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CONTENTS

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Contents

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Fossil Eggs in the Lower Cretaceous of Utah

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Brigham Young University

ABSTRACT.—Discovery of fossil eggshell localities in the Lower Cretaceous of Utah is a major contribution to known fossil eggs. Two recent discoveries of eggshell lie about 145 miles apart in equivalent, transitional formations of the basal Cretaceous. These materials are more varied in external ornamentation and display features of shell structure not observed in the Upper Cretaceous eggshells reported earlier from Utah (Jensen, 1966).

Organic residue and variable shell microstructure of these new materials suggests a complex uterine histology not apparent in modern avians. Century-old avian eggshell nomenclature is inadequate and does not effectively describe their nature.

Rapid formation of an egg, as compared to the slow growth of the skeleton, justifies detailed studies of fossil eggshell microstructure and chemical content, as a means of obtaining valuable paleophysiological information. Subseasonal variation in environment, as well as metabolic fluctuation due to nutrition and health, is reflected in the fast growing eggshell but not so much in the slow growing bony skeleton.

Studies of fossil reptilian and pro-avian eggshells may also provide a better understanding of the development of modern egg forms.

A system for assignment of convenient names will be used in this paper which will not involve fossil eggs in vertebrate taxonomy but make a more exact reference possible in comparative work.

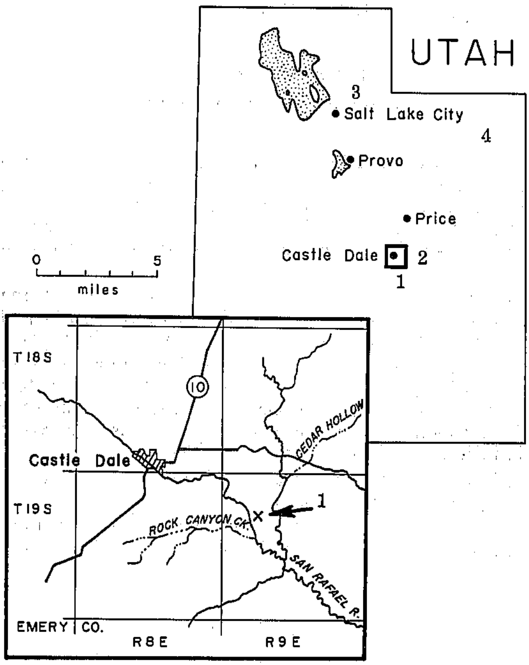
CONTENTS

TEXT

ILLUSTRATIONS

INTRODUCTION

Fossil egg fragments were first discovered in the Lower Cretaceous of North America in 1965 by Mr. Carlyle Jones. They were found in the Cedar Mountain Formation near Castle Dale, Utah. The following year Dr. Robert E. Sloan recognized eggshell fragments among fossils collected from the Lower Cretaceous Kelvin Formation, east of Coalville, Utah. These localities are both in the basal section of the Cretaceous and lie about 145 miles apart. Structural deformation has left the Kelvin vertically disposed at the egg locality, providing only a small collecting area. Shell fragments occur at random in a thin, clay-pebble conglomerate and apparently represent several varieties of vertebrates.



TEXT-FIGURE 1.—Locality map. 1—Upper Cretaceous North Horn Formation locality (Jensen, 1966); 2—Lower Cretaceous, Cedar Mountain Formation locality; 3—Lower Cretaceous, Kelvin Formation locality and 4—Dinosaur National Monument Quarry.

Materials were collected for a distance of about 380 meters along the strike of the beds.

Rocks at the Cedar Mountain egg locality are nearly horizontal, with channel sands occurring at random in soft shales of the fossiliferous area. Eggshells collected were completely weathered from their original matrix so the exact horizon of their source can not be determined. It appears, however, that they originate directly below the channel sands and so would occur in the uppermost Cedar Mountain beds.

This eggshell discovery lies within twenty miles of fossil egg localities in the Upper Cretaceous North Horn Formation (Jensen, 1966). The chief value of this proximity may be an opportunity to observe certain aspects of vertebrate evolution during the Cretaceous as it occurred in one geographic region. The two formations are separated stratigraphically by approximately 5,000 feet of Upper Cretaceous sediments, with the intervening Mancos Shale representing a major marine invasion between two periods of terrestrial egg production. Sandstones of the Mesaverde Group overlie sands and shales of the Mancos Group.

The Cedar Mountain Formation was described by Stokes (1944) and is equivalent to the Burro Canyon Formation of Stokes and Phoenix (1948) in other areas of Utah and western Colorado. The Cedar Mountain Formation is transitional from the Upper Jurassic Morrison formation to the basal Cretaceous.

DESCRIPTION

Landois (1865) described the depth of eggshell above the mammillae as being the "spongy layer" of the avian egg. He made this designation after hard calcium salts had been dissolved leaving a spongy mass of protein fibers. The name thus applies to a residue rather than a complete structure and although it has been in general use for a century by avian physiologists it is nonetheless unrealistic and misleading. The upper zone is actually a compact spherolithic, crystalline structure, easily seen in magnified thin sections, which becomes quite dramatic under polarized light. Crystalline structure is the main characteristic of this "upper" zone before chemical alteration. It has therefore been termed the "prismatic zone" in more recent times by van Stralen (1925).

