

REVISION OF THE WIND RIVER FAUNAS, EARLY
EOCENE OF CENTRAL WYOMING. PART 8. FIRST FOSSIL
LIZARD EGG (?GEKKONIDAE) AND LIST OF
ASSOCIATED LIZARDS

KARL F. HIRSCH¹

LEONARD KRISHTALKA

Associate Curator, Section of Vertebrate Fossils

RICHARD K. STUCKY

Assistant Curator, Section of Vertebrate Fossils

ABSTRACT

A small fossil egg from the Lostcabinian (early Eocene, CM loc. 1040) of the Wind River Formation, Wyoming, is the first unequivocal record of a fossil lizard egg. It has a shell structure similar to that of rigid-shelled eggs of modern geckos, especially *Tarentola delalandii*. The unique eggshell structure of Recent geckos warrants recognition of a fourth type of rigid eggshell in addition to those of chelonians, crocodilians and birds. At least 22 species of lizards are represented by skeletal material at the fossil egg locality, including anguids, necrosaurids, agamids, varanids, xantusiids, xenosaurids, iguanids, and teiids.

INTRODUCTION

In 1984, paleontologists from The Carnegie Museum of Natural History collected several fossil eggs from early Eocene (late Wasatchian, Lostcabinian) horizons of the Wind River Formation in central Wyoming. One of these eggs is small (8–9 mm diameter), has a rigid eggshell, and represents the first unequivocal record of a fossil lizard egg. It resembles eggs of living geckos, the only extant lizards with rigid eggshells. Other fossil squamate eggs have been mentioned in the literature (Meyer, 1867) and identified in some collections on the basis of gross features of the specimens, which may not be diagnostic.

The eggshell structure of only a few species of squamates has been studied in detail; that of geckos has been mentioned only briefly (Schmidt, 1957; Hirsch, 1983, 1985; Packard et al., 1982). However, studies of the shell microstructure (Erben and Newesely, 1972), and the biominerals of the shell membrane and calcitic layer (Krampitz et al., 1972, 1974) established that gecko eggshells differ from those of birds, crocodilians and chelonians, and represent a fourth type of rigid eggshell.

Fossil geckos are first known from the late Paleocene of Brazil and the late Eocene of Europe (Estes, 1983). In North America, the earliest geckos are known from the early Miocene of Florida, but have been identified with question from the late Middle Eocene of the Mission Valley Formation, California.

¹ University of Colorado Museum, Campus Box 218, Boulder, Colorado 80309.
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Table 1.—*Fossil lizards known from skeletal material from the B-2 horizon at Buck Spring (CM loc. 1040), Lost Cabin Member, Wind River Formation.*

Taxon	No. specimens
Anguidae	
Diploglossinae sp.	18
<i>Xestops</i>	14
? <i>Ophisaurus</i> sp.	3
<i>Machaerosaurus</i> sp.	2
<i>Glyptosaurus donohoei</i>	1
cf. <i>Gerrhonotus</i> sp.	1
Anguinae sp.	1
Xantusiidae	
Xantusiidae sp. A	9
Xantusiidae sp. B	3
Xantusiidae sp. C	3
Xenosauridae	
<i>Exostinus</i> sp.	6
Agamidae	
<i>Tinosaurus</i> n. sp.	4
Iguanidae	
Iguanidae sp. A	7
Iguanidae sp. B	4
Iguanidae sp. C	3
<i>Parasauromalus</i> sp.	1
Varanidae	
Varanidae sp.	3
Necrosauridae	
<i>Necrosaurus</i> sp.	2
Teidae	
?Teidae sp.	1
Sauria	
<i>Oligodontosaurus</i> sp.	2
"Scincomorpha" sp.	3
Sauria n. gen.	2
Sauria undetermined	100+

LOCALITY AND ASSOCIATED FAUNA

The fossil egg was recovered from the Buck Spring Quarries (Quarry 1, Horizon B-2, CM loc. 1040) in the type area of the Lost Cabin Member of the Wind River Formation. As described elsewhere (Stucky and Krishtalka, 1987; in press), the geology of the locality and mode of preservation of the fossil vertebrates are unique among known Wind River Formation localities. The eggshell-bearing horizon consists of alternating thinly-laminated mudstone and limestone couplets, which were apparently deposited in freshwater ponds and/or well-drained swamps within 250 m of the nearest permanent stream.

