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SCANNING ELECTRON MICROSCOPY OF EGGSHELLS OF CONTEMPORARY REPTILES

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Abstract

Eggshells of contemporary turtles and squamate reptiles (lizards, snakes, and the tuatara) are either flexible or rigid, and usually are composed of both a fibrous shell membrane and an overlying calcareous layer. The calcareous layer of turtle eggs is calcium carbonate in the form of aragonite, whereas the crystalline material of squamate eggs generally is calcite. Both rigid and flexible shells of turtle eggs are composed of individual building blocks or shell units. Shell units of rigid shells abut tightly, and few pores penetrate the calcareous layer. In contrast, flexible shells exhibit large numbers of spaces or pores in the crystalline material. Rigid eggshells of squamates are characterized by interlocking columns of calcareous material that yield a compact, non-compliant matrix. Pores are presumed to penetrate the crystalline layer but have yet to be described in such eggshells. Flexible-shelled eggs laid by squamates exhibit the greatest variability in gross morphology of all reptilian eggs examined to date. The crystalline layer may occur as a thin, relatively unstructured crust overlying the shell membrane or may exhibit protrusions or nodes of variable morphology. In some cases, the crystalline material exists as widely dispersed aggregates separated by uncalcified areas. Pores as distinct structural entities similar to the pores of turtle eggshells do not occur, but holes and pore-like structures, as well as cracks and fissures, presumably provide for transport of gases and water between eggs and their environment.

KEY WORDS: reptilian, eggs, eggshells, morphology, ultrastructure, turtle, lizard, snake, squamate, testudinian

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Introduction

Eggshells from contemporary reptiles can be categorized in the broadest terms as either flexible or rigid. This description provides a convenient and easy means of classifying reptilian eggs, but obscures an incredible diversity in morphology and structure of eggshells. Our objective here is to provide an overview of morphology and ultrastructure of eggshells of contemporary reptiles, pointing out common themes as they exist but emphasizing diversity over similarity. We will focus on eggs of testudinians (turtles) and squamates (lizards, snakes and the tuatara) and refer readers to Ferguson (1982, 1985) for reviews of structure of shells of crocodilian eggs. More space will be devoted to squamate eggshells because more than 95 percent of the 6000 species of living reptiles belong to the Order Squamata and it is within this group that we encounter the broadest range of structural diversity of eggshells and the greatest difficulty in making generalizations.

Shells of eggs of most reptiles consist of a multi-layered, fibrous shell membrane overlain by some sort of crystalline material. The crystalline material may occur as a relatively thick layer organized into columns that penetrate the shell membrane, as a thin crust covering the membrane, or as isolated aggregates dispersed over the membrane (Packard et al., 1982c). Although occurrence of both a fibrous and a crystalline layer is the norm, eggshells of some squamates may lack a crystalline layer altogether (Packard et al., 1982c). Unfortunately, results of many studies are incomplete because authors did not address directly the question of presence or absence of a surface crystalline layer or the techniques used were inadequate to demonstrate the presence of such a layer (Allison and Greer, 1986; Andrews and Sexton, 1981; Cuellar, 1979; Guillette and Jones, 1985; Sexton et al., 1979; Trauth and Fagerberg, 1984).

The crystalline material of squamate eggs generally is calcium carbonate in the form of calcite whereas that of testudinian eggs is aragonite (Erben, 1970; Ferguson, 1982, 1985; Packard et al., 1982c; Solomon and Baird, 1976; Young, 1950). However, eggshells of pythons may be entirely aragonitic or comprised of calcite with traces of aragonite (Solomon and Reid, 1983), and eggshells from farm-reared sea turtles contain areas of both calcite and aragonite (Baird and Solomon, 1979). The profound differences in structure of eggshells of captive and wild sea turtles raises the possibility that some of the variability in the crystal morph of python eggshells stems from the fact that the eggs were obtained from zoo animals (Solomon and Reid, 1983).

Structure of Testudinian Eggshells

Eggs of carettochelids, chelids, dermatemydids, kinosternids, testudinids, and trionychids are characterized by rigid shells whereas those of cheloniids, chelydrids, and dermochelyids have flexible shells. Pelomedusids and emydids produce eggs with both kinds of shells (see Ewert 1979, 1985; Packard et al., 1982c).

The calcareous layer of rigid eggshells is composed of closely apposed shell units of aragonitic crystallites radiating outward from a common center (Figs. 1-4; Erben and Newesely, 1972; Ewert, 1985; Ewert et al., 1984; Hirsch, 1983; Kriesten, 1975; Krampitz et al., 1972; Packard and Packard, 1979; Packard et al., 1982c, 1984a, b; Silyn-Roberts and Sharp, 1985; Woodall, 1984; Young, 1950). In some species, the outlines of individual shell units are readily apparent in surface view whereas in others sculpturing of the outer surface obscures the identity of shell units (Figs. 1, 2). Pores through the crystalline layer provide for the movement of gases and water between the egg and its environment. The crystalline layer is bounded at its inner aspect by a fibrous, multilayered shell membrane that comprises only a small fraction of total shell thickness (Figs. 3, 4). Shell units of rigid eggshells tend to be taller than they are wide (Figs. 3, 4). During shell formation, individual shell units grow into the shell membrane for a short distance, as well as away from the membrane, thereby providing for a firm attachment between the calcareous layer and the membrane (Fig. 3; Packard et al., 1984a).

