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REVIEW OF FOSSIL EGGS AND THEIR SHELL STRUCTURE

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Abstract

Of the established eggshell groups (membrane-like, pliable, and rigid), the rigid eggshell group has the best chance of fossilizing. Fossils of this group, with modern-type structure, extend back into the Eocene (crocodiles, gecko) and even into the Cretaceous (birds, turtles).

Structural types which differ from modern types are found as late as the Eocene, and in the Cretaceous they are numerous. These Cretaceous eggshells have, for the most part, been assigned to dinosaurs often without consideration of other egg-laying animals of that time. Only a few eggs and eggshells have been reported from the Jurassic and older periods.

Polarizing and scanning electron microscopy complement each other. For example, the polarizing light microscope shows the extinction pattern and the larger units of the shell structure whereas the scanning electron microscope allows a detailed study of the microstructure which may enable us ultimately to identify specimens to lower taxonomic groups.

KEY WORDS: fossil eggs, eggshell structure, diagenesis

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Introduction

The purpose of this paper is to provide a general review of the present status of the fossil eggshell record and to point out the problems and limitations encountered in studying fossil eggshell structure.

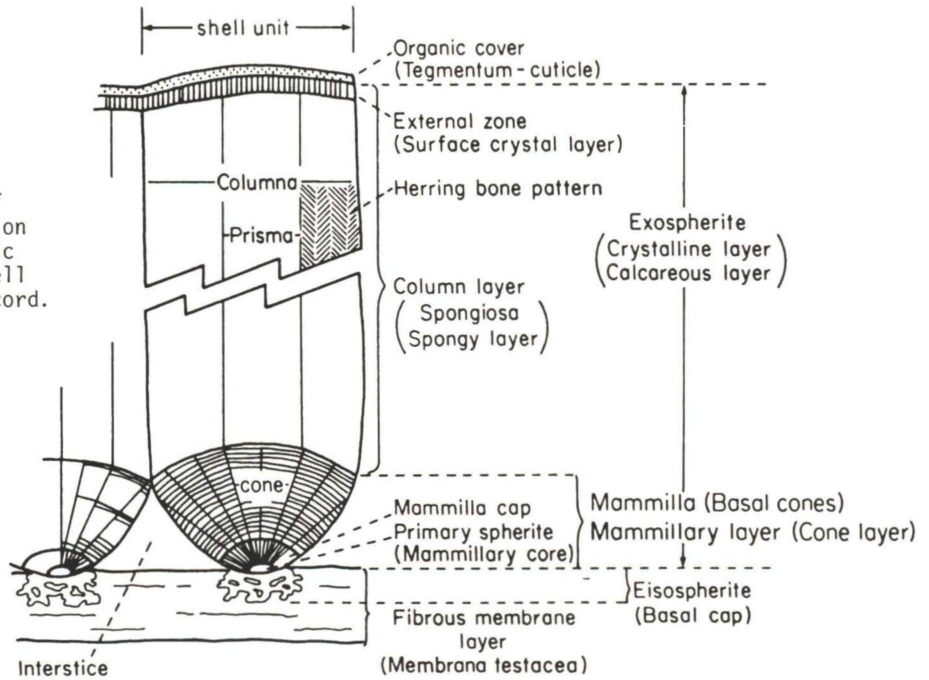
Our studies are based on knowledge of modern eggshells and are severely limited by a number of factors. The organic matter of modern shells such as shell membrane, cuticle, pore coverings, and organic network within the crystalline layer is, as a rule, not preserved in fossils. This leaves only the crystalline calcareous layer, part of the crystalline layer, or in some cases only a "steinkern" for study. Differences in the sediments in which the eggshell is buried and diagenesis may result in variations in preservation of the crystalline layer, sometimes even within the same specimen. The physical condition of the specimen -- embedding matrix, contamination by secondary shell-like layers, filling of the pore canals -- often makes it impossible to prepare the specimen properly or study certain aspects of structure. In addition, some specimens are unique or rare and care must be taken to inflict as little preparation damage as possible on them.

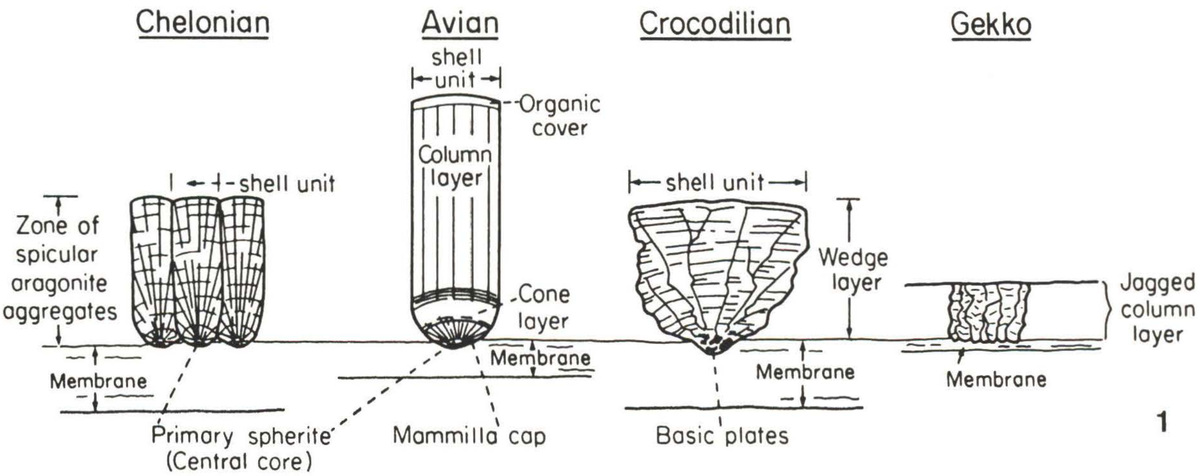
The study of eggshell microstructure is still a relatively young discipline, encompassing only a few of the numerous kinds of amniote eggshells. This lack of comparative data, the fact that many egglaying animals are extinct, and the possibility of evolutionary or adaptive changes in shell structure make it almost impossible to assign most fossil eggs to taxonomic groups below the ordinal level. In addition, only the rigid-type eggshell has a good chance of fossilization, thus leaving large gaps in the fossil record, especially in older periods.

Terminology and Methods

Terminology used for the well-studied avian eggshell has become a standard, as has the eggshell structure itself (Fig. 1). Methods described in Pooley (1979) and Hirsch (1979, 1983, 1985) have been followed in preparing the specimens; they are also listed in Table 1.

Figure 1. Terminology of eggshell structure based on avian eggshell. Stylistic drawings of modern eggshell types found in fossil record.





It is important that specimens are studied using both polarizing light microscopy (PLM) and scanning electron microscopy (SEM). Each technique has its advantages and complements the other. The characteristic features of the extinction pattern in eggshells is visible only under polarized light. The contrasting images of size, shape and arrangement of the shell units, their nucleation centers and growth lines viewed under normal and polarized light are often sufficient for assigning eggshells to a taxonomic category such as chelonians, crocodilians, birds and geckos (Fig. 1). The SEM allows one to study the eggshell uncut and in three dimensions, rather than in the single plane of a thin section. Here one can study the specimen in its original state, on fresh fractures, or after chemical treatment has enhanced certain features of the organic or inorganic matter. Pooley (1979) demonstrated this technique well in his study of the microstructure of modern bird eggshells. The SEM also allows one to see in detail the micro-crystalline arrangement of the larger units within the eggshell and thus to study crystal growth units and diagenetic changes. This may enable researchers one day to differentiate between the shell structures of lower taxonomic groups perhaps even to species level.

Description and Discussion

Although many amniote eggshells, especially those of lizards, snakes and monotremes have not yet been studied, three groups of eggshells can be recognized so far.

Soft, parchment- or membrane-like eggshells

The eggs of snakes, most lizards, and perhaps monotremes belong to this group. The

Table 1

Techniques for recent and fossil eggshell studies

Polarizing light microscopy (PLM) and light microscopy
    Examination of radial and tangential thin sections with and without chemical treatment or staining

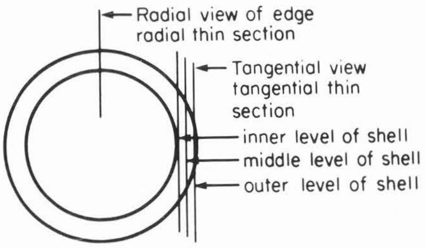
Scanning Electron Microscopy (SEM)
    1. Examination of surface and radial (edge) views with or without chemical treatment
    2. Examination of epoxy-embedded material after polishing or etching

Elemental and mineralogical analyses

Biochemical analyses

Geneva Lens Measure
    Used to estimate egg size from large shell fragments

Features to be noted, preferably following ultrasonic cleaning:
1. Shape and size of egg or shell fragment
2. Thickness of shell layer
3. Sculpturing on outer surface; size, distribution, shape of pores
4. Arrangement of crystalline material (columns, wedges, radiating pattern, herringbone pattern, horizontal layering)
5. Size, shape, density of mammillae on inner surface of eggshell
6. Internal matrix of specimen (imprints of inner shell surface, structure and arrangement of filling material)



calcite occurs in these single or multi-layered, fibrous shell membranes as floating crystals (Figs. 2, 3), concentrations in the outer layer, or as an outer crust (Andrews and Sexton, 1981; Sexton et al, 1979; Packard and Packard, 1980; Packard et al, 1982b, c; Hirsch, 1983). The amounts of calcite are so minute, or in such a disorganized form, that it is impossible to trace or identify them after the organic matter has decayed.

There are no positively identified fossil specimens from this group with the possible exception of the yet undescribed Triassic eggs from South Africa (Kitching, 1979). The results of a study of these specimens, which have supposedly a membrane-like shell layer and contain embryonic remains, may allow us to assign the oldest vertebrate egg (Romer and Price, 1939) also to this group. Hirsch (1979) was unable to establish an undoubted fossil status for this specimen.

Eggshells with a pliable calcerous layer

Most turtles and perhaps the tuatara belong to this group (Hirsch, 1983; Packard and Packard, 1980; Packard et al., 1982a, b). The eggshell shows a clear separation into a thick membrane and a thinner crystalline layer. The latter is composed of more or less tightly abutted shell units (Figs. 4, 5). The chance of fossilization is slim since the calcareous layer, which is not interlocked, will most likely disintegrate with the decay of the membrane.