At least 22 species of lizards are known from dental and skeletal remains from the B-2 horizon (Table 1). This is the highest diversity recorded among known Eocene lizard faunas. However, no gekkonid skeletal material has been positively identified from this horizon. One of the lizards, *Glyptosaurus*, is here considered a senior synonym of *Eoglyptosaurus*. Study of the type species of the latter, *E.*

Table 2.—Size, shell thickness and status of modern gecko and fossil egg.

Specimens	Egg size (mm)	Shell thickness (mm)	Status of egg
Eocene egg			
CM 46668/HEC 321	8 × 9	0.04–0.05	—
<i>Tarentola delalandii</i>			
UCM OS1142/HEC 357	9 × 10	0.06–0.07	hatched
<i>T. mauritanica</i>			
UCM OS1129/HEC 408	11 × 12	0.09–0.1	?infertile
<i>Phelsuma madagascariensis</i>			
UCM OS1130/HEC 125	13 × 15	0.14–0.16	hatched
<i>Gekko gekko</i>			
UCM OS1143-1/HEC 391-1	21 × 19	0.27–0.34	?infertile
<i>G. gekko</i>			
UCM OS1143-2/HEC 391-2	21 × 19	0.27–0.34	?infertile
<i>G. gekko</i>			
UCM OS1143-3/HEC 391-2	21 × 19	0.27–0.34	embryo/early stage
<i>Lepidodactylus lugubris</i>			
Erben and Newesely, 1972	—	?0.9	—
<i>Hemidactylus turcicus</i>			
Packard et al., 1982	—	?0.06	—

donohoei (including the holotype, USNM 18316), reveals that it has a linear band of pterygoid teeth, a feature also found in *G. sylvestris*, the type species of *Glyptosaurus* (Sullivan, 1986). Sullivan erred in separating *Eoglyptosaurus* from *Glyptosaurus* on this characteristic, as well as on the presence of raised subconical osteoderms, which appears to vary allometrically in *G. donohoei* (Stucky, unpublished data).

In addition to the lizard eggshell and skeletal material, relatively complete and well preserved specimens of fossil mammals, turtles, birds, snakes, amphibians, crocodilians and fish have been recovered from the Buck Spring Quarries. The B-2 horizon also preserves fossil roots and stems of plants (carbonate-replaced and lignified), avian eggshells, algal skeletal grains, and rarely, gastropods and decapod exoskeletons.

MATERIAL AND TECHNIQUES

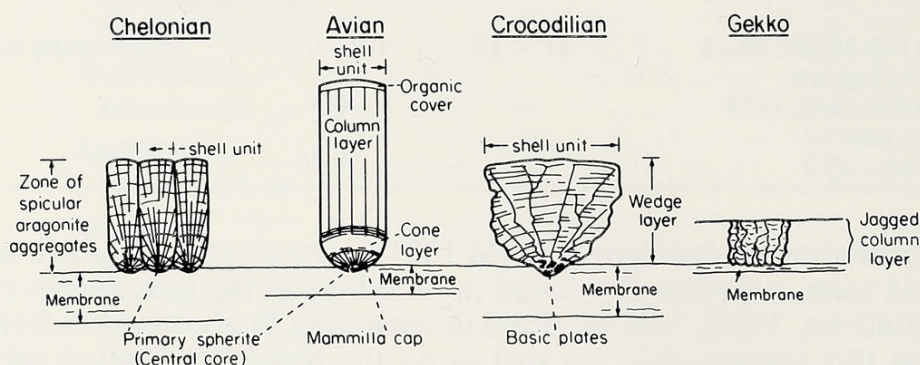
Specimens of modern and fossil eggshell (Table 2) were studied using polarizing light microscopy (PLM), scanning electron microscopy (SEM) and X-ray diffraction (XRD). Methods described in Hirsch (1979, 1983) and Packard et al. (1984) were followed as far as the very delicate and fragile nature of the specimen allowed. Three small shell fragments were detached from the fossil egg, the remainder of which is still preserved in the surrounding block of matrix (CM 46668, Fig. 1). These fragments were too fragile to be treated with chemicals or cleaned in an ultrasonic bath. Thus the outer and the inner surfaces are somewhat contaminated by secondary deposits or preservatives. However, fresh fractures of the shell permitted examination of radial (edge) sections. Tangential sections of the fossil specimen could not be prepared. The status of the egg (fertilized or unfertilized, stage of incubation) was known in three cases for the modern eggshells.

