural configuration.

The rigid chelonian egg shell is formed of spherulitic, or radial aggregates of needle-like crystals of aragonite that radiate outward from central cores (Young 1950; Erben 1970; Erben and Newesely 1972; Watabe and Dunkelberger 1979; Hirsch 1983; Packard et al. 1984) (Fig. 16). The cores are located slightly above the level of the outermost fibers of the membranous layer, and the crystals that grow downward from the cores form small basal caps that serve to bind the shell to the membranous layer (Packard 1980; Packard et al. 1984). The crystals that radiate outward from the cores form spherulitic units that comprise the entire thickness of the shell (Fig. 16).

In tangential section, the crystals of each unit display incremental lines as they pass from the core (Fig. 17), and where the crystals of adjacent units meet they form distinct boundaries (Figs. 17 and 18). Thus, the crystals of any one unit do not encroach upon the structural integrity of contiguous units.

The structure of the rigid chelonian egg shell (Fig. 19) is quite distinctive, and readily distinguishable from that shown by other rigid sauropsid eggs (cf. Figs. 7, 13 and 15). The calcareous portion of the chelonian shell appears to be made up entirely of what would be referred to as the mammillary layer in crocodylian and avian eggs.

#### Structure of the Rooidraai Egg Shells

The external surfaces of the Rooidraai shells are reasonably well-preserved, although each shows some degree of degradation that is probably attributable to postdepositional weathering (Fig. 20). Patent respiratory pores are visible on the external surfaces of the shells and, in the two specimens measured, they are spaced, on average, some 0.45 mm to 0.50 mm apart. The Rooidraai shells present no evidence of the erosion craters displayed by incubated crocodylian eggs.

Radial sections of the preserved shells reveal them to be very thin

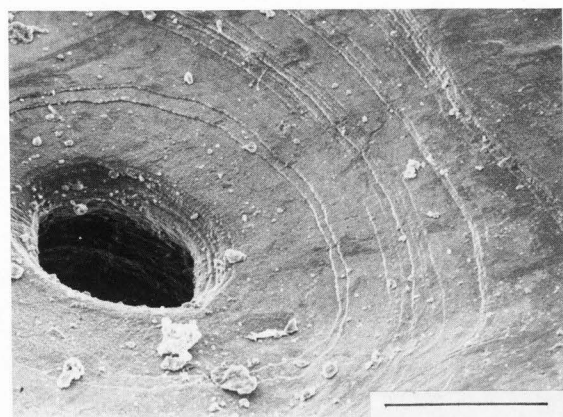
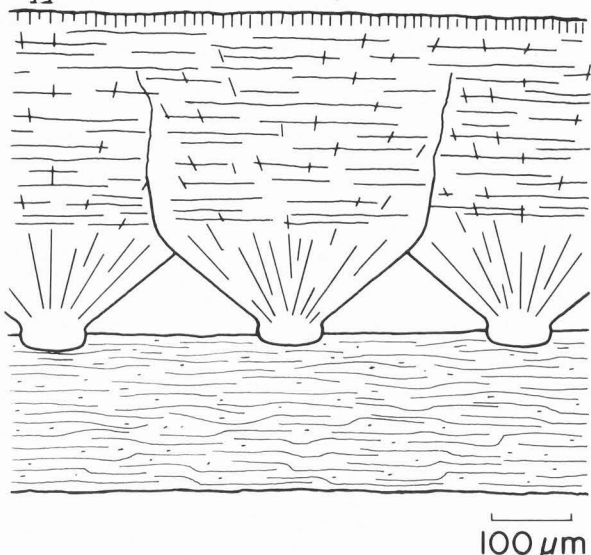


Fig. 12. Extrinsic erosion crater development around the mouth of a respiratory pore on *Crocodylus niloticus* egg shell. Bar = 100  $\mu$ m.



*Crocodylus niloticus*

Fig. 13. Diagrammatic representation of a radial section through a crocodilian egg shell.

(circa 0.2 mm to 0.3 mm) in relation to their overall size (some 65 mm by 55 mm (Kitching 1979)). Examination of radial sections revealed an apparent absence of distinct, well-formed mammillary processes (Fig. 21), although the inner surface follows an undulating contour. The apparent absence of these processes, and the relatively thin nature of the shell may be attributable to the inner portion of the shell having been at least partially decalcified during the incubation of the eggs.