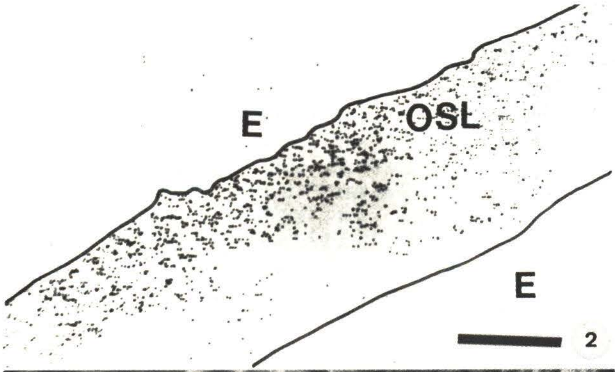
Here again we have no positively identified fossil specimens, although some chelonian eggs may belong to this group (Hirsch, 1983).

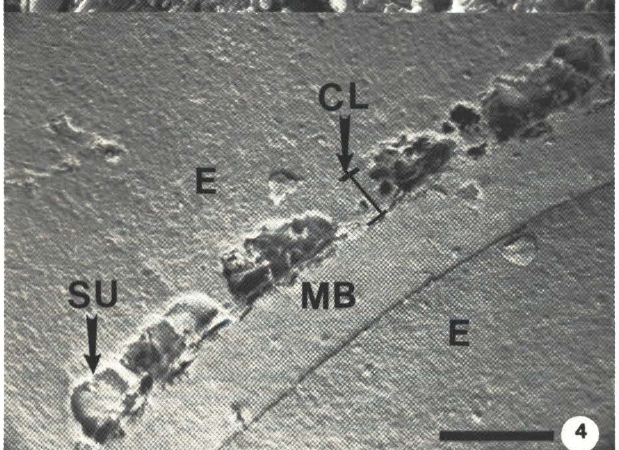
Eggshells with a rigid calacerous layer

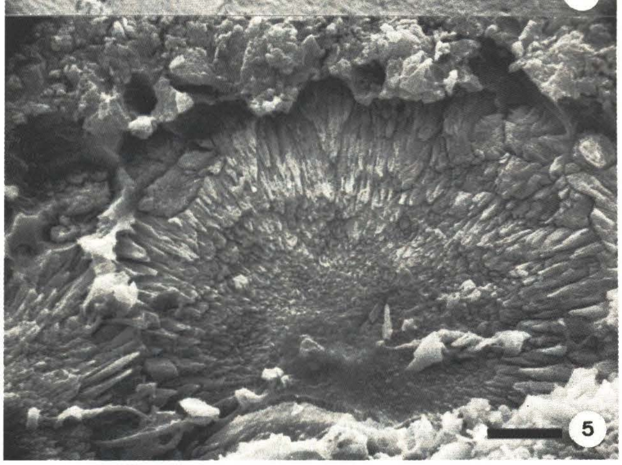
Some turtle, some gecko, all crocodile, all bird, and all identified dinosaur eggshells belong to this group (Hirsch, 1979, 1983; Packard and Packard, 1980; Packard et al., 1982b). The crystalline layer is composed of a single layer of well-defined and tightly abutted shell units. The crystals of the adjacent units interlock, thus forming a rigid non-pliable shell. This structure becomes diversified such that geckos, chelonians, crocodilians and birds each have their own identifiable structure (Fig. 1). Variations within the lower taxa of these groups exist although systematic definitions are, as yet, not possible. The chance of fossilization is very good and the microstructure is in many cases remarkably well preserved.

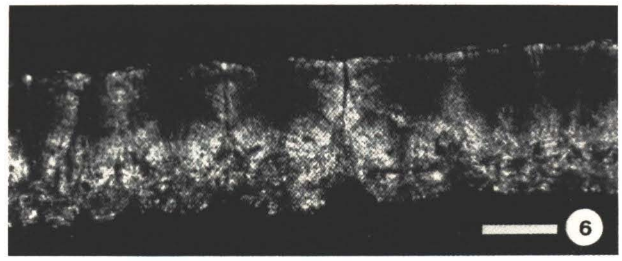
Chelonian eggs. Descriptions of fossil chelonian eggs in the older literature, which in most cases have been surprisingly identified correctly, were based more or less on the comparison of macro-features, especially comparisons with different shapes of modern specimens (Buckman, 1860; Meyer, 1860, 1867; vanStraelen, 1928). Hirsch (1983), using detailed PLM and SEM analyses, was the first to describe preserved modern-type structure and diagenetic changes in Cretaceous, Oligocene and Pliocene turtle eggshell. In the chelonian eggshell the calcium carbonate is in the form of aragonite (cf. Figs. 6, 7); all other amniote eggshells are composed of calcite. Aragonite is metastable and is thought to change fairly quickly to calcite. However, a specimen from the Middle Cretaceous clays of Folkstone in England still displays typical aragonitic structure (Hirsch, 1983), as does a Cretaceous egg from Japan studied by Obata (personal communication). Specimens from Gran Canaria, Canary Islands (Figs. 8, 9) (Hirsch, 1987) and others, illustrated here (Figs. 10- 13), display all stages, from totally aragonitic to totally calcitic.

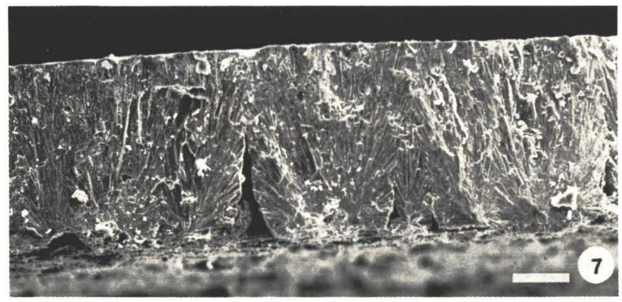
Gecko eggs. Descriptions of modern gecko eggshell structure are still very scanty. However, based on comparative studies by the author (in preparation) it was possible to identify an egg found in the Eocene of Wyoming as "gecko-like" (Fig. 14). A very thin eggshell











<u>Notes and abbreviations for figures</u>

In radial views, the outside of the eggshell is always up. The following abbreviations have been used: AH CCCP = Paleontological Institute, Academy of Sciences, USSR; CMNH = Cleveland Museum of Natural History; LACM = Los Angeles County Museum; MCZ = Museum of Comparative Zoology; MOR = Museum of the Rockies; NMNH = National Museum of Natural History; PU = Princeton University; UCM = University of Colorado Museum.

<u>Figure 2</u>. Eggshell embedded in epoxy (E); SEM; snake (<u>Elaphe obsoleta quadrivatta</u>, UCM-OS1126). Lapped; radial view mapped for calcium. Note concentration of calcium in outer shell layer (OSL). Bar=100 µm.

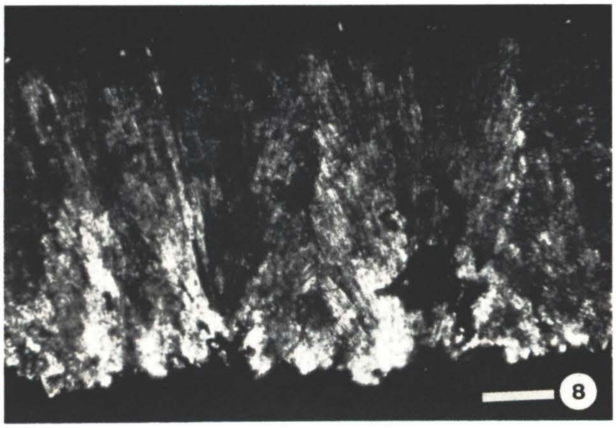
<u>Figure 3</u>. Same specimen as in Figure 2; SEM; treated with KOH; radial view. Note calcite crystals floating within shell membrane (arrows). Bar=10 µm.

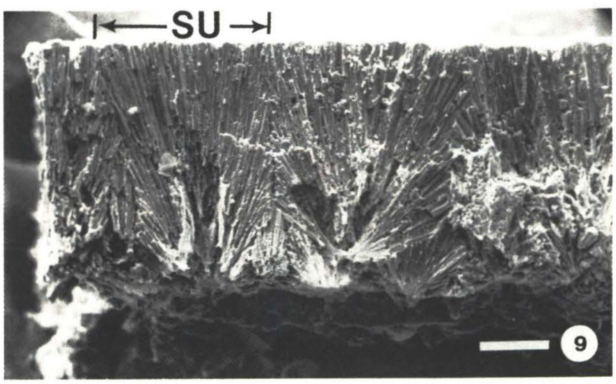
<u>Figure 4</u>. Eggshell embedded in epoxy (E); SEM; sea turtle (<u>Lepiodochelys kempi</u>, UCM-OS480). Lapped, etched with EDTA. Radial view. Note separation into membrane layer (MB) and crystalline layer (CL) with loosely arranged shell units (SU). Bar=100 µm.

<u>Figure 5</u>. Enlarged shell unit of specimen in Figure 4. Bar=10 µm.

<u>Figure 6</u>. Radial thin section; PLM; turtle <u>Kinosternon hirtipes</u> (UCM-OS1127). Polarized sweeping extinction pattern. Bar=100 µm.

<u>Figure 7</u>. Freestanding eggshell; SEM; same specimen as in Figure 6. Radial view. Bar=100 µm.