Flexible-shelled eggs are similar in gross detail to rigid-shelled eggs in that these shells also are composed of individual shell units (Figs. 5, 6; Hirsch, 1983; Packard, 1980; Packard et al., 1982c; Solomon and Reid, 1983; Young, 1950). However, shell units of flexible eggs abut one another loosely, if at all, yielding a relatively open crystalline layer with numerous spaces or pores (Figs. 5, 6). However, pores of flexible-shelled eggs are less structured than those of rigid-shelled eggs (cf. Figs. 1, 2, 5). The shell membrane of flexible eggshells is proportionately thicker than that of rigid shells, and individual shell units tend to be more-or-less as wide as they are tall (Fig. 6).

Eggshells of sea turtles represent a special subclass of flexible-shelled eggs and are quite different morphologically from those of other turtles with flexible-shelled eggs (Baird and Solomon, 1979; Hirsch, 1983; Packard et al., 1982c; Solomon and Baird, 1976). The organization of the crystalline layer into individual shell units is less obvious in the scanning electron microscope (SEM). Shell units generally are smaller, the crystallites of aragonite are larger and more variable in size, and pores do not exist as distinct, morphological entities (Figs. 7, 8). Nonetheless, numerous spaces penetrate the loosely-organized crystalline layer (Figs. 7, 8).

Structure of Squamate Eggshells

Some gekkonid lizards lay eggs with rigid shells (Erben and Newesely, 1972; Krampitz et al., 1972; Packard et al., 1982c), but other lizards and all snakes lay flexible-shelled eggs (Andrews and Sexton, 1981; DeSalle et al., 1984; Krampitz et al., 1973; Packard et al., 1982a, b, c; Sexton et al., 1979; Trauth and Fagerberg, 1984). Little is known of the surface morphology of rigid-shelled eggs, but the radial or cross-sectional faces tend to be quite similar among the species studied so far. On the other hand, surface morphology of flexible-shelled eggs is quite variable, but cross-sectional views tend to be rather similar in gross morphology.

The outer surface of rigid-shelled eggs of the gecko *Hemidactylus tursicus* is composed of criss-crossing fibers with large numbers of small, block-like crystals interspersed among the fibers (Fig. 9). In contrast, the outer surface of rigid eggshells from the gecko *Lepidodactylus lugubris* seems to be covered by a relatively amorphous (possibly organic) layer and the calcareous material is organized into a series of humps or protrusions (Fig. 10). The cross-sectional face of eggshells of both species reveals jagged, interlocking columns of crystalline material arranged so as to yield a compact, non-compliant matrix (Figs. 10, 11).

Figure 3. Radial or cross-sectional view of rigid eggshell of the turtle *Trionyx spiniferus* showing tightly abutting shell units. The fibrous shell membrane has pulled away from the calcareous layer, carrying with it remnants of the crystalline material (arrow). Bar = 40 µm.

Figure 4. Radial view of rigid eggshell of the turtle *Sternotherus minor* showing crystallites of shell units radiating outward from a common center. Shell membrane is visible at inner aspect of crystalline layer (arrow). Bar = 50 µm.

Figure 5. Outer surface of eggshell of flexible-shelled egg of the turtle *Chrysemys picta* showing loosely-organized shell units and large numbers of spaces or pores through calcareous layer. Bar = 100 µm.

Figure 6. Radial view of shell of flexible-shelled egg of the turtle *Emydoidea blandingi*. Bar = 100 µm.

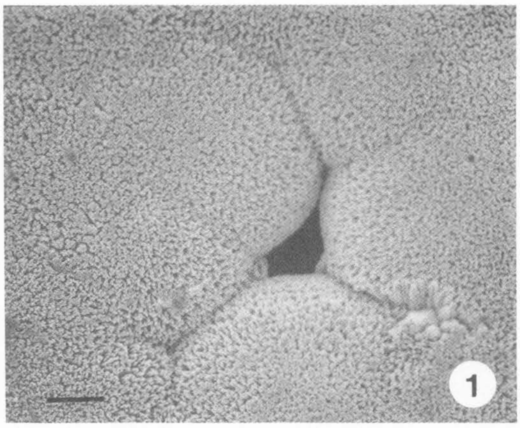


Figure 1. Outer surface of eggshell of rigid-shelled egg of the turtle Trionyx spiniferus showing pore at the intersection of 4 shell units. Bar = 50 μm.