The simplest and most effective description of Utah Cretaceous eggshell structure is attained by designating an *upper* and *lower* prismatic zone rather than by use of the terms "mammillary layer" and "spongy layer." These Utah materials are more complex than those of modern avians with many layers which divide easily into two zones. The use of two "layers" is therefore inadequate in any description of their microstructure. This paper will depart from the customary avian eggshell nomenclature by defining shell structure on the basis of *upper* (outer) *prismatic zone,* or *upper zone,* and *lower* (inner) *prismatic zone,* or *lower zone.* "Mammillae" is a useful term, but no reference will be made to "spongy layer."

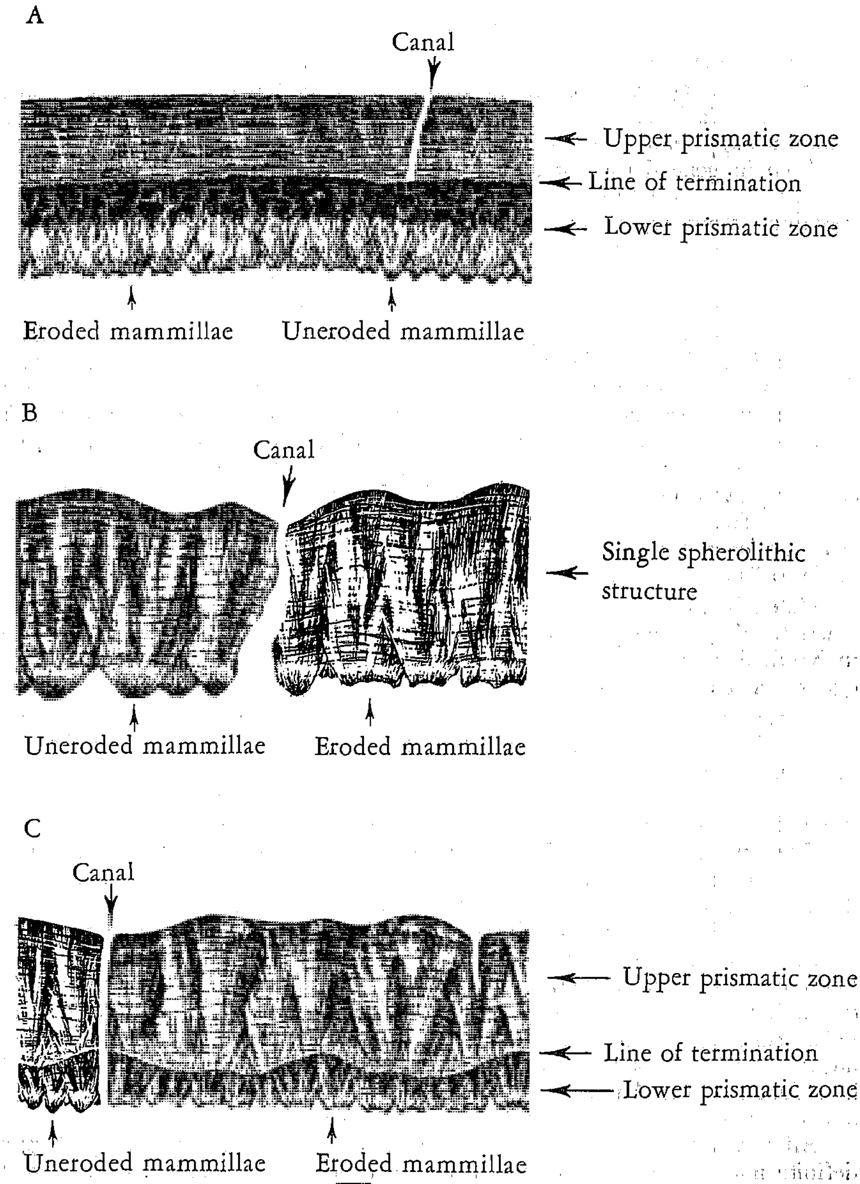
Materials from the Cedar Mountain and Kelvin formations represent the oldest fossil egg fragments which may be attributed to birds or dinosaurs found in North America, although a clear distinction cannot yet be made between the eggs of these two groups.

A variety of ornamentation and microstructure is present in shells from both localities, indicating the existence of several genera and species of unknown egg-laying vertebrates in the lower Cretaceous. Most shell fragments display a deeply textured or sculptured surface (Plates 1 to 3) with the smooth surfaced, avian-like forms of the Upper Cretaceous (Jensen, 1966) being rare.

The structure of certain Upper Cretaceous eggshells indicates that calcification of the prismatic zone progressed with little interference after formation of the mammillae. Their prismatic spheroliths appear to be continuations of a radial, crystalline structure originating within the mammillae (Text-fig. 2, C).