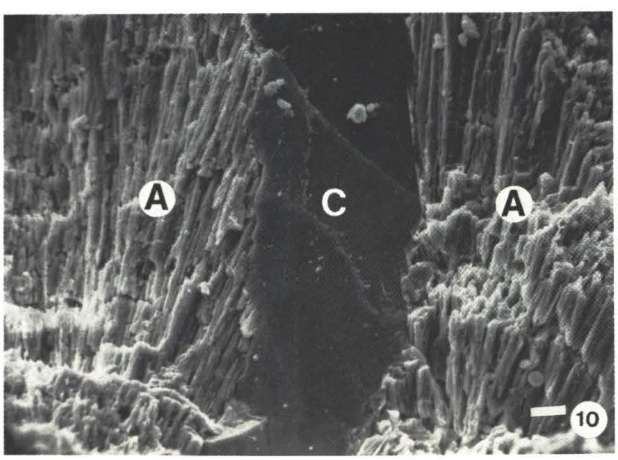
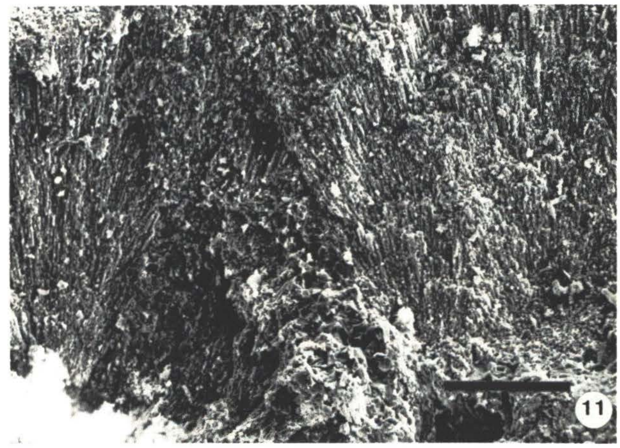
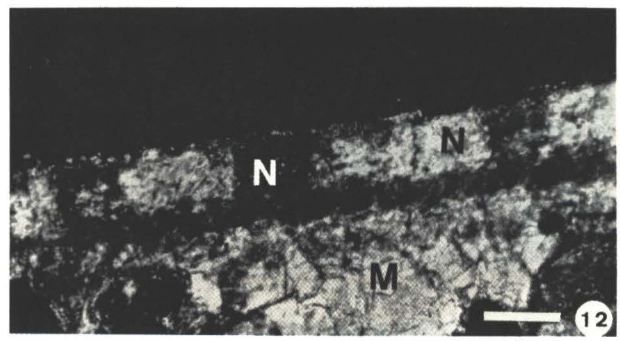


Figure 8. Radial thin section; PLM; fossil turtle, Pliocene, Gran Canaria, Canary Islands (UCM 54313). Polarized. Note aragonite; sweeping extinction pattern of radiating structure. Bar=100 μm.

Figure 9. Freestanding eggshell; SEM; same specimen as in Figure 8. Radial view. Shell unit = SU. Bar=100 μm.

Figure 10. Freestanding eggshell; SEM; fossil turtle, Ethiopia (CMNH AL363). Radial view. Note calcite (C) and aragonite (A); replacement by calcite started in pore and is extending to both sides. Bar=100 μm.





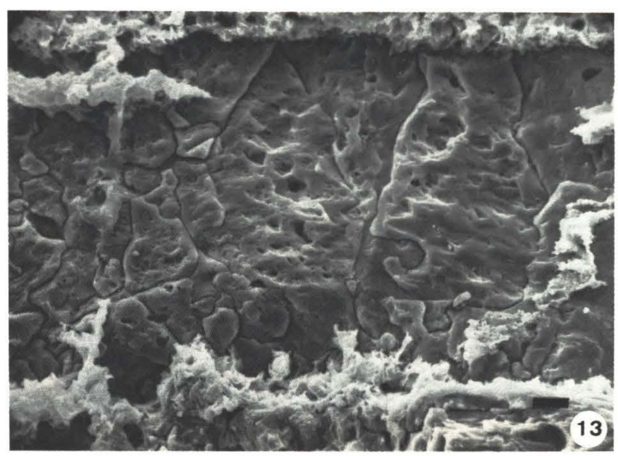
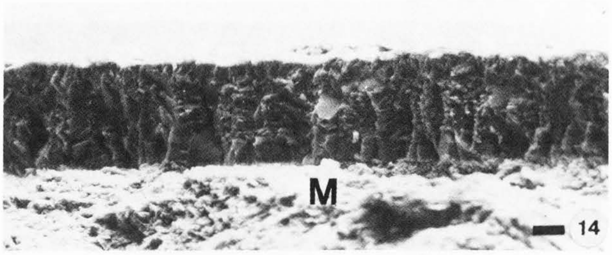
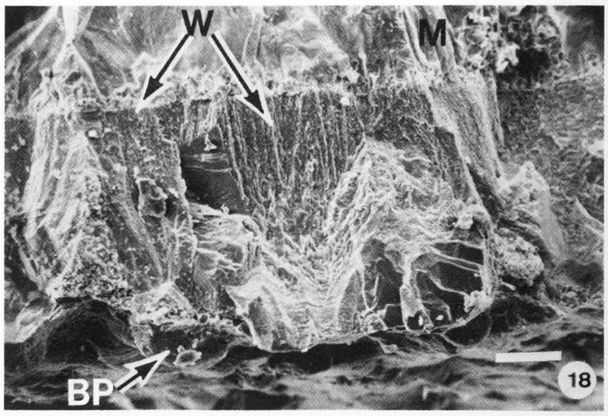


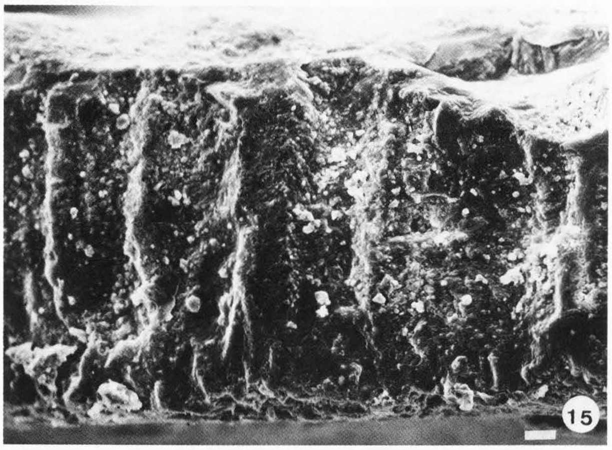
Figure 11. Freestanding eggshell; SEM; fossil turtle, Pliocene, Lanzerote, Canary Islands (UCM 54314). Radial view. Note completely replaced by calcite; needle-like crystal structure preserved. Bar=100 μm.

Figure 12. Radial thin section; PLM; fossil turtle, PlioPleistocene, Kanapoi, Africa (MCZ 156-66K). Polarized. Note completely replaced by calcite and sharply extinguishing neomorphs (N). Matrix = M. Bar=100 μm.

Figure 13. Eggshell embedded in epoxy; SEM; same specimen as in Figure 12. Lapped, etched with EDTA. Radial view. Note irregular structure of neomorphs. Bar=100 μm.


M
14


W
M
BP
18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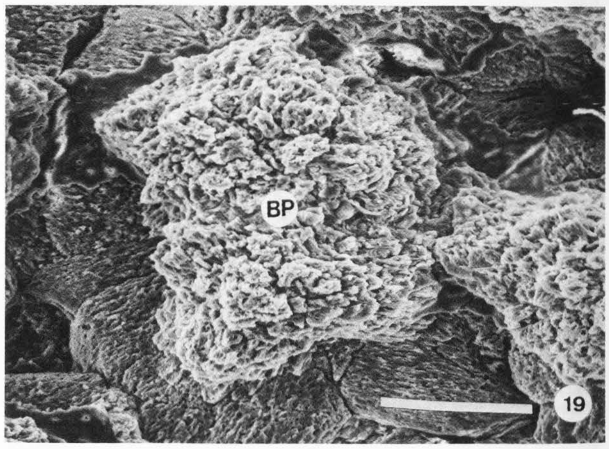
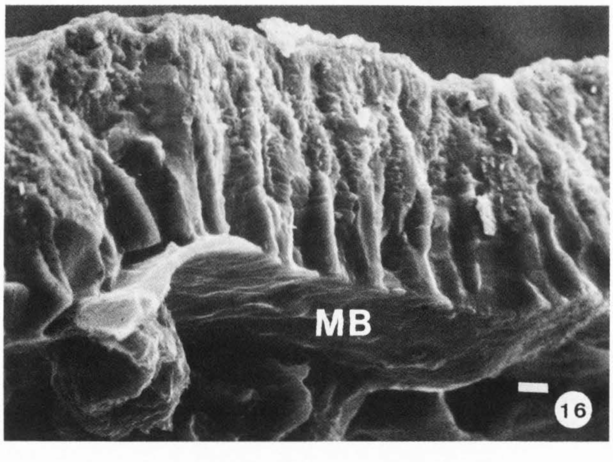
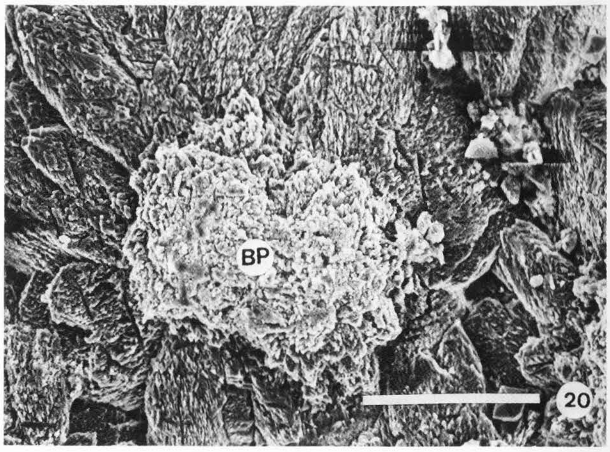
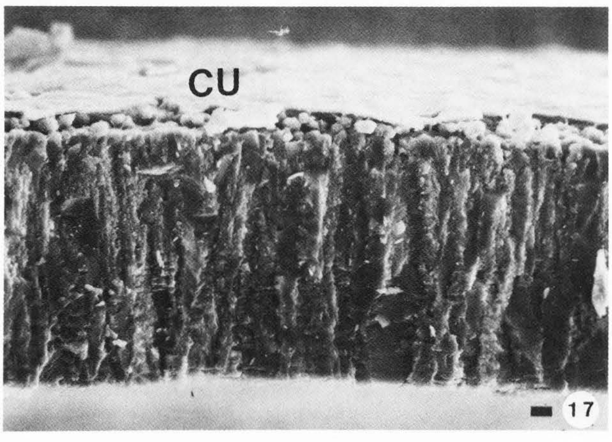

BP
19


MB
16


BP
20


CU
17

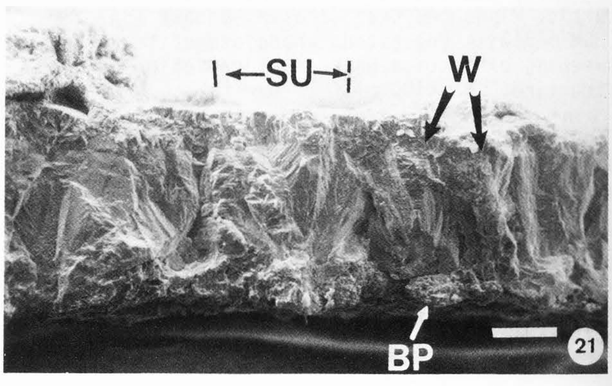

SU
W
BP
21

Figure 14. Freestanding eggshell; SEM; fossil gecko-like, Eocene, Wyoming (UCM 54315). Radial view. Matrix = M. Bar=10 μm.