Abbreviations: CM, The Carnegie Museum of Natural History; HEC, Hirsch Egg Collection; UCM, University of Colorado Museum; USNM, U.S. National Museum.

RESULTS

Modern Rigid-Shelled Gecko Eggs

The rigid eggshell, one of the three main kinds of amniote eggshells (Hirsch, 1983, 1985; Packard and Packard, 1980), is the most likely to become fossilized. The calcareous layer of these eggshells is very thick in comparison to the underlying membrane and is composed of well-defined, interlocking, more or less spherulitic



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Fig. 1, 2.—1. Fossil egg embedded in matrix. Scale = 1 mm. 2. Terminology and structure of the four types of modern rigid eggshells.

shell units that are nucleated on the membrane. Among amniotes with rigid-shelled eggs, a typical shell structure has been recognized for birds, crocodilians and turtles (Schmidt, 1943, 1957; Schmidt and Schoenwetter, 1943; Erben and Newesely, 1972; Hirsch, 1983, 1985). The characteristic structure of rigid-shelled gecko eggs differs from these types and warrants classification as a fourth type (Fig. 2; see also Erben and Newesely, 1972; Krampitz, 1972).

Gecko eggshells are composed of a thin inner membrane overlain by a comparatively thick calcareous layer (0.06–0.34 mm, see Table 2), which is covered by a more or less fibrous, organic cuticle. The surface of the cuticle can be an open network of fibers, or relatively smooth, or bumpy as a result of the nodes of the underlying calcareous layer.

The calcareous layer, as in the avian eggshell, is made up of tightly abutted calcite columns extending from the membrane to the outside of the shell. In edge view, the columns interlock along uneven, jagged surfaces (Fig. 4, 5) and thereby differ from the spherulitic, even, interlocking crystal pattern found in avian eggshells. The jagged columnar structure is typical for the first four species examined in Table 2 and has also been observed in *Lepidodactylus* and *Hemidactylus* (Erben and Newesely, 1972; Packard et al., 1982). In radial view the columns show horizontal and sometimes almost lamellar layering. Under PLM, faint columnar extinction patterns can be observed. In tangential thin sections, the pattern of the columns is polygonal, but randomly interlocking. As in all other shell types, the gecko eggshell varies from one point to another in columnar size and shell thickness.