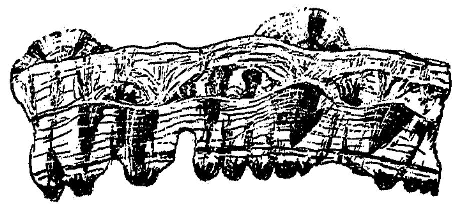
All materials from the Cedar Mountain and Kelvin formations display a lower prismatic zone with the most remarkable definition of any examined by the author. The basis for this unusual structure is a variety of laminate and radial cuneate, protein-rich fibers. These probably resulted from a complex uterine histology, not yet observed in avians, which will be discussed in detail in a future paper. Analyses of protein and amino acid residues in Utah Cretaceous eggshells are presently being carried out and will be discussed later.

All Lower Cretaceous Utah materials studied display evidence suggesting a definite interruption after formation of the lower zone. Examination of radial thin sections under polarized light reveals that spheroliths of the lower zone were terminated before deposition of the upper zone began. The top of the lower zone then presented an undulating or mounded appearance. In cross-section this terminal surface appears as a rather distinct, undulating line marking an interval between lower and upper shell formation (Text-fig. 2, C). The egg may have paused for a time before entering the uterus or passed through a section of oviduct devoid of calcification cells.



TEXT-FIGURE 2.—Radial sections of fossil eggshell drawn with polarized light. A—Upper Cretaceous, smooth-shell variety. Pore canal, or tube, penetrates only upper zone. Dense concentration of protein residues in upper part of lower zone. Very small mammillae. Approx. thickness = 2.0 mm. B—Upper Cretaceous, ornamented-shell variety. Simple crystalline structure. Large mammillae. Large, tapered pore canal, penetrating entire depth of shell. Approx. thickness = 2.1 mm. C—Typical structure of all Lower Cretaceous specimens regardless of shell thickness or the great variation in external ornamentation. Small undulating "line of termination" marks the crystallization materials from both localities. A similar "line" occurs in some Upper Cretaceous *avian-like* eggshells except it is almost straight instead of undulating.

A

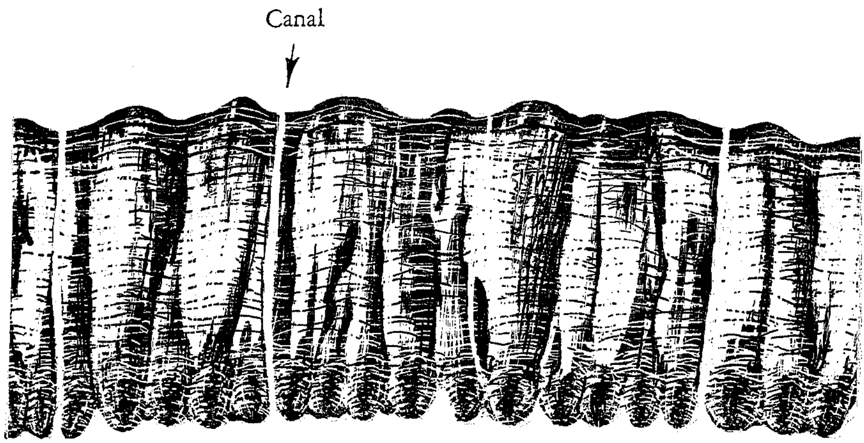


Modern alligator (polarized light) X 20

B

Modern Emu (polarized light) X 20

C



Dinosaur, late Cretaceous, France. (polarized light) X 20

TEXT-FIGURE 3.—Radial sections comparing modern reptile and flightless bird eggshells with one from a dinosaur. A—Alligator eggshell has complex crystalline structure. Mammillae are well defined but interrupted by large inzones of crystallization. Approx. thickness = .82 mm. B—Ratite eggshell. Simple crystalline structure similar to a dinosaur. Approx. thickness = 1.0 mm. C—Dinosaur eggshell with well defined mammillae but no exact distinction between an upper and lower zone. Approx. thickness = 2.3 mm.

After an indeterminate interval, formation of the upper zone began with a continuation of the deposition of thin horizontal protein sheets, but with a total absence of the thin, radial plumes of protein found in the lower zone.

Dense, radial, protein-rich fibers darken the proximal mammillar points whereas the content of laminated, organic matter in the upper zone is sufficient to color the shell a dark, brownish gray. Specimens of fossil eggshell examined by the author from the Cretaceous of Mongolia and France were observed to be light to dark tan. There is no apparent explanation for the greater protein density in Utah materials.

In the outer zone of the Lower Cretaceous eggshells, stratified proteins do not flow conformably across the undulating line of contact between the zones but instead appear to lie horizontally in its valleys. These proteins were deposited simultaneously with the growth of the upper or outer zone rather than prior to it.