The calcite crystals that comprise the shells are arranged in broadly wedge-shaped units, and they display a

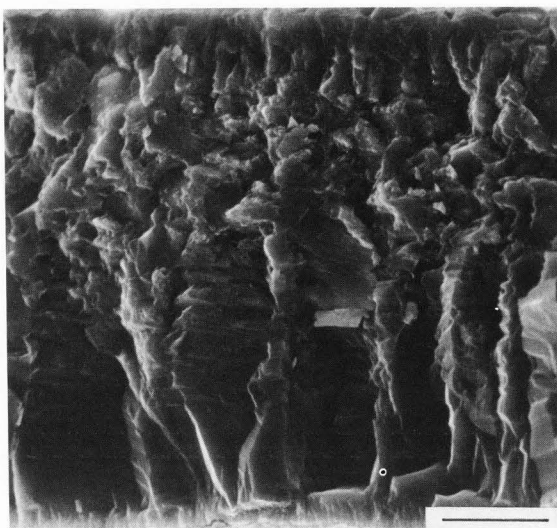
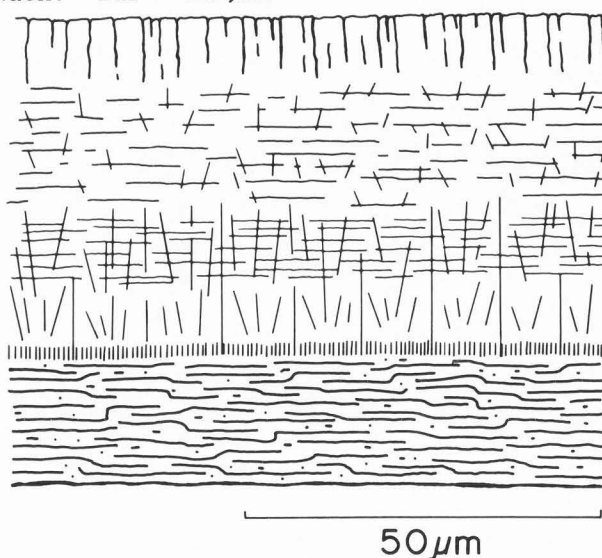


Fig. 14. Naturally fractured radial section of *Hemidactylus mabouia* egg shell. Membranous layer removed by NaOH. Bar = 10  $\mu$ m.



*Hemidactylus mabouia*

Fig. 15. Diagrammatic representation of a radial section through a gekkonid squamate egg shell.

tabular rather than a spherulitic configuration (Figs. 21 and 22). The bulk of what is judged to be the palisade layer shows a roughly lamellate crystal packing arrangement, with the cleavage patterns of the crystals resulting in what appears to be equivalent to the 'herring-bone pattern' described by Schmidt (1964) for avian eggs.

Etched tangential sections of the Roodraai shells reveal irregularly shaped aggregates of crystals (Fig. 23),

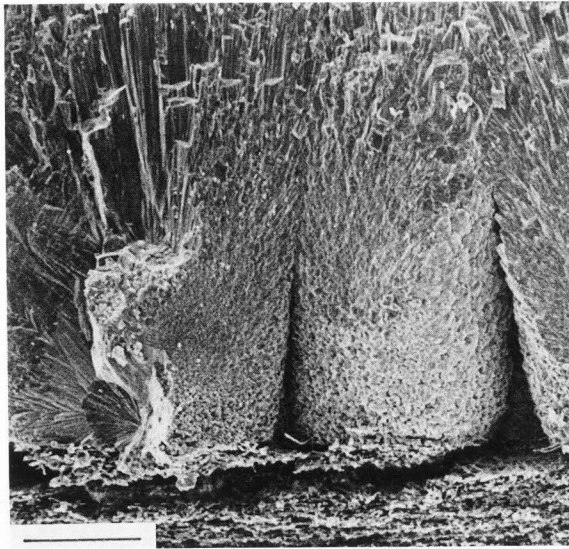


Fig. 16. Naturally fractured radial section of *Testudo pardalis* egg shell. Bar = 100  $\mu\text{m}$ .