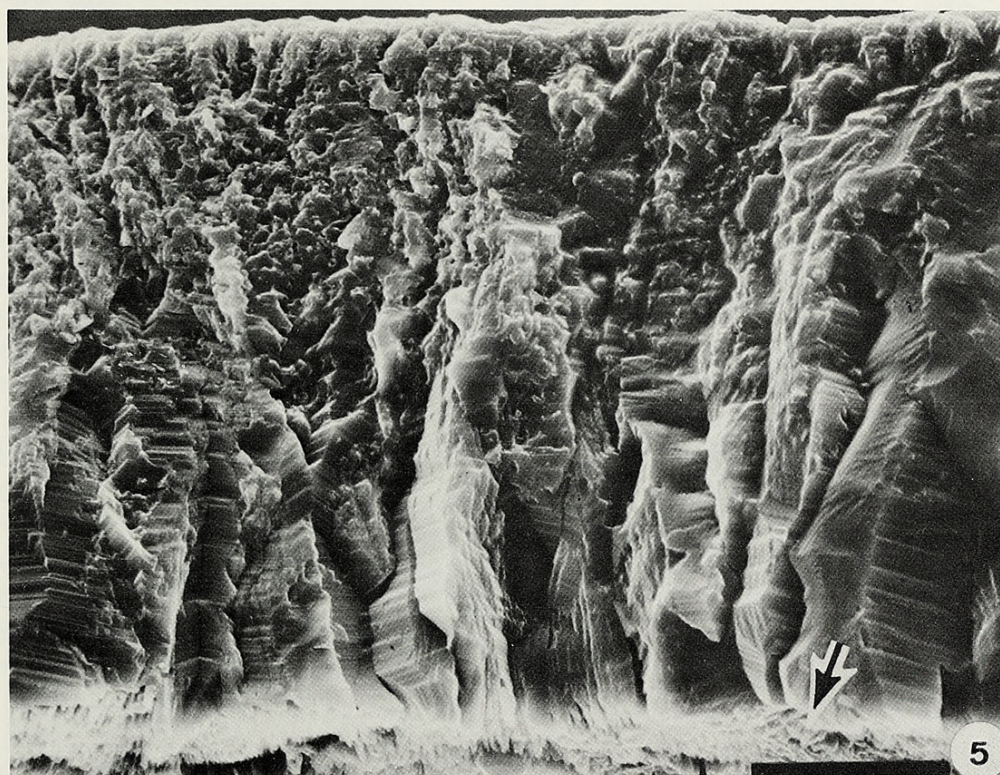
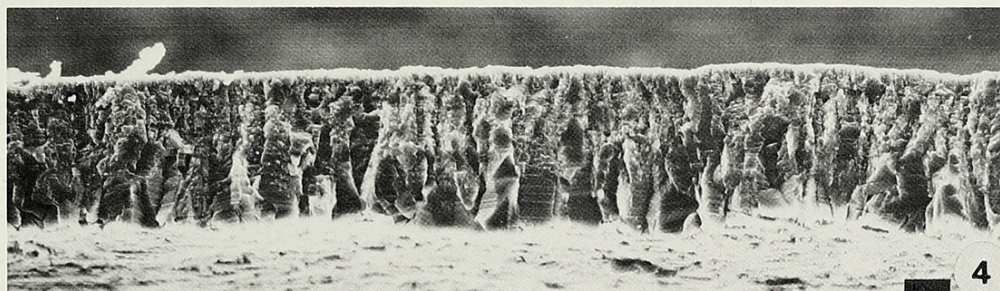
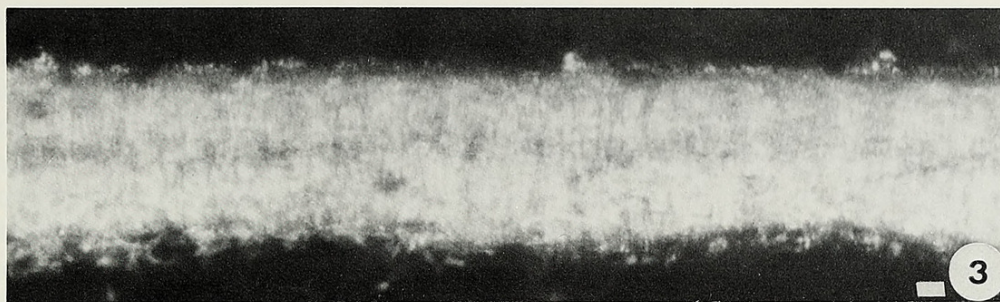


Fig. 3--5.—*Tarentola delalandii* eggshell (scale = 10 μ). Outside of shell is up. 3. Radial thin section viewed under polarized light. Note that columnar structures are somewhat narrower than in the fossil egg (see Fig. 6). 4. Photomicrograph of radial view (edge) of eggshell. 5. Enlargement of Fig. 4. Note the minute crystals on mammillary column faces (arrow).