Deposition of the combined organic and mineral content of the upper zone was registered within the interstices of a loose, fibrous latticework of protein. Various respiratory pores, produced by later shrinkage of some of these matrix fibers, penetrate directly from the shell membrane to the outer surface of the shell. Apparently a three-dimensional protein structure was produced upon the surface of the membrane prior to the beginning of hard shell deposition or at least concurrent with the origin of mammillae. This lattice provided for complete communication of the intermammillary ventilation system with the externally vented pores. It seems unlikely that such a well-organized system was the result of a gradual addition to individual fibers during the entire crystalline growth of the upper zone. Some device involving ionization may have provided

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Explanation of Plate 1

EXTERIOR VIEWS OF DINOSAUR EGGSHELLS

All photographs x5

FIG. 1.—*Oolithes carlylensis* n. sp. is the first variety of eggshell named from the Cretaceous of Utah. Pattern channels partially obstructed by calcite crystals. Cedar Mtn. Fm., central Utah. Approx. thickness = 2.3 mm. BYU E-200, holotype.

FIG. 2.—A variation of *Oolithes carlylensis* n. sp. Subcircular to subangular mushroom nodes are more independent than figure 1. Cedar Mtn. Fm. Approx. thickness = 2.8 mm. (Coated with ammonium chloride for photographic purposes.) BYU E-201.

FIG. 3.—Indefinite pattern. Irregular depressions of random size and shape, subtuberculose in form. Rounded ridges. Cedar Mtn. Fm. Approx. thickness = 2.0 mm.

FIG. 4.—Distinct, raised pattern. Circular to subcircular nodes arranged among intermittent, subparallel to sinuous, truncate ridges. Cedar Mtn. Fm. Approx. thickness = 1.8 mm.

FIG. 5.—Natural erosion pattern. (Coated) This pattern is a striking contrast to dissolution surface seen in figure 8. These patterns result from a differential solubility of crystalline structure.

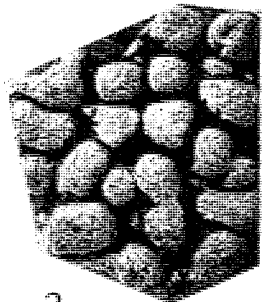
FIG. 6.—Definite pattern of variable sized, oblong nodes. Axes of nodes oppose each other at various angles. Cedar Mtn. Fm. Approx. thickness = 2.3 mm.

FIG. 7.—Indefinite pattern. Irregular pits and cavities of random size and shape. Similar to sculptured surface on an amphibian skull. Ridges tend to sharpness rather than roundness as in figure 3. Small mammillae. Cedar Mtn. Fm. Approx. thickness = 1.8 mm.

FIG. 8.—Natural erosion pattern. (Coated for photo.) Contrast with soluble surface on figure 5. Cedar Mtn. Fm. This pattern obviously originates from a different structure than that of figure 5.

PLATE 1

1



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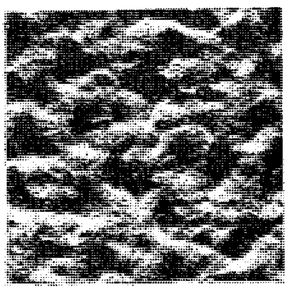

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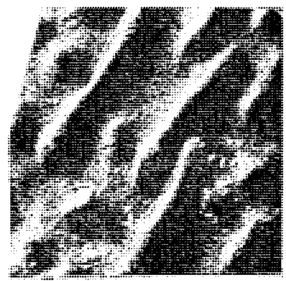

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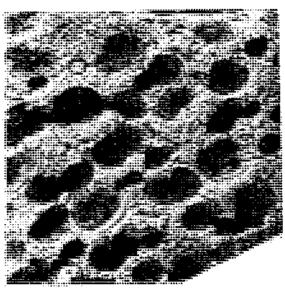

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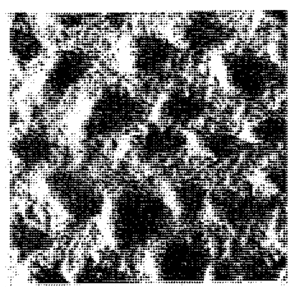

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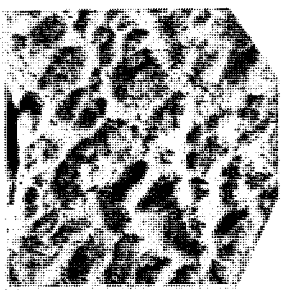

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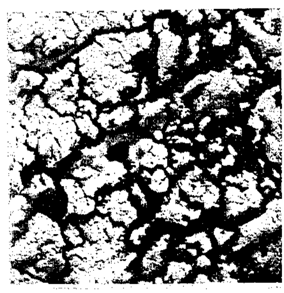

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a means for fusing collangen-like protein granules to the radial tips of lattice fibers during prismatic growth; otherwise, it seems more reasonable that these rod-like fibers originated in tubular cells of the caudal isthmus.

A latticework of fibers, formed amid the surface of developing mammillae, would ultimately provide a ventilating system by fiber shrinkage, but it may also have affected the total shell thickness. Stimulation of the uterine epithelium by a surface of radial fibers on the shell membrane may have caused it to produce the necessary calcium salts until the irritating fibers were completely imbedded. This process is suggested by the formation of a conical orifice seen around many pore openings prior to deposition of the final layer. This is visible in exfoliated shells (Text-fig. 4).