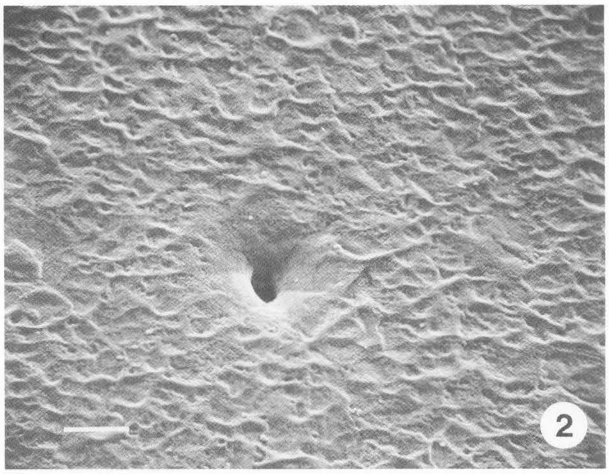
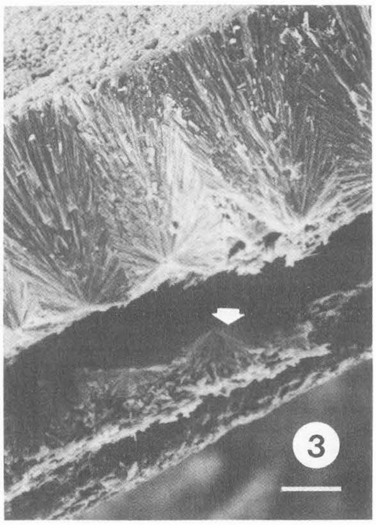
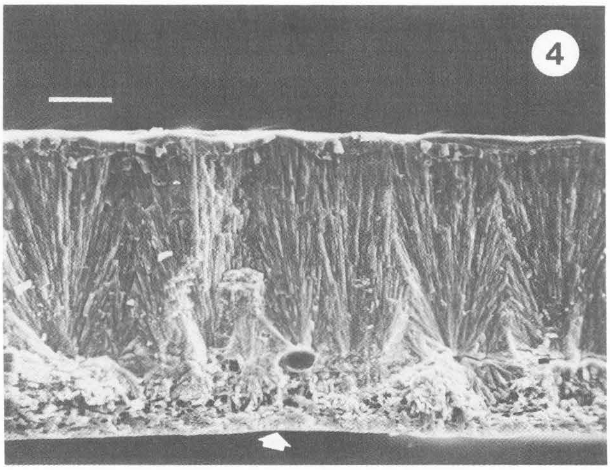
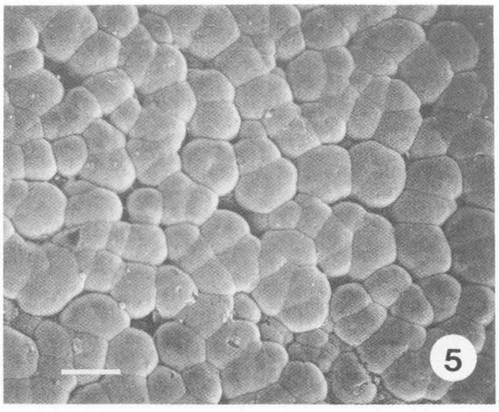
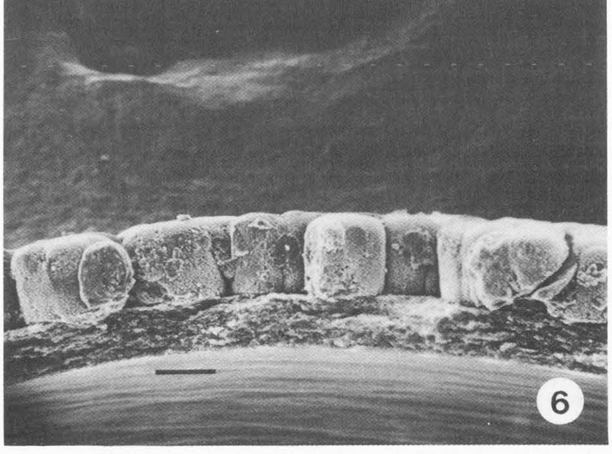


Figure 2. Outer surface of eggshell of rigid-shelled egg of the turtle Kinosternon flavescens showing sculpturing of calcareous material and pore at intersection of 4 shell units. Bar = 100 μm.









These eggshells are similar in radial view to rigid eggshells of another gecko, Tarentola mauretanica (Erben and Newesely, 1972; Krampitz et al., 1972). We assume that some sort of fibrous shell membrane is attached to the inner surface of the calcareous layer of these eggs, but details of the structure and arrangement of such a membrane have not been reported. Similarly, pores must surely penetrate the crystalline layer, but have not yet been described.

The crystalline material of eggshells of the tuatara (Sphenodon punctatus) also is organized into columns. However, the columns do not interlock and they penetrate deeply into the fibrous shell membrane (Packard et al., 1982b). The inner aspect of the columns is interwoven with fibers of the shell membrane whereas the outer portion is more compact and lacks fibers (Fig. 12; Packard et al., 1982b). Structurally tuatara eggshells are intermediate between rigid-shelled eggs with relatively little penetration of the crystalline layer into the shell membrane and other flexible-shelled eggs with a crystalline layer confined solely to the outer surface of the membrane.