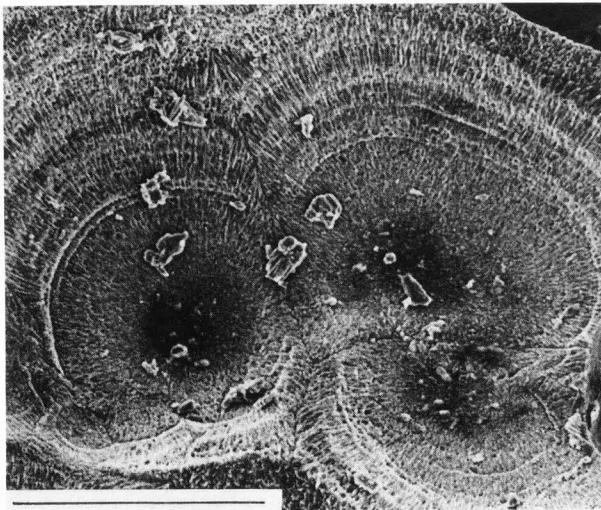


Fig. 17. Etched tangential section of *Testudo pardalis* egg shell showing relationships of individual shell units. Note depth of section from fibers of membranous layer visible on right. Bar = 50  $\mu\text{m}$ .

that bear a superficial resemblance to the individual crystal 'prisma' observed by Schmidt (1962a) in avian eggs. These aggregates, however, are extremely irregular in outline compared to those found in avian shells. (We assume that the HCl used as an etchant on the Rooidraai specimens has accentuated the 'natural' boundaries between contiguous units, although it is possible that these boundaries are merely artefacts of the etching regimen.)

The outer portion of the shell

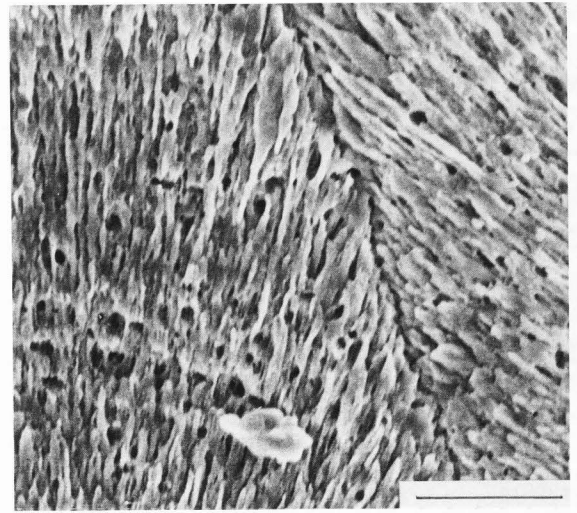
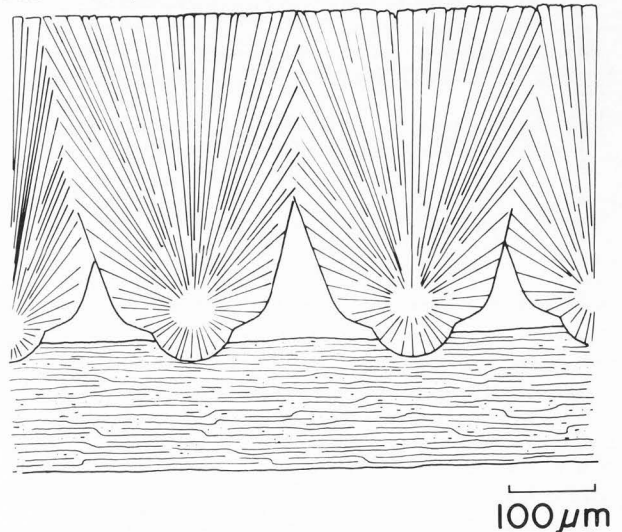


Fig. 18. Enlargement of tangential etched section of *Testudo pardalis* egg shell showing boundary between aragonite crystals of two contiguous shell units. Bar = 10  $\mu\text{m}$ .



### *Testudo pardalis*

Fig. 19. Diagrammatic representation of a radial section through a chelonian egg shell.

possesses a thin (circa 10 to 20  $\mu\text{m}$ ) layer of crystals that are orientated perpendicular to the external surface. In this respect, the Rooidraai shells are similar to those of both avians and crocodylians.