Hereditary factors strongly influence total shell thickness (Taylor and Lerner, 1939) in avian eggs, but little is known about exactly how they are involved. If a three-dimensional latticework of protein fibers was formed prior to the hard shell, as suggested above, it may be that the hereditary depth prescribed for this structure would represent a constant factor determining shell thickness. Less constant factors governing thickness are mainly environment, nutrition, and disease.

Very little variation is observed in the stratified combination of protein and mineral in the upper zone of shells from either Lower Cretaceous locality. Certain Upper Cretaceous eggshells, in contrast (Jensen, 1966), display dramatic variations in the thickness of their different layers. This remarkable characteristic will be examined in a future paper.

The relatively smooth surface of most avian eggs is marked by shallow depressions containing pore openings. These pores are formed in places where

EXPLANATION OF PLATE 2

EXTERIOR-INTERIOR VIEWS OF DINOSAUR EGGSHELLS

All photographs x5

FIG. 1.—Distinct, tuberculate pattern. A thin shell. There is a slight directional tendency to the right. Cedar Mtn. Fm. Approx. thickness = 1.0 mm.

FIG. 2.—Internal, mammillar surface of figure 8. Mammillar cones of variable size and shape present a compact surface with only small inter-mammillary chambers visible. Kelvin Fm. Approx. thickness = 2.2 mm.

FIG. 3.—Torose or mounded surface. Pores occur at random without particular regard for mounds. Canals are subcircular of variable size. Cedar Mtn. Fm. Approx. thickness = 2.0 mm.

FIG. 4.—Exfoliated shell. Natural erosion has split a massive layer of fine laminae from upper zone exposing mounded structure deep within, indicating an early origin of surface pattern. Cedar Mtn. Fm.

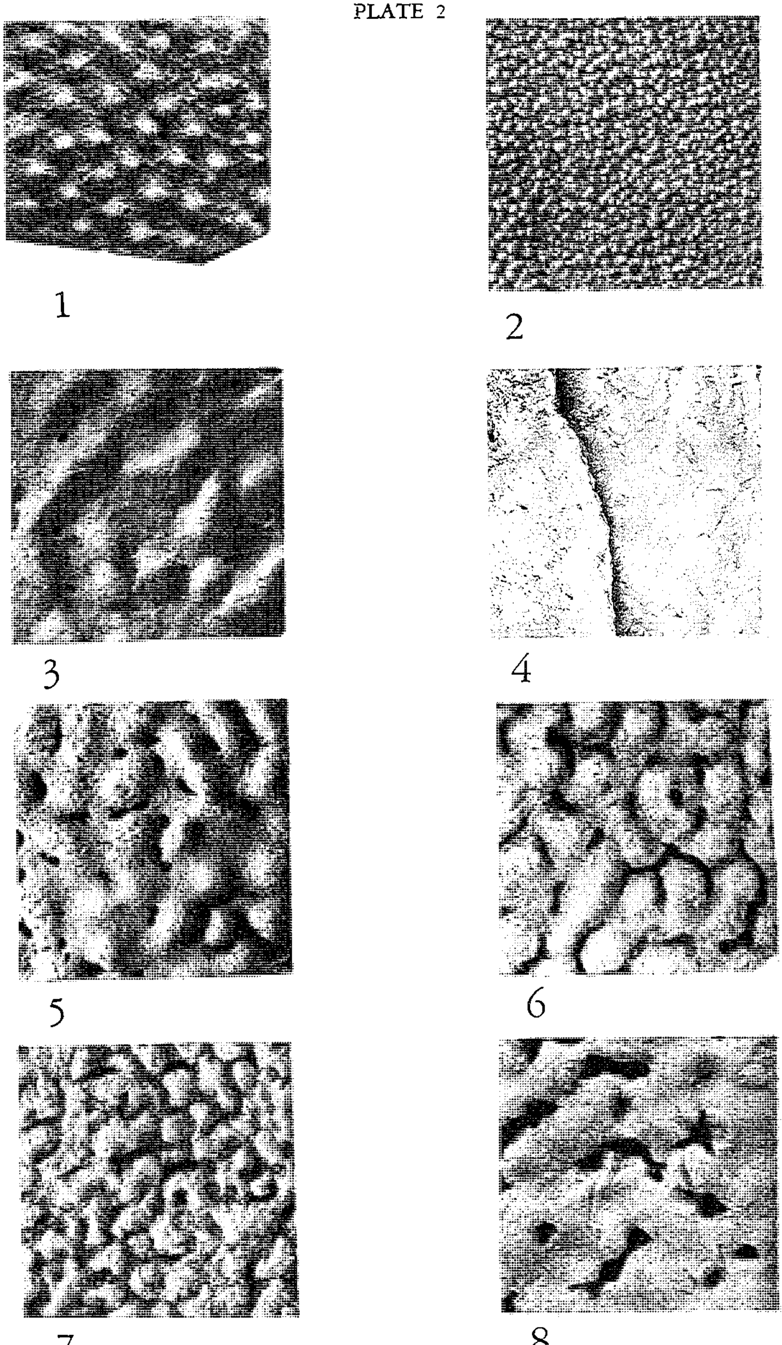
FIG. 5.—Spheroidal to elongate mounds with subcircular pores having a strong tendency to pairing. Joining of several pairs may develop deep, irregular slots in the valleys. Cedar Mtn. Fm. Approx. thickness = 1.5 mm.