Flexible-shelled eggs of other squamates consist of a thin crust of crystalline material overlying a relatively thick, fibrous shell membrane (Figs. 13-27). However, the morphology of the outer surface is highly variable both within and among species (Figs. 13-27; Packard et al., 1982a, b, c). For example, Solomon and Reid (1983) report that the crystalline layer of eggs from the royal python (Python regius) is composed of calcified protrusions surrounded by a complex crystalline cuff, but the crystalline layer of python eggshells that we examined does not fit this description (Figs. 16, 17).

Shells of python eggs in our collection exhibited calcified areas as well as areas devoid of calcareous deposits (Figs. 14-17). Areas containing crystalline material were chalky-white in color and effervesced vigorously in dilute acid whereas non-crystalline areas were yellow and did not effervesce. In the SEM, uncalcified areas were characterized by an amorphous, slightly rugose layer covering the shell membrane (Figs. 14, 15). Calcified areas, however, were considerably more rugose, with large, ridged deposits of crystalline material overlying an amorphous ground substance similar to that characterizing uncalcified areas (Figs. 16, 17).

Differences between eggshells examined in this study and those examined by Solomon and Reid (1983) could stem from differences in how animals had been maintained in captivity and/or from the fact that Solomon and Reid (1983) examined shells of freshly oviposited eggs whereas we used shells from eggs incubated to hatching. Alternatively, this variability in structure could simply reflect natural variability among different females. In any case, this example illustrates the difficulty encountered in characterizing a "typical" squamate eggshell.

The morphology of the crystalline layer of eggshells of other squamate reptiles ranges from relatively amorphous in the SEM to rather highly sculptured. For example, the calcareous material of flexible-shelled eggs of the gecko Eublepharis macularius is organized into irregular plaques or plates broken by fissures and pore-like structures (Figs. 18, 19). At low magnification, the crystalline layer appears to be relatively unstructured, but at higher magnification, the calcareous material seems to be comprised of an aggregation of small spheres (Fig. 19). In contrast, the crystalline layer of eggshells from the snake Hydrodynastes gigas is composed of relatively amorphous areas broken by a series of nodes similar in many respects to the "pustules" described recently on shells of eggs of an Australian skink (Figs. 20-23; Allison and Greer, 1986). These nodes are extensions or outgrowths of the surrounding crystalline material and are somewhat recessed in the center (Figs. 22, 23). Nodes are not uniformly distributed over the surface of the eggshell, and some areas lack nodes altogether (Fig. 24). Pores of irregular size and shape are found in the calcareous layer and seem to form at discontinuities between otherwise overlapping and abutting plates of crystalline material (Fig. 25). Pores also have been described in flexible eggshells of the snake Elaphe obsoleta (Lillywhite and Ackerman, 1984). It is not clear if such pore-like structures penetrate directly through the calcareous layer, as do pores of turtle eggshells.

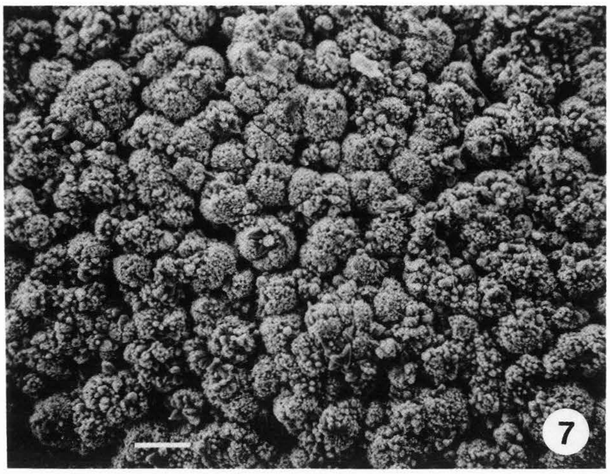
Calcareous nodes or rosettes also characterize eggshells of the snake Coluber constrictor, but the rosettes are not extensions of a surrounding crystalline layer (Fig. 26). When eggshells are placed in dilute acid, effervescence occurs only at the nodes. Thus, the amorphous substance between nodes presumably is organic in nature (Fig. 27; Packard et al., 1982c). The nodes of these eggshells are quite large and give eggshells a nubbly texture to the unaided eye. In contrast, the nodes on Hydrodynastes are not readily apparent without magnification.

Figure 9. Outer surface of eggshell of rigid-shelled egg of the gecko Hemidactylus tursicus. Bar = 4 μm.

Figure 10. Radial view of rigid eggshell of the gecko Lepidodactylus lugubris showing jagged columns of crystalline material and humps or protrusions of calcareous layer at outer surface. Bar = 12.5 μm.

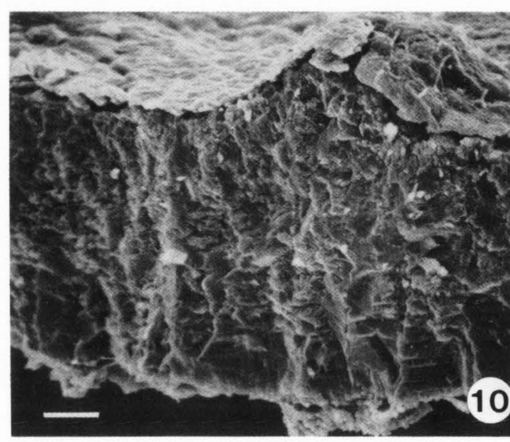
Figure 11. Radial view of rigid eggshell of the gecko Hemidactylus tursicus. Bar = 12.5 μm.