Figure 15. Freestanding eggshell; SEM; fossil ?gecko-like, Upper Cretaceous, Nagpur, India (UCM 54316). Radial view. Bar=10 μm.

Figure 16. Freestanding eggshell; SEM; gecko (Tarantola mauritanica, UCM-OS1129). Radial view. Membrane = MB. Bar = 10 μm.

Figure 17. Freestanding eggshell; SEM; gecko Phelsuma madagacariensis, UCM-OS1130). Radial view. Cuticle=CU. Bar=10 μm.

Figure 18. Freestanding eggshell; SEM; fossil crocodile, Eocene, Colorado (UCM 47523). Radial view. Note shell units, basal plate groups (BP) and wedges (W). Matrix = M. Bar=100 μm.

Figure 19. Inner surface of eggshell; SEM; fossil crocodile, Eocene, Colorado (UCM 44945). Note basal plate group (BP) and crystalline structure. Bar=100 μm.

Figure 20. Inner surface of eggshell; SEM; fossil crocodile, Eocene, Geiseltal, East Germany (UCM 54317). Note basal plates (BP) and crystalline structure. Bar=100 μm.

Figure 21. Freestanding eggshell; SEM; fossil crocodile, Eocene, Wyoming (NMNH 12597). Radial view. Note shell units (SU), basal plate groups (BP) and wedges (W). Bar=100 μm.

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from the Cretaceous of India (Sahni et al., 1984) may also fall into this eggshell type (Fig. 15) but more study is necessary to establish this identification. Two different types of recent gecko eggshells are shown in Figs. 16, 17.

Crocodilian eggs. Only two reports of fossil crocodilian eggs (Heller, 1931; Erickson, 1978) could be found in a literature search. Detailed SEM and PLM studies (Hirsch, 1985) describe four crocodilian eggs from the Eocene of Colorado (Figs.18, 19). Studies of other specimens (Hirsch, in preparation) show that eggs from the Eocene of the Geiseltal in East Germany are similar in shape, size and structure to this Colorado form (Fig. 20). However, four eggs from the Eocene of Wyoming, because of their difference in size and structure, seem to belong to a different crocodialian species (Figs. 21, 22).

The extinction pattern of crocodilian eggshells cannot always be differentiated from avian eggshells under the PLM. However, under the SEM the similarity between recent and fossil crocodilian eggshell structure is very apparent in radial views (Figs. 18, 21, 23) and in views of the inner shell surface (Figs. 19, 20, 22, 24, 25).

Avian eggs. Avian eggshells, because of their especially rigid interlocking structure, are fairly common. However, identification of avian eggshells from the Cretaceous is problematic since many dinosaur eggs also have an avian-like shell structure and we have not, as yet, been able to distinguish between them. In spite of this, Beetschen et al (1977) have identified a thin eggshell found in the Upper Cretaceous of France as avian.

Elzanowski (1981) described embryonic bird skeletons from the Upper Cretaceous of Mongolia. However, the eggshell was not well enough preserved to describe its microstructure. We have also been unable to define the shell layer on egg fragments from the same locality. This shell may have a new type of structure or it may just be badly abraded (Figs. 26, 27). An egg similar in size and shape was found in the Upper Cretaceous of Montana (Figs. 28, 29, 30). The shell structure is avian-like. However, since the radiograph did not show any embryonic remains, the identification of this egg is still an open question. Dughi and Sirugue (1962) found avian eggs and eggshell in the Eocene of France and attributed them to Diatryma, a large voracious groundbird.

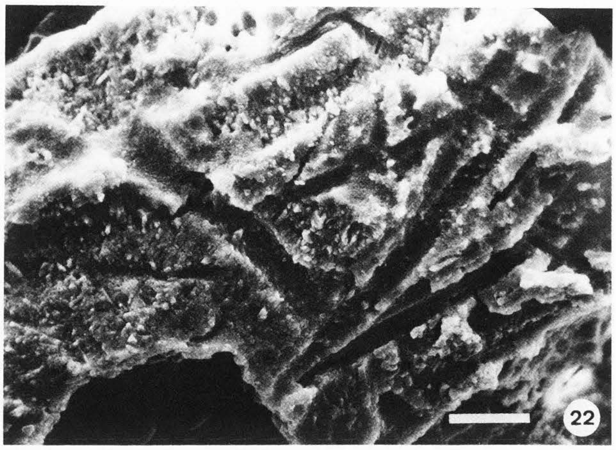
Much has been published on ratite eggs and their thick eggshells (e.g., Dughi and Siruge, 1964; Erben, 1970; Schmidt, 1957; Sauer, 1972, 1976, Tyler and Simkiss, 1960). Thick eggshell fragments with a ratite pore pattern have been found in the Eocene of Wyoming and Colorado (Hirsch, unpublished).

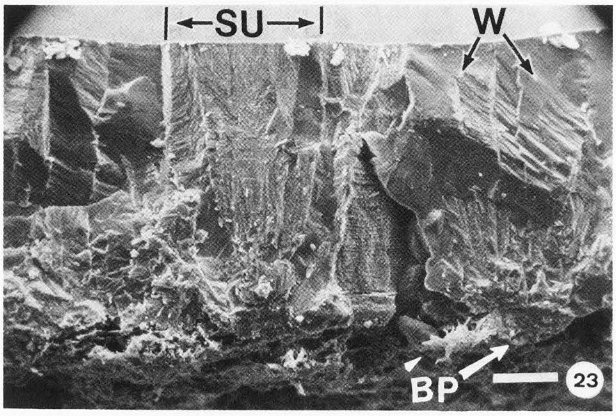
Although neognathan eggs are smaller, and thus more fragile, they have been reported from numerous places around the world, especially from the Tertiary. VanStraelen (1928) summarizes this literature and suggests that these eggs are so abundant because they come from ground nests belonging to water or shore birds. We have studied a number of neognathan eggshells from the Ceozonic of North America. These are summarized generally below:

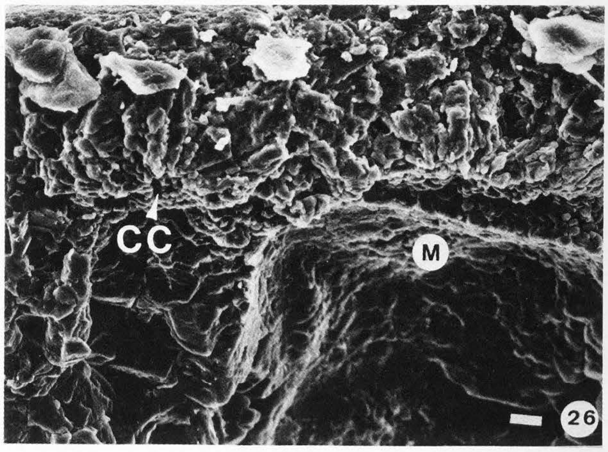
Crane-like fossil eggs (one of them with embryonic remains) from the Eocene of Wyoming have been described in a preliminary report by Hirsch and Bowles (1978). Although the mammillae of a sandhill crane (Fig. 31) are very similar to those of the Eocene eggshell (Fig. 32), the structure in radial view (Figs. 33, 34, 35, 36) differs somewhat. However, on a similar scale structural divergence has been observed in seven different modern crane species (Miller, pers. comm.; Hirsch, preliminary unpublished study).

In the Eocene of Colorado we found an egg, eggshell, and some bird bone embedded in very fine sandstone. The sediments suggest a nesting site on a sandy river beach, point bar, or island. Another site produced eggshell with an avian-like structure but with an unusually structured outer surface (Figs. 37, 38).

Numerous eggs have been reported from the Oligocene Badlands in South Dakota and Nebraska (Farrington, 1899; Troxell, 1916). We have examined over 100 of them and can distinguish four different types. The spheroidal egg type is always identified as a turtle egg. However, two of these in which we have studied the microstructure are definitely avian and could be owl eggs (Hirsch, unpublished). In other eggs the calcareous layer, and often the whole egg,







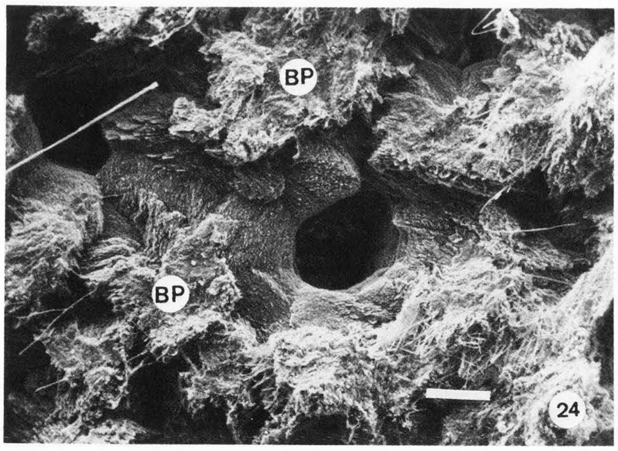


Figure 22. Same specimen as in Figure 21. Inner surface of eggshell; SEM; Note impressions of fibers on basal plate group. Bar=10 µm.

Figure 23. Freestanding eggshell; SEM; alligator (*Alligator mississippiensis*, UCM-OS479). Radial view. Note shell units (SU), basal plate groups (BP) and wedges (W). Bar=100 µm.

Figure 24. Inner surface of eggshell; SEM; crocodile (*Crocodylus niloticus*, UCM-OS478). Note crystalline structure and basal plate groups (BP). Bar=100 µm.