The overall structure preserved by these early Jurassic egg shells (Fig. 24) is notably dissimilar to that which characterizes both chelonian and squamate eggs (cf. Figs. 15 and 19). At the same time, the Rooidraai shells are structurally similar to those of

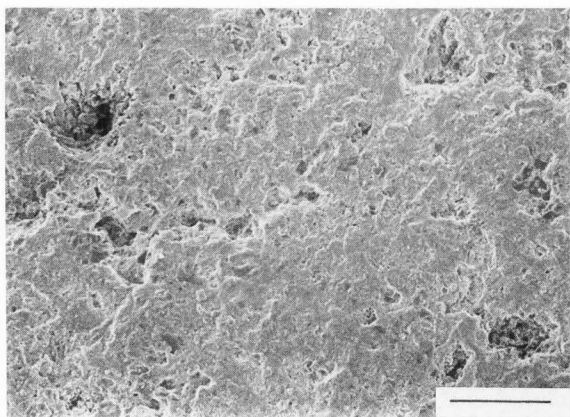


Fig. 20. External surface morphology preserved by the Rooidraai egg shells. Respiratory pore mouth visible in upper left corner. Bar = 100  $\mu$ m.

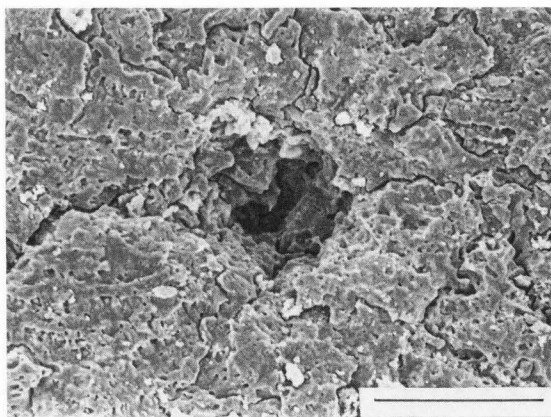


Fig. 23. Polished and etched tangential section of Rooidraai egg shell showing the irregularly shaped crystal aggregates surrounding a respiratory pore. Bar = 50  $\mu$ m.

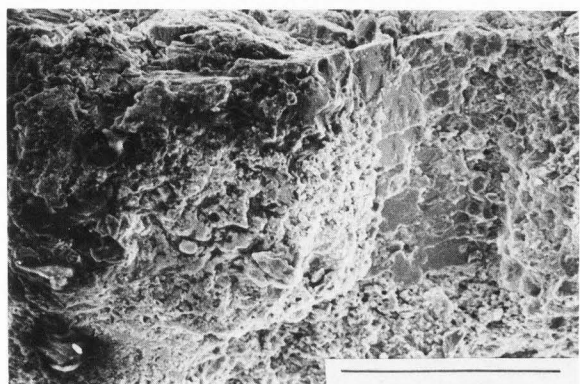


Fig. 21. Naturally fractured radial section through the preserved Rooidraai egg shell. Bar = 100  $\mu$ m.

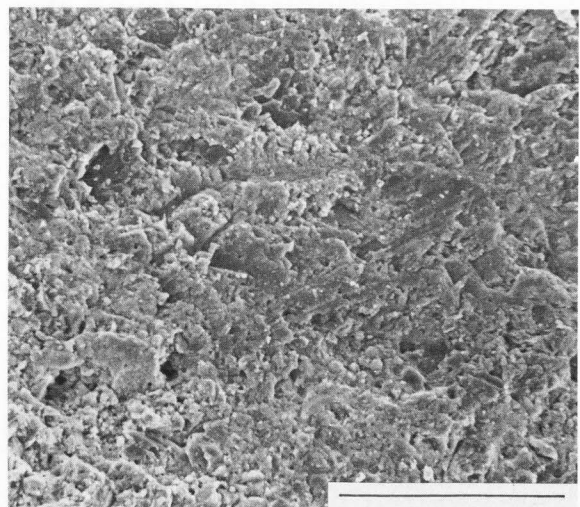
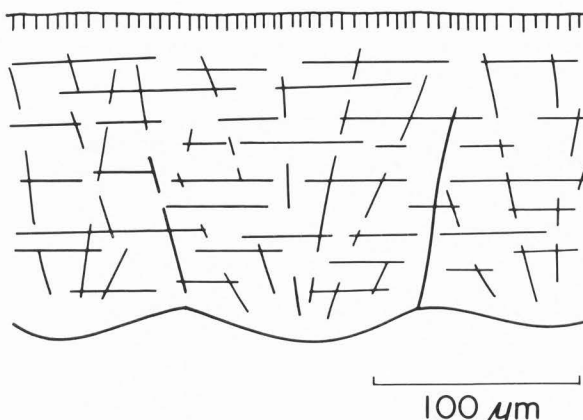


Fig. 22. Tabular calcite crystal arrangement shown by cut, etched radial surface of Rooidraai egg shell. External surface of shell above. Bar = 50  $\mu$ m.