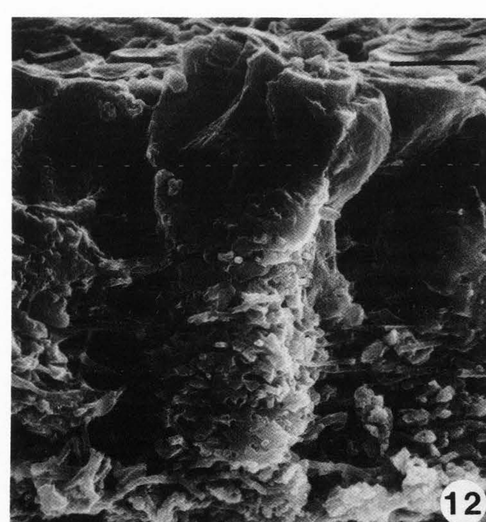
Figure 12. Radial view of flexible eggshell of the tuatara Sphenodon punctatus showing columns of crystalline material penetrating the fibrous shell membrane. Bar = 10 μm.



igure 7. Outer surface of eggshell of the sea urtle Caretta caretta. Bar = 100 μm.

Figure 8. Higher magnification view of outer surface of eggshell of the sea turtle Caretta caretta. Bar = 25 μm.





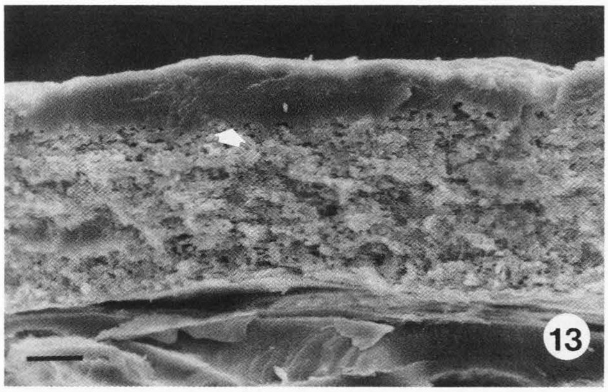


Figure 13. Radial view of flexible eggshell of the lizard Python regius showing thin crystalline layer and thick, fibrous shell membrane. Arrow indicates interface between calcareous layer and shell membrane. Bar = 47 µm.

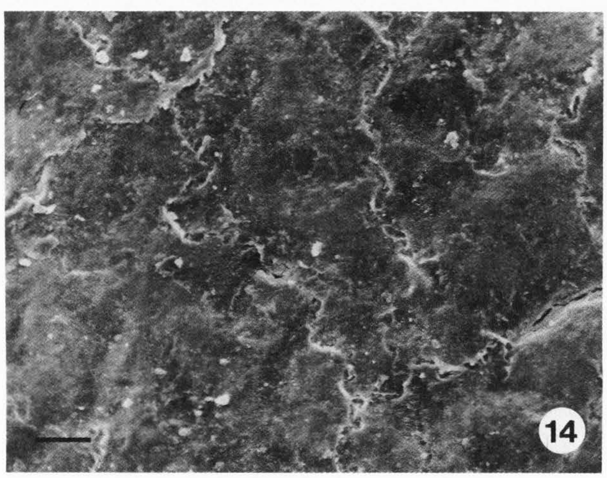


Figure 14. Outer surface of uncalcified area of flexible eggshell of Python regius. Bar = 100 µm.

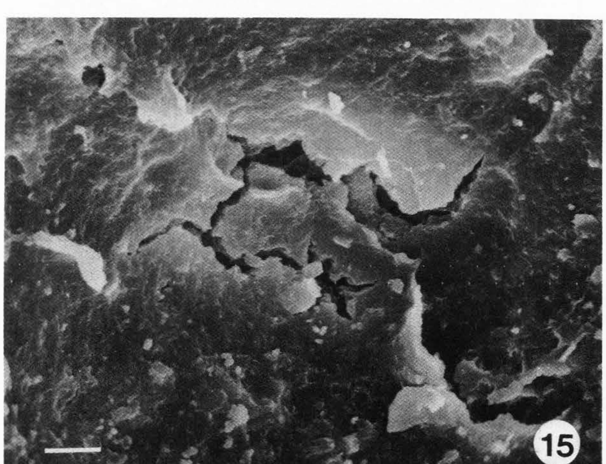


Figure 15. Higher magnification view of uncalcified area of eggshell of Python regius. Bar = 12 µm.

Figure 18. Outer surface of flexible eggshell of the gecko Eublepharis macularius showing irregular plates or plaques of crystalline material with numerous fissures and pore-like structures. Bar = 50 µm.

Figure 19. Higher magnification view of outer surface of eggshell of Eublepharis macularius. Bar = 2 µm.