FIG. 6.—Similar to figure 5 with extensive, irregular slots which strictly follow valley patterns. Cedar Mtn. Fm. Approx. thickness = 1.9 mm.

FIG. 7.—Tuberculate nodes. No definite channel pattern. Pores not apparent. Diagonal corners eroded, upper left and lower right. Kelvin Fm. Approx. thickness = 2.2 mm.

FIG. 8.—Mildly undulating surface. Large pores occur at random and join in various ways to produce large irregular openings. Twining apparent. Kelvin Fm. Approx. thickness =2.2 mm. (Exterior view of figure 2.)

PLATE 2



the eggshell, in the process of formation, is in contact with the uterine epithelium (Romanoff and Romanoff, 1949). The highly textured surfaces of most Utah Cretaceous eggshells display a great variety of nodes, channels, ridges, or rugose sculpturings, which are often developed without regard to the occurrence of pore openings. These surface patterns are established well before the final layer, as the shells are laminated similar to the annular rings of a plant. Undulating sheets of protein follow these subsurface patterns. The surface pattern is generated near the base of the upper zone and is intensified during the zones' stratified deposition. Thus, if one or several layers are peeled off, the surface pattern remains the same (Text-fig. 4). In the case of deeply channeled surfaces, the pores open at random into the depths and are not easily observed (Text-fig. 5 and Plate 2, fig. 2). Pores may occur in an irregular fashion through nodes or alongside them with a general disregard for shell thickness or design.

Ornamentation in certain Upper Cretaceous eggshells (Jensen, 1966) has been divided into three general groups according to gross physical structure. Variation among Lower Cretaceous materials is too complex to attempt such a division.

EXPLANATION OF PLATE 3
EXTERIOR-INTERIOR VIEWS OF DINOSAUR EGGSHELLS
All photographs x5

FIG. 1.—Mildly undulating surface. Single pores of various diameters with a great variation of subparallel, multiple-pore slots. These crescentic to angular slots conform generally to the eggs long axis. Axis of egg vertical in figure. Kelvin Fm. Approx. thickness = 1.9 mm.

FIG. 2.—Irregular, verruculate nodes raised from a rugose background. Pores are not very apparent as warty nodes obscure their definition. A reconstruction was made from large shell fragments of this variety resulting in an egg measuring 113 mm at its equatorial diameter and 224 mm at its polar diameter. Kelvin Fm. Axis of egg horizontal on figure. Approx. thickness = 2.6 mm.

FIG. 3.—The only smooth shelled variety collected from the lower Cretaceous of Utah. Surface slightly pitted by post depositional formation of calcite crystals. The near-circular pores vary a great deal in diameter. All pores are single. Kelvin Fm. Approx. thickness = 1.9 mm.

FIG. 4.—Oblong nodes occurring at random. Pores vary from single, circular, to multiple, irregular slots. Cedar Mtn. Fm. Axis of egg horizontal in figure. Approx. thickness = 2.2 mm.

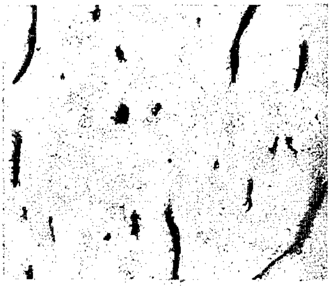
FIG. 5.—Internal, mammillar surface of figure 6. Mammillar cones are eroded exposing slightly concave surfaces. Several circular, radial-canal mouths, or pores, can be observed. These penetrate directly through the entire shell appearing on the surface and can be seen in figure 6. Mammillae are not compact. Kelvin Fm.

FIG. 6.—Simple pattern of low-profile, gently meandriform ridges. Pores vary in size and shape from circular to elongate slots and occur at random, opening within valleys or on slopes and ridge tops. This pattern resembles that of the famous "Protoceratops eggs" of Mongolia. Kelvin Fm. Axis of egg vertical in figure. Approx. thickness = 1.45 mm.

FIG. 7.—Irregular, sub-parallel, tuberous ridges with varying slopes and overhanging sides. Pores generally open beneath overcast edges. Some radial canals exit through twin pores on opposite sides of a ridge. Ridges parallel to long axis of egg. Cedar Mtn. Fm. Approx. thickness = 2.0 mm.

FIG. 8.—Random, circular to oblong, bulbous nodes of high profile. Pores generally open beneath overcast edges. Axis of egg horizontal to figure. Cedar Mtn. Fm. Approx. thickness = 2.2 mm.