### Elliot Formation Rooidraai Shell Clutch

Fig. 24. Diagrammatic representation of a radial section through the shell preserved by the Rooidraai eggs.

crocodilians and birds (cf. Figs. 7 and 13). Insofar as they resemble avian shells, the Rooidraai eggs are structurally comparable also to those of Cretaceous dinosaurs.

In that the Rooidraai shells appear to be composed of broadly wedge-shaped and ill-defined units, they are seemingly more similar to crocodilian than to avian eggs. At the same time, however, the Rooidraai shells differ from those of crocodilians and resemble those of avians in that they lack the distinct horizontal lamellar configuration that characterizes the

palisade layer in the former. In this respect, and in the apparent 'herring-bone pattern' displayed by the orientationally dictated cleavage of the calcite crystals, the Rooidraai shells resemble those of birds and dinosaurs.

#### Summary and Conclusions

Amongst extant sauropsids, avians and crocodylians, as well as some chelonians and squamates lay eggs that possess a rigid calcareous shell. The structure of the shells differs between these various sauropsid groups in such a way that the eggs of chelonians and squamates can be readily distinguished from those of crocodylians and birds.

In chelonians, as exemplified here by Testudo (= Geochelone) pardalis, the calcareous shell is composed of spherulitic, or radial aggregates of needle-like aragonite crystals that splay outward from central cores. The crystals of each shell unit (i.e. those that are related to a single core) do not impinge upon the structural integrity of contiguous units. Each of these shell units appears to be homologous with the mammillary process that forms the innermost portion of the shell in crocodylians and avians (Erben 1970).

In Hemidactylus mabouia, as in other gekkonids, the calcareous egg shell is made up of primarily columnar units, the innermost crystals of which are aligned perpendicular to the internal surface of the shell. In these specimens, the internal vertical arrangement of the crystals is gradually masked by a lamellar configuration, such that the basic columnar structure becomes less evident towards the outer aspect of the shell. Gekkonin egg shells, though composed of calcite, differ substantially from those of avians and crocodylians not only in their vertically columnar structure, but also in their apparent lack of distinct mammillary processes.

The shells of crocodylian and avian eggs are structurally similar to one another, especially in comparison to the shells of chelonians and squamates, although they differ in several respects. In crocodylians (e.g., Crocodylus niloticus) and birds (e.g., Coturnix coturnix, Gallus domesticus and Struthio camelus) the inner portion of the calcareous shell is composed of distinct mammillary processes, whilst the bulk of the shell thickness is comprised of the palisade layer. The calcite crystals that grow outward from the mammillary cores initially form well-shaped (idiomorphic) structures, with a gradual alteration in crystal alignment in the palisade layer. While

the palisade layer is structurally continuous with the mammillary processes in both crocodylians and avians, in the former the crystals of the palisade layer form distinct tabular lamellae that are orientated parallel to the outer surface of the shell. In radial section, crocodylian shells appear to be made up of broadly wedge-shaped and extremely ill-defined primary units. In avian eggs some of the crystals of the palisade layer are outwardly continuous with those of the mammillary processes, the lamellar configuration being less well defined than in crocodylians. Whereas some of the crystals are approximately parallel to the outer surface in avian shells, others run at angles to them, resulting in the 'herring-bone' crystal cleavage pattern of the basically columnar shell units.

Numerous fossil eggs of Cretaceous age have been attributed to dinosaurs. While not all of the specimens that have been described as such are necessarily referable to dinosaurs, those whose dinosaurian attribution is reasonably well established possess shells that are structurally very similar to the shells of birds.