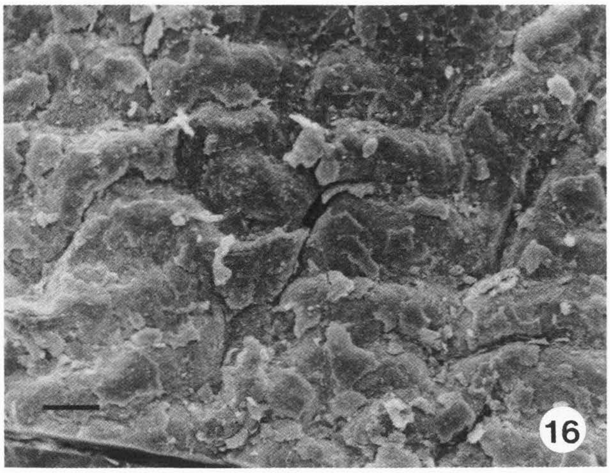
Figure 20. Radial view of flexible eggshell of the snake Hydrodynastes gigas showing crystalline material and thick shell membrane. Bar = 100 µm.

Figure 21. Outer surface of eggshell of Hydrodynastes gigas showing nodes and amorphous appearance of crystalline material in internodal areas. Bar = 50 µm.

Concluding Remarks

A common theme links shells of eggs of oviparous reptiles in that most eggshells are composed of both inorganic and organic components. However, the organization and arrangement of these components is highly variable. We can organize chelonian eggshells into three convenient morphological categories encompassing rigid-shelled eggs, flexible-shelled eggs, and flexible-shelled eggs unique to sea turtles. Eggshells of squamate reptiles also can be categorized as rigid or flexible, but no broad grouping characteristic of certain species--and certain species only--currently is possible.

Research in this field has been devoted largely to purely descriptive accounts of gross morphology of eggshells. Such accounts have contributed importantly to our understanding of shell structure, and have occasionally provided insights into potential mechanisms of shell formation (Packard and Packard, 1979; Packard et al., 1984b; Solomon and Baird, 1976). Nonetheless, major questions concerning structure of reptilian eggshells remain unanswered. These include (but are not limited to) the contribution of diet and nutrition to variability in structure and crystal morph of eggshells, the chemical milieu in which shell formation takes place, the source(s) of the calcium used in formation of the crystalline layer, and the mechanism of shell formation in those species that seemingly lack discrete nucleation sites for crystal deposition. Additional research into these and other questions is required before a fully synthetic treatment of this subject can be attained.



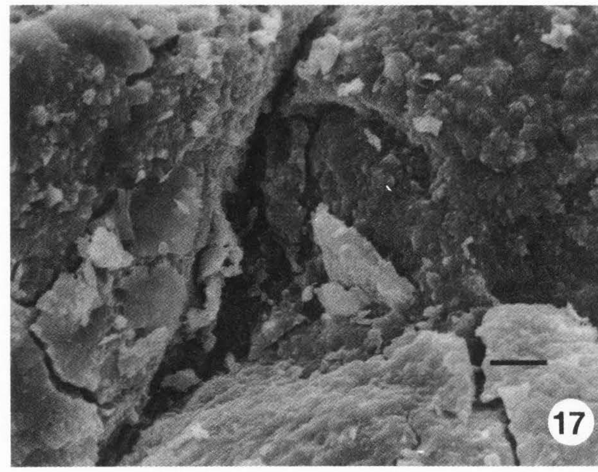
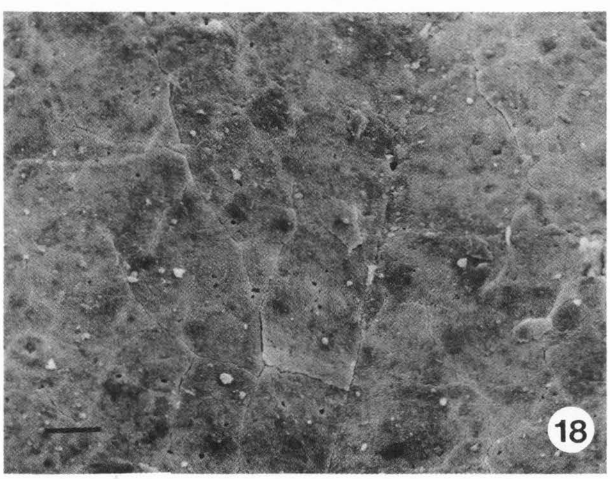
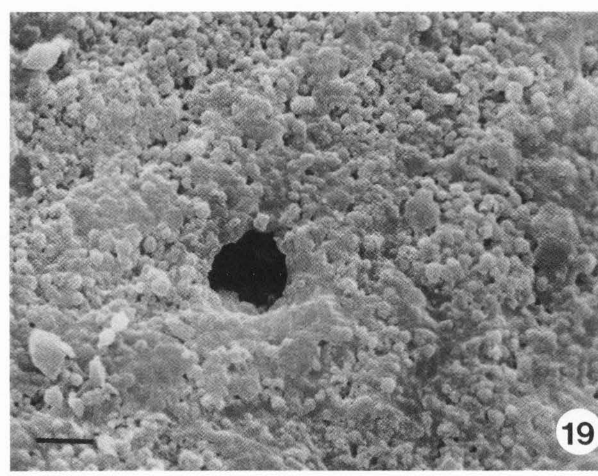
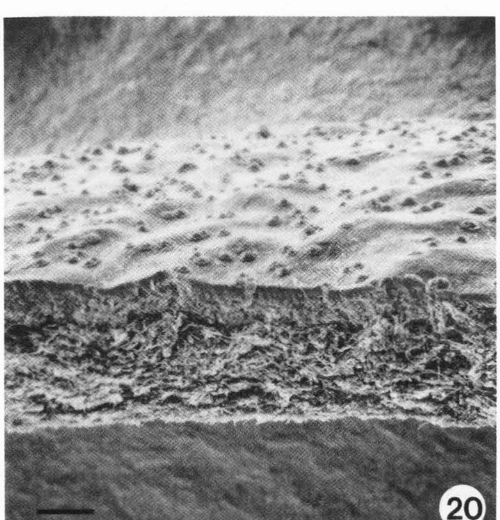