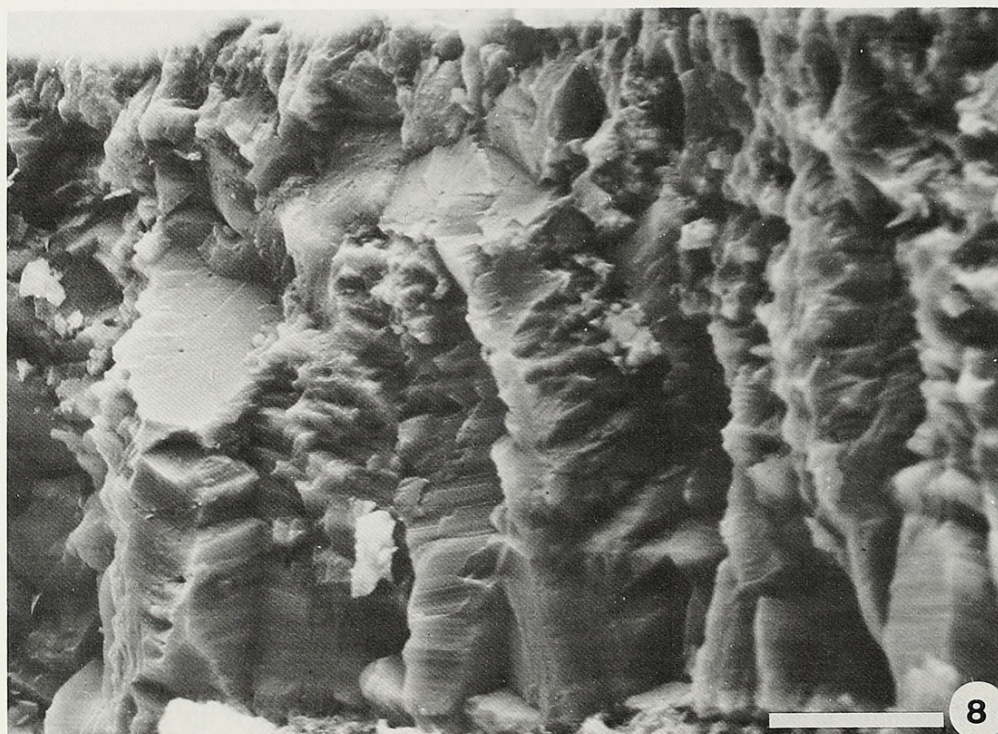
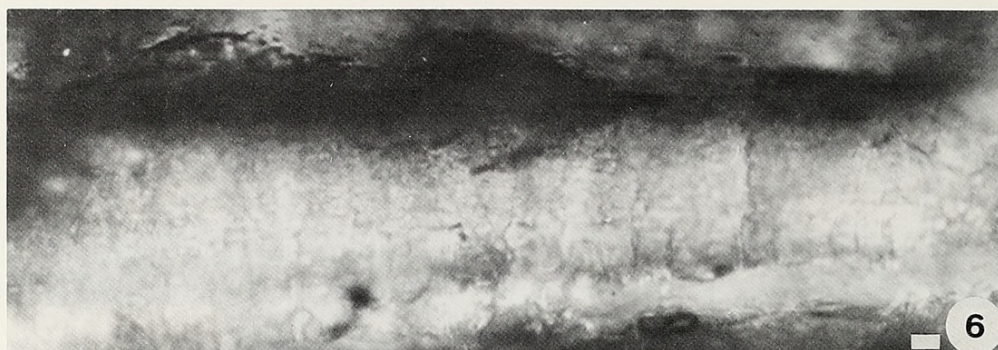


Fig. 6-8.—Fossil eggshell (scale = $10\ \mu$). Outside of shell is up. 6. Radial thin section viewed under polarized light. Note faint columnar structures. 7. Micrograph of radial view (edge) of eggshell. Note similarity to radial view in Fig. 4. 8. Enlargement of Fig. 7. Note jagged columnar structure and horizontal layering.