PLATE 3



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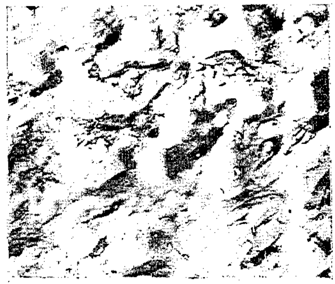

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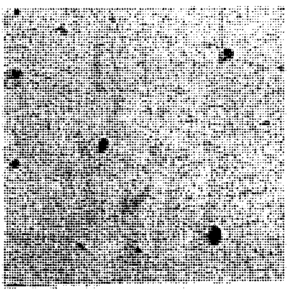

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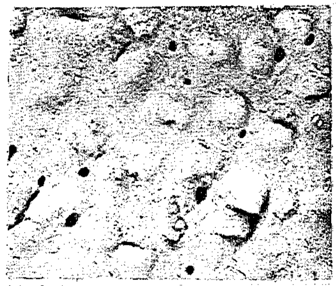

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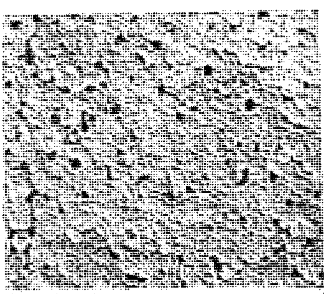

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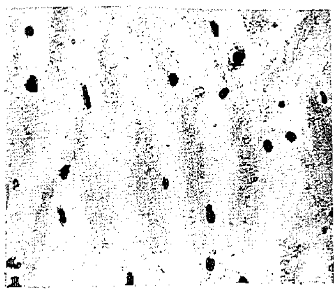

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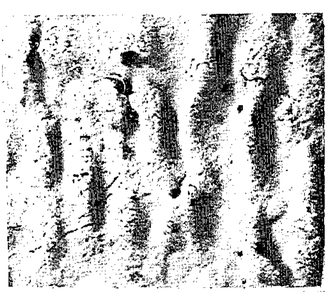

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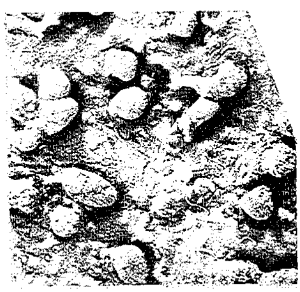

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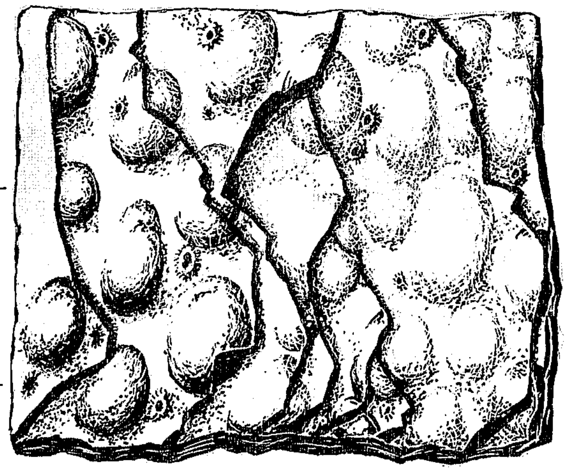
Conical orifice

Terminal layer

Depressed orifice



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TEXT-FIGURE 4.—Exfoliated Upper Cretaceous eggshell showing laminate structure of upper zone. Pores or canal mouths, in subsurface layer, exhibit a depressed orifice. Nodes in surface pattern are developed near base of upper zone and become more distinct toward the surface. This exfoliation results from natural erosion.

Fossil eggs cannot be assigned to an exact parentage, other than by circumstantial evidence; therefore, this paper will identify certain distinct varieties by another method. This is being done for convenience only in present and future reference and will not involve fossil eggs in vertebrate taxonomy.

Young (1965) used *Oolithes* as a designation for fossil eggs, adding a species based upon shell structure or locality. Thus, he named *Oolithes megadermus* and *Oolithes nanhsiungensis* (Young, 1965). The author will follow his example.

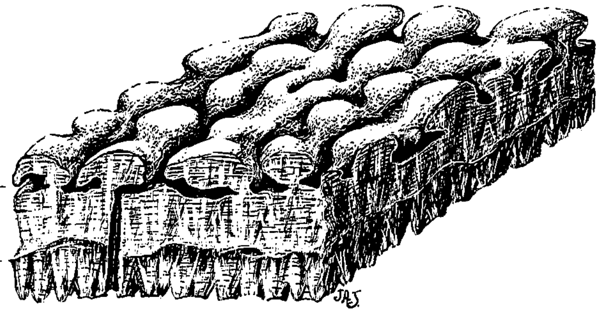
SYSTEMATIC DESCRIPTION

OOLITHES CARLYLENSIS, n. sp.

Pl. 1, figs. 1, 2, Text-fig. 5.

Description.—Ornamentation characterized by deep meandriform channeling amidst truncated ridges. Profile of ridges varies from moderate mushroom to aphanite chambering produced beneath radically overcast edges. External pore openings occur only in channel depths indicating a strict megastructural regard for protein fibers produced early in shell formation.