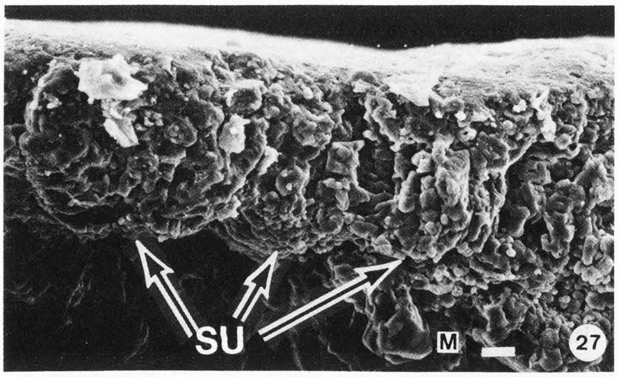
Figure 25. Inner surface of eggshell; SEM; alligator (*Alligator mississippiensis*, UCM-OS1049). Treated with KOH. Note impressions of fibers on basal plate group. Bar=10 µm.

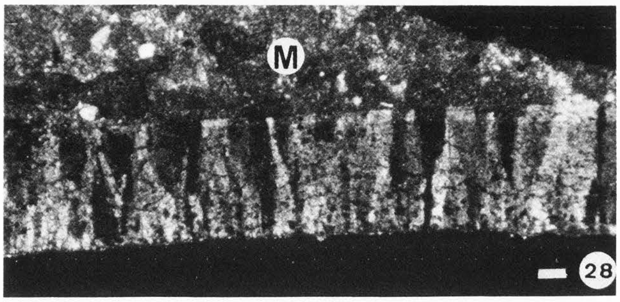
Figure 26. Freestanding eggshell; SEM; fossil bird, Upper Cretaceous, Mongolia (AH CCCP 3142/410). Radial view. Note ?central core (CC) of mammillary cone or ?shell unit. Matrix = M. Bar=10 µm.

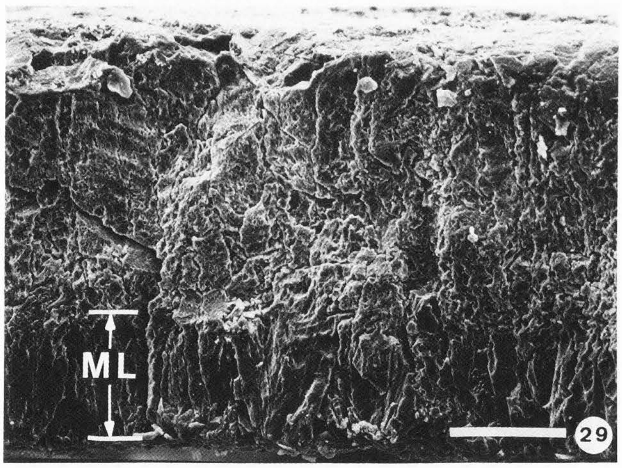
is replaced by agate; but in a few cases a faint indication of the original shell structure can still be observed (Hirsch, 1979).

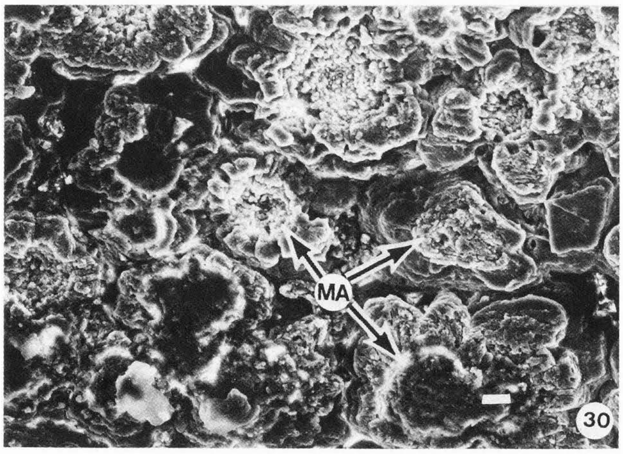
In general neognathan eggshell in North America is known mainly from the Eocene and Oligocene and reveal a divergency of forms. They are poorly known and badly in need of study.

Upper Cretaceous eggshell. The Cretaceous has produced an abundance of eggs and eggshells. The large *Hypselosaurus* eggs from France and the nesting sites with complete clutches in Mongolia and China have received









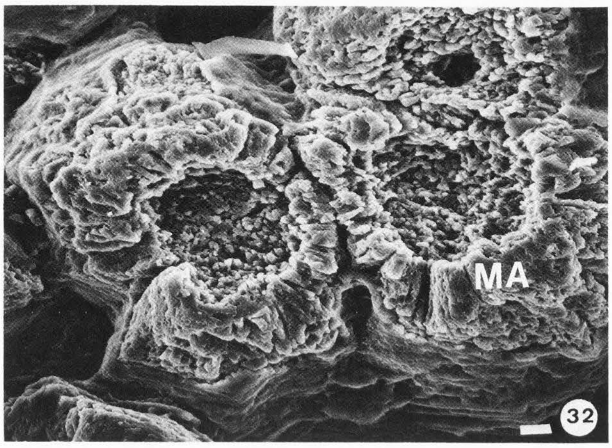


Figure 27. Freestanding eggshell; SEM; same specimen as in Figure 26. Radial view. Note ?shell units (SU) or mammillary cones. Matrix = M. Bar=10 μm.

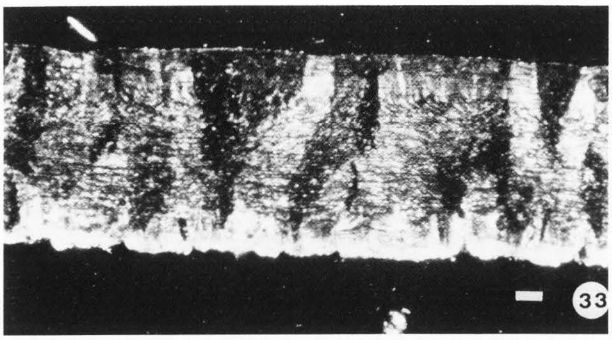
Figure 28. Radial thin section; PLM; fossil ?bird, Upper Cretaceous, Montana (PU 23396). Polarized. Note avian-like extinction pattern. Outer surface of shell embedded in matrix (M). Bar=100 μm.

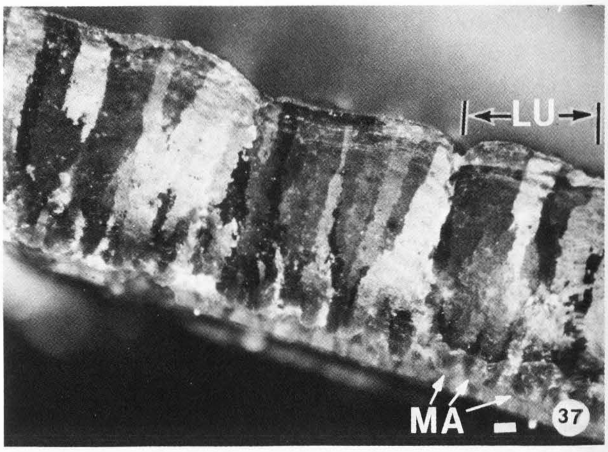
Figure 29. Freestanding eggshell; SEM; same specimen as in Figure 28. Radial view. Note the pronounced layer of slender mammillae (ML). Bar=100 μm.

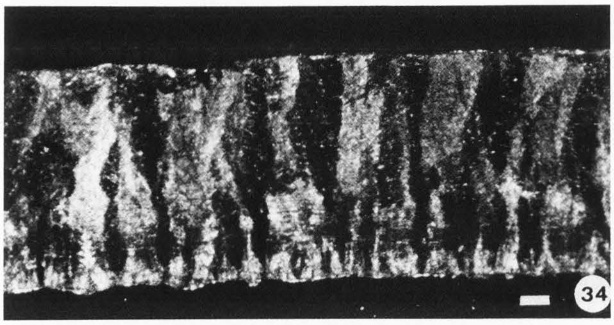
Figure 30. Inner surface of eggshell; SEM; same specimen as in Figure 28. Note the avian-like mammillae (MA). Bar=100 μm.

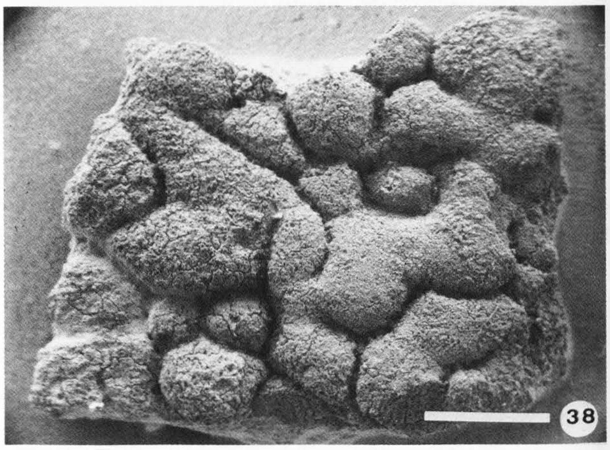
Figure 31. Inner surface of eggshell; SEM; bird (Grus canadensis tabida, UCM-OS1131). Note mammillae (MA). Bar=10 μm.

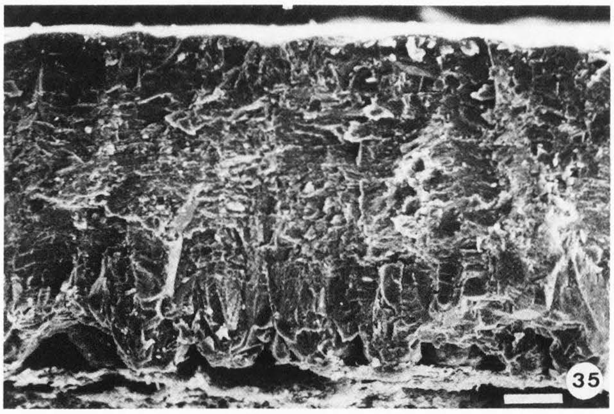
Figure 32. Inner surface of eggshell; SEM; fossil bird, Eocene, Colorado (UCM 47524). Note mammillae (MA). Bar=10 μm.