The structure of the early Jurassic Rooidraai egg shells, as revealed by scanning electron microscopy, is distinctly unlike that shown by the shells of chelonians and squamates. The Rooidraai shells are, on the other hand, structurally comparable to those of crocodylians, birds and other dinosaurs, save for the fact that mammillary processes are not preserved by the Rooidraai specimens.

The Rooidraai shells are relatively very thin (circa 0.2 mm to 0.3 mm) compared to their overall size (circa 65 mm by 55 mm), and this is likely to be related to the absence of discernible mammillary processes. The absence of these processes may be attributable to the inner portion of the shell having been at least partially decalcified during incubation and not preserved in the fossil state. The shells resemble those of crocodylians in that they appear to be composed of ill-defined, broadly wedge-shaped calcareous units. At the same time, however, the calcite crystals comprising the Rooidraai shells do not form the distinct, horizontal lamellae that characterize crocodylian shells. Rather, the tabular crystals reveal a 'herring-bone' pattern of orientationally dictated cleavage, as is shown in the palisade layers of avian and dinosaur eggs.

Thus, while the Rooidraai eggs resemble those of crocodylians in some respects, they are similar to those of avian (and later dinosaurian) taxa in others. The structural similarity of the

## EARLY DINOSAUR EGG SHELL STRUCTURE

Rooidraai egg shells to those of crocodylians, birds and other dinosaurs is perhaps not unexpected in light of their taxonomic attribution. The differential resemblance of the Rooidraai eggs to those of these other closely related sauropsid groups may be pertinent to questions concerning the evolution of egg shell structure within this clade.

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Discussion with Reviewers

**A. Boyde:** To what extent can the (SEM) examination of a fractured, a polished or an etched egg shell be used to diagnose the origin of the shell? For example, can you expect a cladistic diagram showing decisions to be made at each branching point?  
**Authors:** While other techniques, such as the use of polarized light microscopy might have been employed by us, the



methods that were utilized have been so used by other workers in the field, and the results that we present suggest very strongly that observations on structure using these techniques can be used to diagnose the origin of the shell, albeit at a rather 'gross' taxonomic level. Thus, the methods that we used are capable of distinguishing between shells of chelonian, squamate, avian and crocodilian origin. At this point in time, it is very difficult to construct a cladogram that depicts the evolutionary transformation of rigid sauropsid shell structure because of the problems of establishing structural homology. We suspect, as have others, that the chelonian shell represents the primitive morphotype, inasmuch as it appears to be composed entirely of a mammillary process-like structure. But, further work aimed at the problem of developmental and structural homology will have to be undertaken in order to clarify this issue.

A. Boyde: You have not treated any high resolution features. Could these be useful in distinguishing shell types and origins?

Authors: Such features might well prove to be useful in distinguishing amongst shell types, and we hope to be able to pursue this type of investigation in the future.

R.L. Hughes: How important is the failure to demonstrate mammillary bodies in the Rooidraai egg shells to accepting your proposition that this material is structurally comparable to that of crocodilians, birds and other dinosaurs? Also, can a convincing case be made for the possible geological erosion of the mammillary bodies of the Rooidraai egg shells?

Authors: Our examination of the fossil shells leads us to conclude that their lack of mammillary processes is likely due to their having been decalcified and lost during the incubation of the dinosaur embryos. We do not suggest that these processes were lost through geological erosion, and nor do we believe that this would be likely. Apart from their 'apparent' lack of mammillary processes, the Rooidraai shells are structurally very similar to those of birds and Cretaceous dinosaurs, thus we do not feel that because the mammillary processes themselves cannot be identified that this detracts from our conclusions.

K.F. Hirsch: People working on eggshell structure should try to establish a common nomenclature to avoid misunderstandings. An example is the crocodilian eggshell. Neither Erben (1972) nor myself (1985) found central cores but named the mammillary processes or mammillae, since they looked different,

the basal plate group. It is the same feature with a different name.

Authors: We fully agree that a stable descriptive nomenclature is something that should be established. We do not understand, however, why it is necessary to apply different names to the same feature, as Erben and yourself have done with regard to the mammillary processes of crocodilian shells. This makes for unwarranted confusion, especially since you argued in 1985 that the entire shell thickness in crocodilians (the "wedge layer") is homologous with the mammillary process of the avian shell, but you now seem to be implying that you now consider the so-called "basal plate" to be homologous with the mammillary process.