General appearance of external surface is that of a discontinuous chain of subcircular to elongate nodes separated by deep channeling. These nodes average from 2 to 3 mm. on their long axes with an average width of 1.3 mm. Internal structure is typical of all Lower Cretaceous material studied. Upper and lower zones are separated by a "line of termination." Average shell thick-



TEXT-FIGURE 5.—A distinct variety of Lower Cretaceous eggshell from the Cedar Mountain Formation hereby designated as *Oolithes carlylensis* n. sp. Canal mouth, or pore, opens into deep meandriform channeling. Upper and lower zones well defined. Small mammillae. Aphanite, or hidden chambers develop beneath overcast edges of nodular, bulbous ridges. This variety includes modified and exaggerated forms of this illustration. Axis of egg diagonal, from lower left to upper right. Approx. thickness = 2.3 mm.

ness is 2.7 mm. with a plus or minus variation of 0.4 mm. The internal surface displays eroded mammillar points which have been reduced to slight concavities with an average diameter of 0.3 mm. The specific name directs attention to Mr. Carlyle Jones who first discovered fossil egg materials in the Lower Cretaceous of North America.

Occurrence.—Cedar Mountain Formation. Five miles southeast of Castle Dale, Utah. Locality 1, Text-fig. 1.

Repository.—Brigham Young University Earth Sciences Museum collections: Holotype BYU-E 200.

DISCUSSION

The formation of hard shells on eggs of certain Cretaceous vertebrates was a complex matter. Avian eggs generally have more simply organized shells. Cretaceous materials from Utah are characterized by features such as distinct stratification and zonation, well-defined crystalline structure, stratified organic compounds, and a great variation in external ornamentation.

The physiology of hard-shell formation on eggs of large extinct reptiles can only be surmised from inadequate modern examples. With the exception of crocodilians, most reptiles today produce a parchment-covered egg which bears little external resemblance to the great variety of ornamented hard shells on eggs of extinct groups. Our consideration of fossil eggs is therefore based more upon studies of avians than upon those of reptiles. Many competent studies have been made of the avian egg, but the potential for a complete understanding of its diverse nature has not yet been exhausted. Such problems as the development, structure, and function of a respiratory canal system in the shell or the exact mechanism for deposition of its calcium salts have not yet been entirely resolved.

It is, of course, impossible for us to observe egg physiology in extinct animals, but certain well-preserved fossil eggshells provide us with structural information which is in itself a clue to the processes of physiology. Precise stratification, protein residues, distinct separation of upper and lower zones in the shell, a great variation in surface structure and ornamentation are all present in fossil shells to a more remarkable degree than can be observed in modern eggs. Detailed studies of shells produced by ancestral pro-avian forms may contribute to a better understanding of modern avians in the area of physiology. The bony skeleton, by which we know extinct egg-laying vertebrates, was a product of gradual development during the life of the animal, subject to little change from hatch to death by old age. The egg was produced as a result of intermittent soft-tissue functions, according to the female's reproductive cycle. It was developed in a relatively short time, reflecting physiological deviations resulting from nutritional and environmental factors which had little effect upon the bony skeleton. Utah Cretaceous eggshells display remarkable intra-specific variation.

Periodic changes in female avian bone structure has been observed as a result of the reproductive cycle involving the marrow cavities of certain bones in the female bird (Kyes and Potter, 1934). This is the only significent fluctuation reported in avian bone structure and it may or may not have been in use by Cretaceous vertebrates to compensate for the heavy calcium demand during shell formation.

Species of certain Utah Cretaceous eggshells display an almost infinite variation in upper shell structure resulting from some sort of physiological inconstancy among the various females. The author has yet to observe duplication of upper shell structure in any pair of fragments from this group. It appears unlikely that any two eggs of a single nest were identical in shell structure, much less any pair of a particular female's clutch.

There is little value in speculating the possible parents of fossil eggs when the eggs are found associated only with bones of animals readily acceptable as egg layers, such as reptiles. However, if fossil egg materials were found circumstantially related to therapsids, monotremes, mammals or any vertebrate form transitional to placentals, a careful scrutiny of their shell structure and possible origin may then prove worthwhile.

Paleontologists carefully avoid making positive identifications based upon circumstantial evidence when working with bones but such restraint is not always observed when dealing with fossil eggs. Some workers have erected diagrams identifying eggs with various animals such as a sauropod, hadrosaur, carnosaur and in some cases have assigned a fossil egg to a certain species.

The eggshell is an independent solid, formed within soft tissues of the oviduct, and lacks even a single function of any bone in the axial skeleton. It is produced only by the female for a completely different purpose than to function as, or part of, a muscular foundation. The egg relates to bony structure only as it demands adequate passage through the pelvic canal. Even then, we cannot calculate maximum canal diameter but only establish an absolute minimum.

An egg, therefore, cannot be positively assigned to a particular animal on the basis of connecting bone structure, as there is none, nor can parental relationship be determined by color, weight, size or shape of egg or skeleton.

Comparative chemical analyses of original organic compounds in fossil eggshells and those which may be found in fossil bones of the same formation may provide a key suggesting generic or possibly even specific relationships. It does not appear that such a method of parental determination is near at hand nor is there presently any assurance that it is even possible. The main justification for detailed studies of fossil structure presently appears to lie in areas of physiology rather than phylogeny.

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