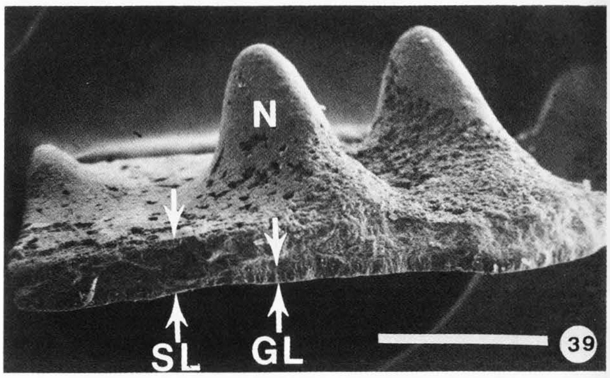


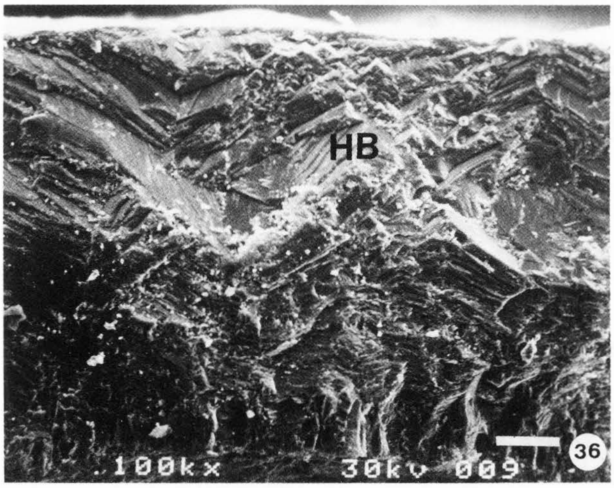












much attention (Dughi and Sirugue, 1957, 1966; Lapparent 1947, 1957; Thaler, 1965; Erben, 1970; Erben and Newesely, 1972; Erben et al, 1979; Sochava, 1969, 1971; Young, 1959, 1965; Zhao, 1979; Kerourio, 1982). In the United States, a Cretaceous eggshell was reported from Montana by Jepsen (1931) and Sahni (1972), and Jensen (1966) has also described an eggshell from the Upper Cretaceous of Utah. A few years ago spectacular finds of nesting sites were reported from Montana (Horner, 1982, 1984; Horner and Makela, 1979).

Figure 33. Radial thin section; PLM; bird (Gymnogyps californianus, UCM-OS1123). Polarized. Bar=100 μm.

Figure 34. Radial thin section; PLM; bird, Eocene, Wyoming (UCM 47602). Polarized. Bar=100 μm.

Figure 35. Freestanding eggshell; SEM; bird (Grus leucogeranus, UCM-OS1133). Radial view. Bar=100 μm.

Figure 36. Freestanding eggshell; SEM; fossil bird, Eocene, Wyoming (UCM 47602). Radial view. Note herringbone pattern (HB). Bar=100 μm.

Figure 37. Radial thin section; PLM; fossil bird, Eocene, Colorado (UCM 47524). Polarized. Note unusual structure pattern probably caused by outer vermiculate sculpturing. Several mammillae (MA) seem to form a larger unit (LU). Bar=100 μm.

Figure 38. Outer surface of eggshell; SEM; same specimen as Figure 37. Note the pronounced vermiculation of surface. Bar=1 mm.

Figure 39. Freestanding eggshell; SEM; fossil, unidentified, Upper Cretaceous, Utah (UCM 54318). Radial view. Note nodes (N) are higher than shell layer (SL), innermost layer is gecko-like (GL). Bar=1 mm.

Several attempts have been made to classify dinosaur eggs, as well as other Cretaceous eggshells. Sochava (1969) divided the eggshells from the Gobi Desert into three groups based on the structure of their air canals. Based on comparison to modern shell, Sochava (1971) recognized two types of eggshell structure, avian-like (ornithoid) and turtle-like (testudoid). Erben et al (1979) classified the eggs from Mongolia, France and Spain into four types, which agreed more or less with Sochava's (1969) divisions according to their microstructure and air canals. In contrast to Sochava and Erben, Dughi and Sirugue (1976) divided the Cretaceous eggshells into avian and reptilian structure without considering the similarity of structure between eggshells of some dinosaurs and birds. Williams et al (1984) distinguished at least four types of eggshell from France based on shell microstructure, porosity and shell thickness, whereas Dughi and Sirugue (1976) recognized about ten types. Young (1959) divided the Chinese dinosaur eggs into two groups based on their shape. Zhao (1979) established three families for these eggs, and a fourth family for the testudoid eggs which are typical for France and Spain. Jensen (1966) divided the eggshells found in Utah by their external shell structure into three classes.

All these attempts are based on selected samples of eggshell from different parts of the world and on different morphological features. As yet there is no useful, worldwide, integrated classification. In the meantime more and more Cretaceous eggshells have been found throughout the world.

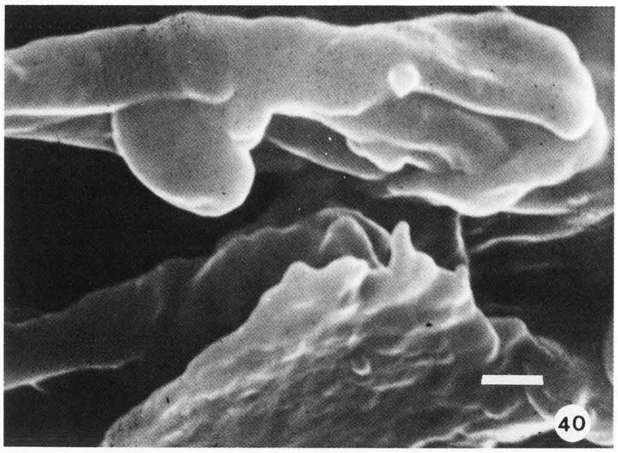
Preliminary examination of three specimens of these new types show that in one specimen the nodes are higher than the eggshell layer is thick (Fig. 39), suggesting that maybe a fibrous organic matrix, as found in some modern geckos, was reinforcing this relatively thin layer. Under high magnification,we detected fiber-like material on the inner surface of this specimen (Fig. 40). Another specimen has a very pronounced nodose outer surface (Figs. 41, 42) with large pore canals penetrating these nodes. In both specimens the shell layer is composed of two structurally different layers, the innermost almost gecko-like. The third specimen shows a pronounced horizontal layering (Figs. 43, 44) not observed before in fossil eggshells (Hirsch, unpublished).

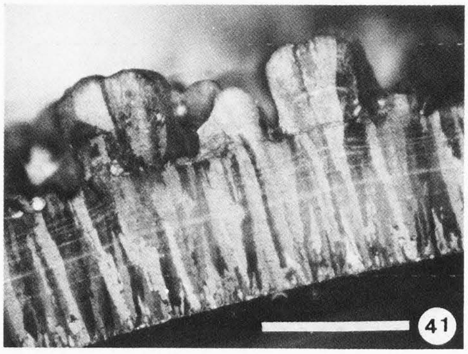
It has to be emphasized that not all Cretaceous eggshell is dinosaurian. It can be assumed that we are also sampling bird, lizard, snake and perhaps other types of eggshell.

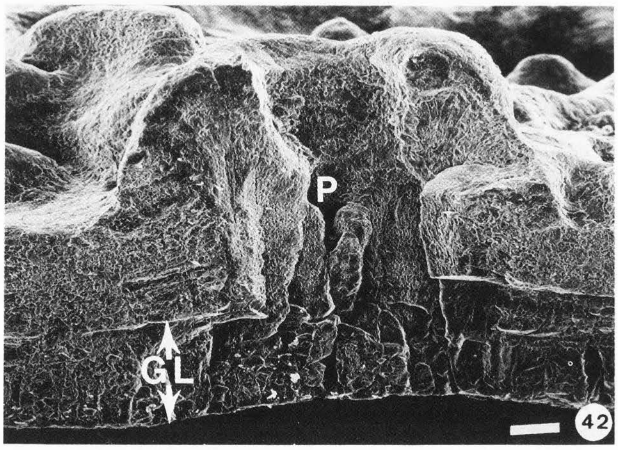
Upper Cretaceous dinosaurian eggshell from Montana. To establish dinosaur egg types complete egg specimens are needed; eggshell fragments are insufficient. Egg size, shape, sculpture of the outer surface, pore pattern, shell thickness, even the preservation of the shell, vary somewhat within the same clutch and even with the same specimen. To assign a particular egg to a particular dinosaur taxon is even more difficult, and to base this assignment on associated fauna or bones is a questionable practice. The only positive identification is if the egg contains identifiable embryonic remains or the nest contains hatchlings. The eggs from France have been assigned to Hypselosaurus based on the associated bones (Dughi and Sirugue, 1957), whereas Sochava (1972) classified an egg as protoceratopsian based on embryonic remains found in it.

The Upper Cretaceous of North America has yielded an abundance of eggshell fragments. However, only recently were complete eggs, some with embryonic remains and hatchlings, found in Montana (Horner, 1982, 1984; Horner and Makela, 1979). In two clutches the eggs had embryonic remains which could be identified as hypsilophodontid; other nests contained hatchlings assigned to a hadrosaur; and a third kind belonged to an unknown dinosaur species (Horner, 1982, 1984).

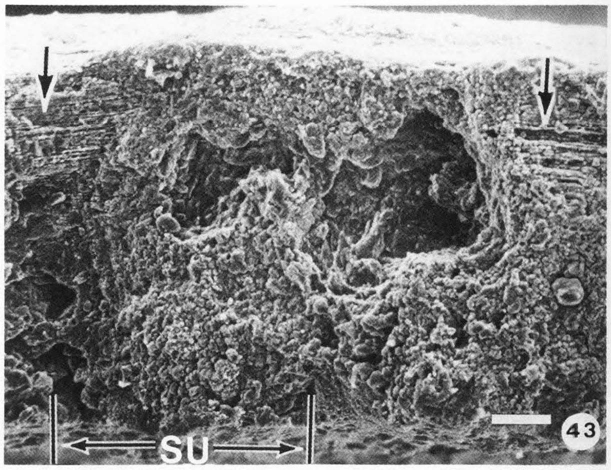
These eggs, which are in the process of being described, differ from each other in size, shape and sculpture of the outer surface. The hypsilophodont egg has a smooth outer surface with faint longitudinal striations. The surface of the hadrosaur egg is sculptured with ridges and the unknown species with nodes (Fig. 45). In radial views the difference between them is even more pronounced. The hypsilophodont egg has a typical avian structure as the polarized photo and the micrograph show (Figs. 46, 47). The eggshell structure is tighter and less porous in the eggs of hypsilophodont and unknown species than in the hadrosaur (Figs. 45, 47-51). The pore canals also differ. In the

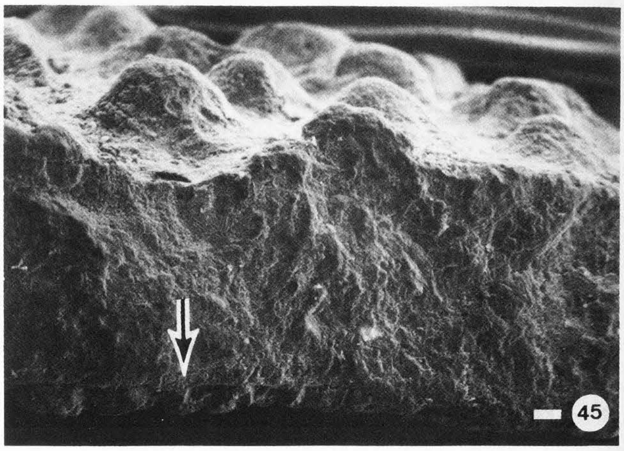






hypsilophodont they are straight and narrow, in the unknown species they are also straight but of larger diameter (Figs. 52, 53). The areation canals of the hadrosaur eggshell are irregular and of varying diameter (Figs. 48, 54). The illustrated inner shell surfaces (Figs. 50, 51) show cratered mammillae, suggesting a resorption of calcium by the embryo (cf. Schwarz and Fehse, 1957). Note the mammilla of an unhatched egg (Fig. 55). The radial view of an eggshell of an unknown species, embedded in epoxy, lapped and etched with EDTA, shows a fibrous-looking layer between the mammillary and shell layer (Fig. 56). This phenomenon could not be observed in the other two shell types although they were





treated in the same fashion.