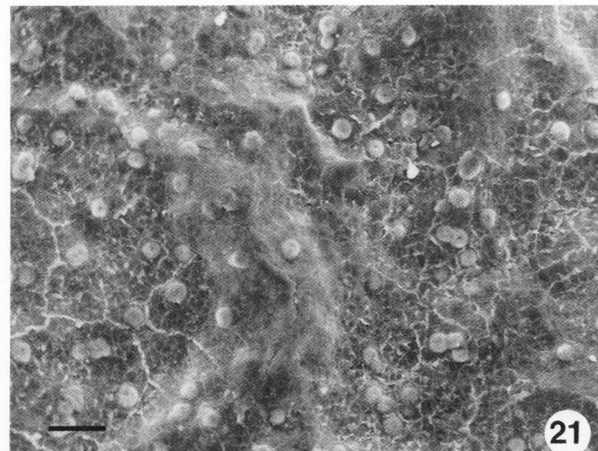
Figure 16. Outer surface of calcified area of eggshell of Python regius. Bar = 100 μm.

Figure 17. Higher magnification view of calcified area of eggshell of Python regius. Bar = 12 μm.









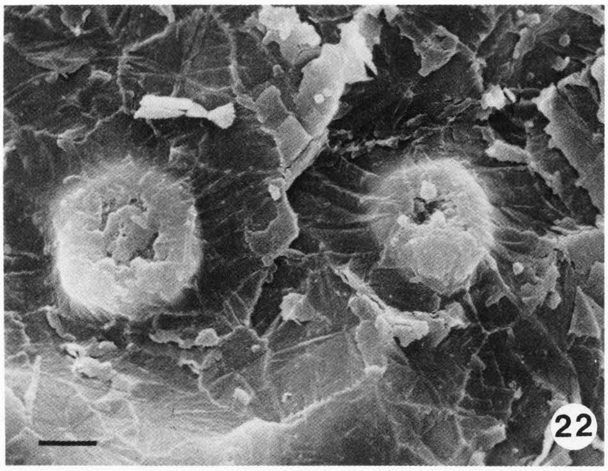


Figure 22. Outer surface of eggshell of Hydrodynastes gigas showing two nodes and abutting and overlapping plates of crystalline material. Bar = 6 μm.

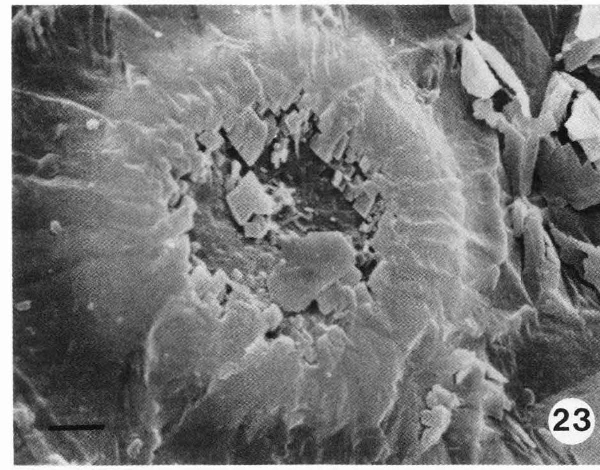
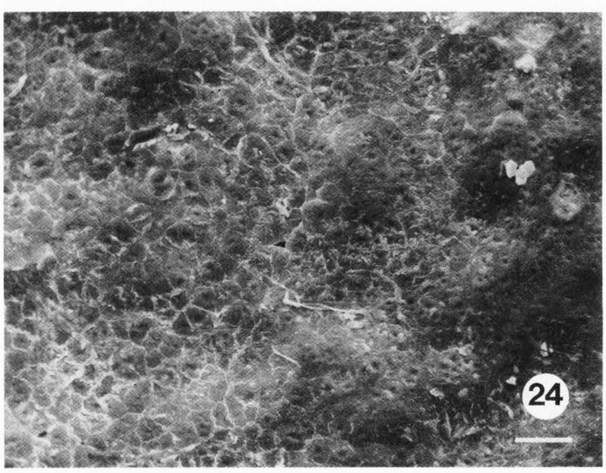
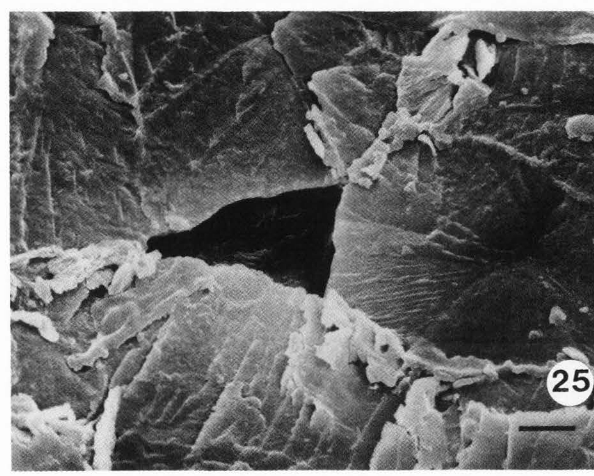
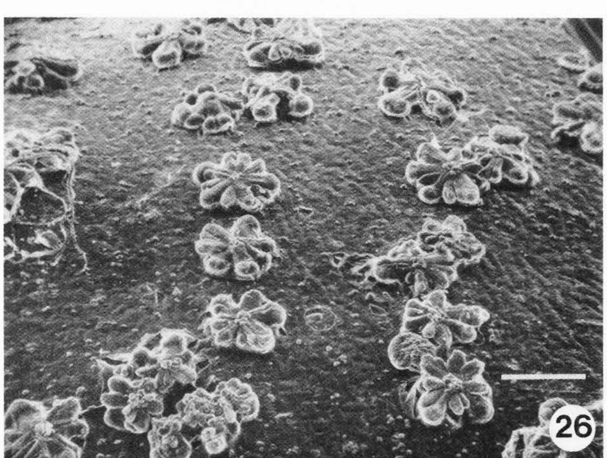