A shell unit structure (see Fig. 2) has not yet been observed in gecko eggshells, either with SEM or PLM. It also has not been established how the calcite columns are nucleated or how they are fastened to the membrane. Central cores, such as occur in avian and chelonian eggshells, and basal plate groups, as in crocodilian eggshells, have not been observed. In unfertilized and fertilized but unhatched eggs the basal tips of the columns are tightly fastened to the membrane; in hatched eggs this membrane is much less securely fastened.

The shape of the basal tip or face of the columns in gecko eggs varies inter-specifically. Variation within a species, observed in several eggs with different incubational histories, may be partly a result of dissolution of columns caused by the withdrawal of calcium from the eggshell by the developing embryo (Packard et al., 1984). In hatched eggs, the basal faces are studded with minute crystals pointing toward the inside of the egg. In eggs of unknown hatching status, round or lumpy tips can be observed.

The Wind River Fossil Egg

The Eocene egg (CM 46668) was compressed during fossilization, but its original shape was apparently spheroidal and measured approximately 8–9 mm in diameter. Eggshell thickness is 0.04–0.05 mm. Like the eggshell of living gekkonids, the fossil eggshell is rigid and does not have the unit structures typical of chelonian, crocodilian or avian eggshells (Fig. 2).

In size and shell structure, the fossil egg is most similar to that of *Tarentola delalandii* (Fig. 4, 5, 7, 8). In both, the columns are wide and strongly jagged, and the horizontal layering (growth lines) is very distinct (Fig. 5, 8). These features are not as pronounced in other living species of geckos that have been studied. Both specimens also exhibit a faint columnar extinction pattern when rotated under crossed nicols (Fig. 3, 6).

The outer surface of the fossil egg is relatively smooth, with no indication of nodes or other sculpturing. Under high magnification, some crystal structure of the column heads is visible.

It is not clear whether the details of the inner surface of the fossil shell reflects original morphology or diagenetic alteration. Low magnification (SEM) reveals a very faint indication of a polygonal pattern, which may represent the faces of dissolved column tips as described above for some hatched gecko eggs. However, unlike *Tarentola* (Fig. 5), high magnification does not reveal distinct small crystals, only small crystalline nodes, perhaps a result of diagenetic recrystallization.

Microprobe and X-ray fluorescence studies determined that the fossil eggshell is composed of calcium carbonate. X-ray diffraction analysis could not distinguish between aragonite and calcite because of the limited amount of fossil material; however, the crystalline structure strongly suggests calcite.

CONCLUSIONS

A preliminary study of modern rigid-shelled gecko eggs indicates that the jagged, columnar structure of the calcareous layer distinguishes them from recognized types of avian, crocodilian and chelonian eggshells. Based on this diagnostic feature, recognition of a fourth type of rigid eggshell is warranted, although interspecific variation in the microstructure of the jagged columns and cuticle occurs among geckos.

The Early Eocene egg from the Wind River Formation is the first such record for fossil lizards. Two of its features—the rigid shell and jagged, columnar structure

of the calcareous layer—are diagnostic. They are known only among extant geckos, and closely resemble the condition in *Tarentola*.

Fossil gecko bones are unknown in the Wind River Formation, although some of the lizard material is provisionally identified and may represent gekkonids. Nevertheless, the fossil egg may have belonged to one of the other lizards recovered from the B-2 horizon in the Wind River Formation at Buck Spring.

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