Older eggshells. Not too many reports of eggshells older than the Late Cretaceous can be found in the literature. Eggshells from the Lower Cretaceous are, as yet, only known from Utah and their macrofeatures have been described by Jensen (1970). Preliminary studies by the authors suggest an even larger variety. However, complete eggs have not yet been found.

Figure 40. Enlargement of Figure 39. ?Petrified membrane and fibers. Bar=1 µm.

Figure 41. Radial thin section; PLM; fossil, unidentified, Upper Cretaceous, Utah (UCM 49395). Polarized. Note extinction pattern continuous through whole shell layer, including nodes. Bar=1 mm.

Figure 42. Freestanding eggshell; SEM; same specimen as Figure 41. Note very nodose surface, pore canal (P) through center of node, gecko-like layer (GL). Bar=100 µm.

Figure 43. Freestanding eggshell; SEM; fossil, unidentified, Upper Cretaceous, Utah (UCM 54319). Note open structure of shell layer, pronounced horizontal layering (arrows), large shell units (SU). Cavities might be caused by dissolution. Bar=100 µm.

Figure 44. Enlargement of Figure 43. Bar=10 µm.

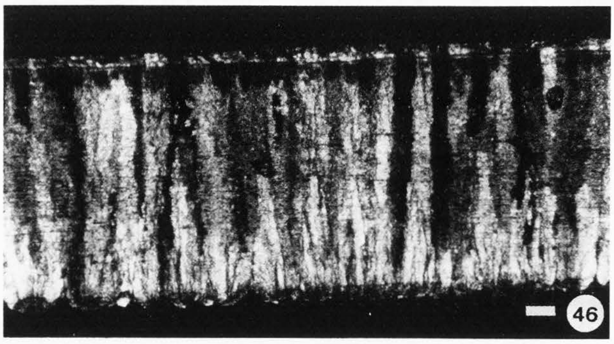
Figure 45. Freestanding eggshell; SEM; unknown dinosaur species, Upper Cretaceous, Montana (UCM 54320). Radial view. Note nodose surface, dense structure of shell layer, and the peculiar layering above mammillary layer (arrow). Bar=100 µm.

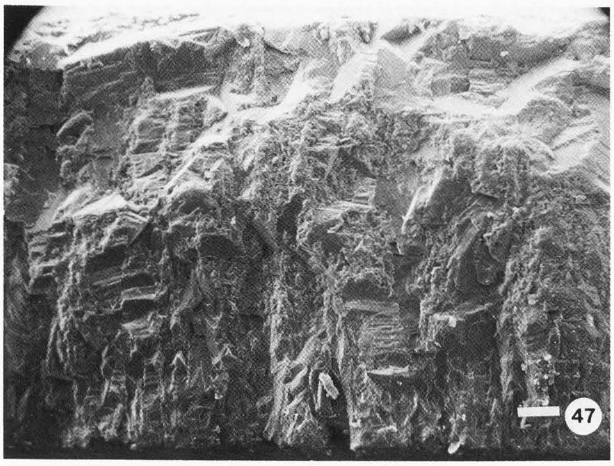
Figure 46. Radial thin section; PLM; hypsilophodont dinosaur, Upper Cretaceous, Montana (PU 22591). Polarized. Note avian-like extinction pattern. Bar=100 µm.

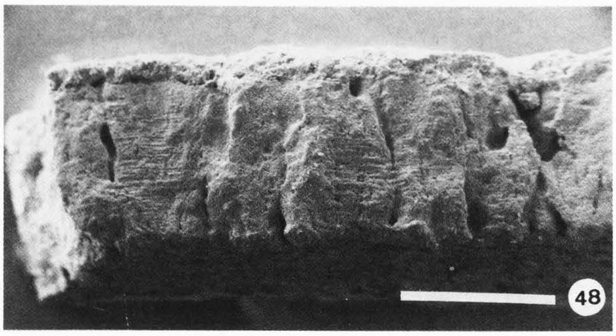
Figure 47. Freestanding eggshell; SEM; same specimen as in Figure 46. Radial view. Note dense structure of shell layer with slender columns. Bar=100 µm.

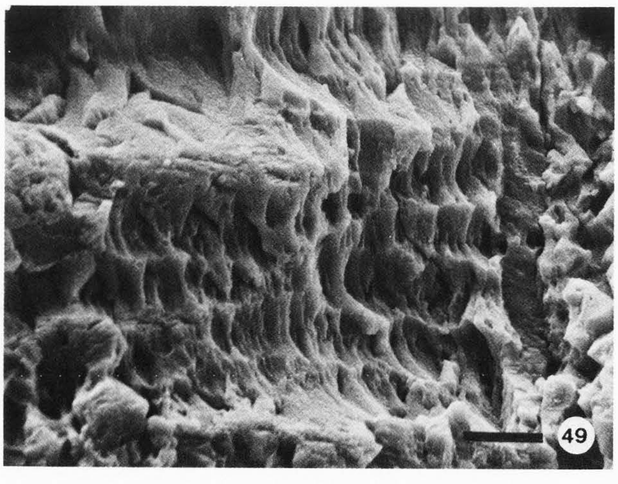
Figure 48. Freestanding eggshell; SEM; hadrosaur dinosaur, Upper Cretaceous, Montana (PU 22432); Radial view. Note horizontal layering, more open structure of shell layer, and irregularity of pores. Bar=1 mm.

Figure 49. Enlargement of Figure 48. Note vesicle holes. Bar=10 µm.



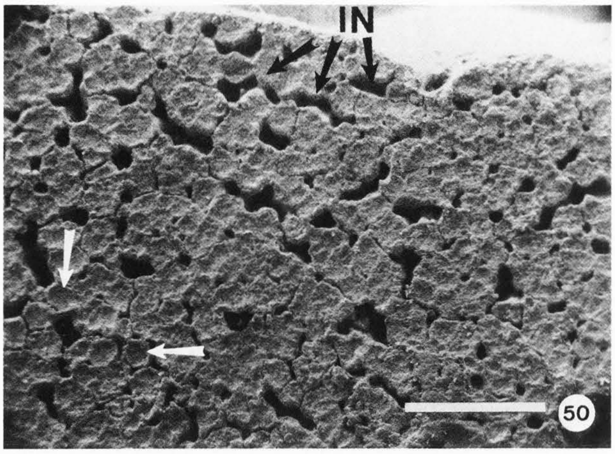


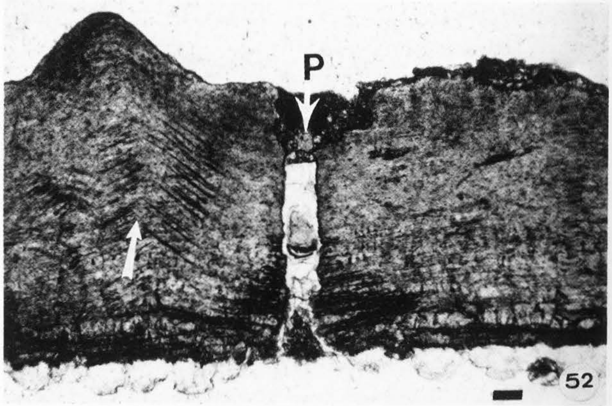


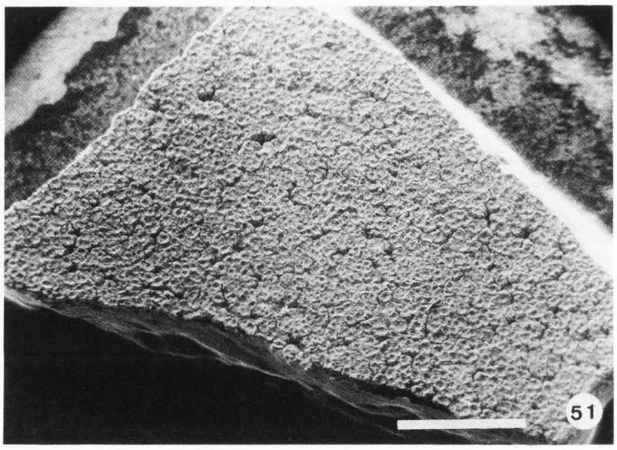


The Jurassic of Colorado has yielded a small amount of eggshell, although too little to study comprehensively. However, preliminary studies indicate that there may be more than one type of shell. Several of the fragments, although they are composed of calcite, may be turtle eggshell (Figs. 57, 58). This assumption was strengthened after etching the specimen and thus exposing a fine radiating crystal structure (Fig. 59). However, it is too early to come to any conclusions.

Triassic eggshell is only reported from Argentina and South Africa. Bonaparte and Vince (1979) described an incomplete juvenile skeleton from a nest with two eggs but the eggs have not yet been described. Kitching (1979) reported six eggs, associated with embryonic remains but has described little about the macrofeatures and the supposedly membrane-like shell of the eggs.