Figure 23. High magnification view of node on outer surface of eggshell of Hydrodynastes gigas showing recessed center. Bar = 2 μm.







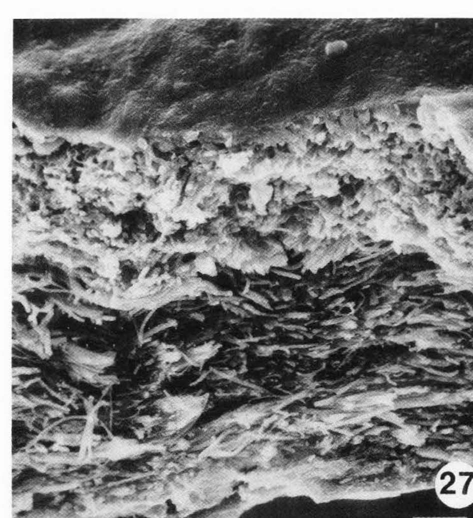


Figure 24. Outer surface of eggshell of Hydrodynastes gigas showing area without nodes. Note pore in center of picture. Bar = 50 μm.

Figure 25. High magnification of pore shown in Figure 24. Bar = 3 μm.

Figure 26. Outer surface of flexible eggshell of the snake Coluber constrictor showing large crystalline rosettes separated by areas of amorphous material. Bar = 500 μm.

Figure 27. Radial view of eggshell of Coluber constrictor showing thin layer of amorphous material overlying thick fibrous shell membrane. Bar = 20 μm.

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Discussion with Reviewers

A. Boyde: I would like to see developmental information in a future publication. Would it be possible to obtain eggs from oviducts for some representative species? It would also be important to characterize the mineral phase before drying occurred.
Authors: Some information on development of eggshells is available for two species of turtles (see Packard et al., 1984b and Solomon and Baird, 1976). Unfortunately, data on development of eggshells for most reptiles will be difficult to come by. Many species cannot be maintained successfully in captivity. Moreover, there is some evidence that captive maintenance can affect shell formation. Thus, there is the potential that information gathered using captive animals will not reflect the wild state. Our limited knowledge about the timing of ovulation and subsequent shell formation in reptiles (in contrast to the situation with the domestic fowl) also complicates studies such as you suggest. In answer to the second part of this question, we are not aware of evidence that the mineral phase of calcium carbonate undergoes changes as a result of drying. If the mineral phase is altered by drying, then it would be important to characterize such changes.
R. L. Hughes: How does the diversity in the morphology of the reptilian egg shell relate to the ecology and embryology of the species concerned? What are the taxonomic and evolutionary perspectives to be deduced from structural diversity of the reptilian egg shells studied?
Authors: Few correlates presently can be made between diversity in morphology of reptilian eggshells and ecology and embryology. Some geckos lay rigid-shelled eggs that they oviposit in relatively exposed sites. Presumably, structure of such eggshells helps to prevent the desiccation that would occur if flexible-shelled eggs were deposited in such sites.

Taxonomic and evolutionary perspectives are a distant goal at this point. Eggshell structure has been examined in only a tiny fraction of the thousands of species of oviparous reptiles. No systematic examination of shell structure has been attempted for a single taxonomic group, much less for several closely related groups. Certainly the structural diversity described thus far indicates that a given problem (packaging of eggs) has a variety of solutions.