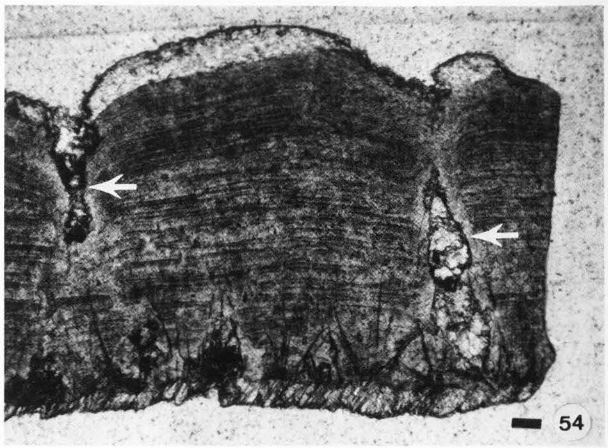


Figure 50. Inner surface of shell; SEM; same specimen as in Figure 48. Note cratered mammillae (arrow) and interstices (IN) between them. Bar=1 mm.

Figure 51. Inner surface of shell; SEM; same specimen as in Figure 46. Note tightly abutted and cratered mammillae pattern with few small interstices. Bar=1 mm.

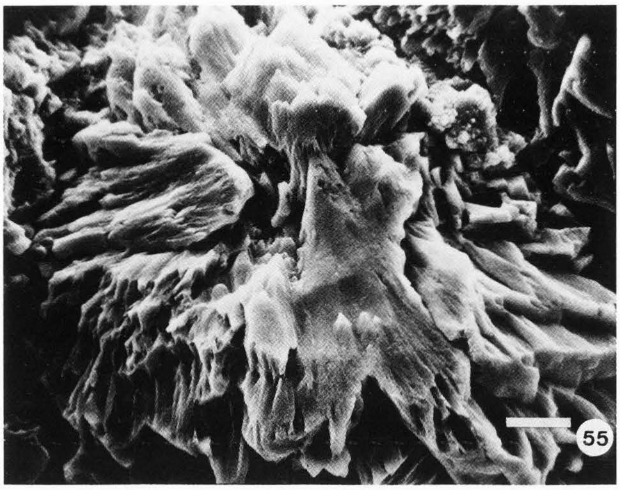
Figure 52. Radial thin section; PLM; same specimen as in Figure 45. Not polarized. Note large straight pore canal (P), herringbone pattern (arrow). Bar=100 μm.

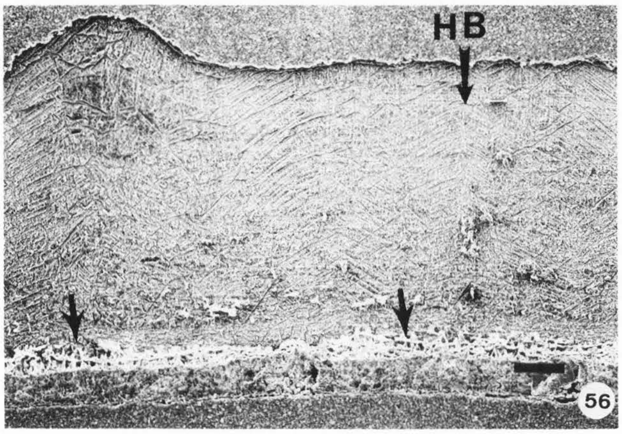
Figure 53. Radial thin section; PLM; same specimen as in Figure 52. Polarized. Note extinction pattern more aberrant. Bar=100 μm.

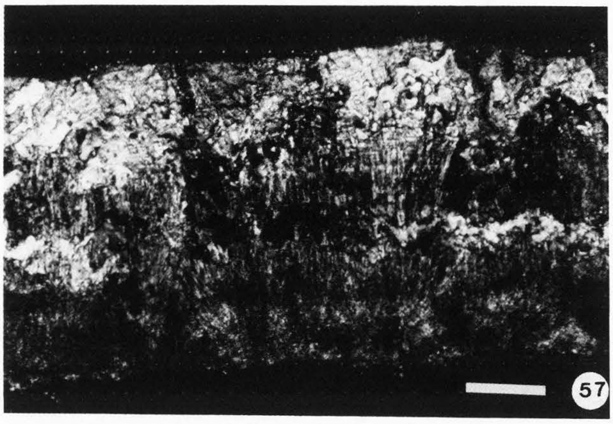
Figure 54. Radial thin section; PLM; same specimen as in Figure 48. Not polarized. Note irregular pore canals (arrows). Bar=100 μm.

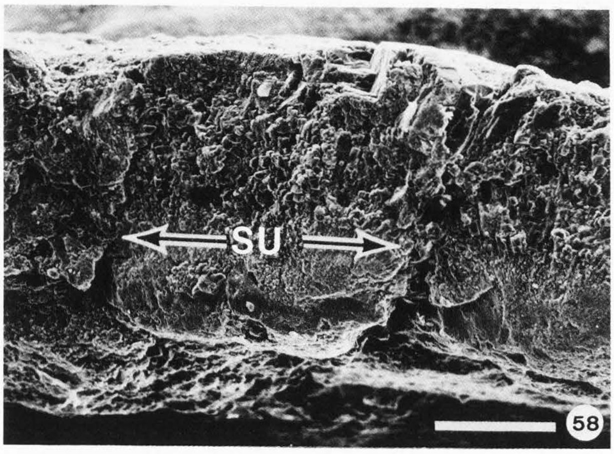
Conclusions

Only the rigid-shelled eggs have a good chance of fossilization. In the other two groups which encompass the majority of amniote eggshells, the organic matter is the dominating element of the eggshell, and the calcareous matter is either poorly organized or not organized. Thus the crystalline matter will not be recognized as eggshell after the organic matter has decayed. Rigid-shelled eggs with modern type eggshell structure can be traced back into the Eocene for geckos and crocodiles and into the Late Cretaceous for turtles and birds.









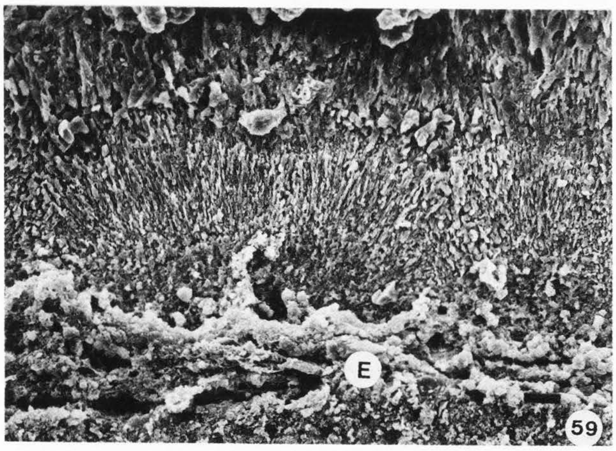


Figure 55. Inner surface of shell; SEM; different specimen of PU 22591. Enlargement of uncratered mammilla. Bar=10 μm.

Figure 56. Eggshell embedded in epoxy; SEM; unknown dinosaur species, Montana (MOR 301). Radial view. Lapped, etched in EDTA. Note herringbone pattern (HB) and membrane-like layer (arrows). Bar=100 μm.

Figure 57. Radial thin section; PLM; fossil ?turtle, Jurassic, Colorado (LACM 120502). Polarized. Note fine radiating structure composed of calcite. Bar=100 μm.

Figure 58. Freestanding eggshell; SEM; fossil ?turtle, Jurassic, Colorado (UCM 54321). Radial view. Note large shell units (SU). Bar=100 μm.

Figure 59. Eggshell embedded in epoxy (E); SEM; fossil ?turtle, Jurassic, Colorado (UCM 54322). Lapped and etched with EDTA. Note turtle-like structure. Bar=10 μm.

Fossil eggshells cannot be interpreted as straight forwardly as modern eggshells. In the first place shell fragments are much more abundant than whole eggs. When working only with shell fragments, we do not know the size and shape of the egg, or if the sculpturing of the outer surface was uniform and continuous over the whole surface or if it was discontinuous or variable. Secondly, diagenesis often changes the eggshell structure or the original mineral may be replaced by another of different chemical composition, as has been demonstrated clearly in the chelonian and avian eggshell. Thirdly, in the older periods we are confronted with the problem of extinct egg-laying animals. Here it is difficult to identify the egg-layers. For example, we are not able to differentiate between avian eggshells and dinosaurian eggshells with avian-like shell structure. Also, there are new structural types with no comparison to modern eggshells as demonstrated by the eggshells from the Upper Cretaceous of Utah. In addition, there may have been changes in the environment which caused changes in eggshell structure.

However, on the positive side we do find, although not often, complete eggs, eggs with embryonic remains, whole nests and even nesting sites as in, for example, the dinosaur material from Montana. Also very important is the progress that has been made in the study of modern eggshells in recent years. In addition, readily available modern techniques such as the SEM, x-radiography, analyses of elements, minerals, amino acids and so on may enable us one day to assign fossil eggs or even eggshell fragments to lower taxonomic units, perhaps even to species.

Eggs and eggshells are more than just curiosities. The nesting sites in Montana have shown that eggs may tell us about the environment and about the habits of the animals that laid the eggs. Finally, fossil eggs and eggshells are more abundant than generally thought and are in dire need of being studied and described.

Acknowledgments

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Discussion with Reviewers

S. E. Solomon: Which methods were used for the determination of the crystal form of the calcium carbonate?
Authors: The mineralogical analyses were made by x-ray diffraction using a Phillips Norelco Generator.

S. E. Solomon: I strongly advise against the use of "chemical" treatment with examining eggshell, since by its very nature, it alters the morphology of the structure being examined.
Authors: Indeed, excessive chemical treatment will alter eggshell structure; however, to study certain features, this is done differentially for either the organic or inorganic matter, either one or the other must be reduced or removed. As long as this is done in a judicious manner, there is no reason not to use these techniques.

F. E. Grine: I would like to see a bit more interpretation of the fossil material. For example, there is at present some question as to whether the dinosaurs are more closely related to birds or to crocodiles. Does the comparative structure of known (i.e. unquestionable) dinosaur eggshells shed any light on this question?
Authors: Before inferences may be drawn regarding the evolutionary significance of eggshell structures, many unquestionable samples will have to be located and correlated world-wide. At present, the study of eggshell structure, modern or fossil, is in its infancy, and too few specimens are currently available to make the desired inferences.