Taphonomy of Extant Desert Tortoise (*Gopherus agasinii*) and Loggerhead Sea Turtle (*Carette caretta*) Nesting Sites: Implications for Interpreting the Fossil Record

Authors: Frankie D. Jackson, David J. Varricchio, Robert A. Jackson, Andrew D. Walde, & Gale A. Bishop

This is a postprint of an article that originally appeared in [Palaios](#) in May 2015.

Jackson, Frankie D., David J. Varricchio, Robert A. Jackson, Andrew D. Walde, and Gale A. Bishop. "Taphonomy of Extant Desert Tortoise (*Gopherus agasinii*) and Loggerhead Sea Turtle (*Carette caretta*) Nesting Sites: Implications for Interpreting the Fossil Record." *Palaios* 30 (May 2015): 207-223.

DOI: <https://dx.doi.org/10.2110/palo.2014.048>

Made available through Montana State University's [ScholarWorks](https://scholarworks.montana.edu)
scholarworks.montana.edu

Taphonomy of Extant Desert Tortoise (*Gopherus agassizii*) and Loggerhead Sea Turtle (*Caretta caretta*) Nesting Sites: Implications for Interpreting the Fossil Record

Frankie D. Jackson, David J. Varricchio, Robert A. Jackson: Department of Earth Sciences, Montana State University, Bozeman, MT, USA

Andrew D. Walde: Walde Research and Environmental Consulting, Atascadero, CA, USA

Gale A. Bishop: St. Catherines Island Sea Turtle Program, Midway, GA, USA

ABSTRACT: Dinosaur reproductive biology is often inferred from the biology of extant taxa; however, taphonomic studies of modern nest sites have focused exclusively on avian, rather than reptilian species. We documented eight Agassiz's desert tortoise (*Gopherus agassizii*) nests and ten loggerhead sea turtle (*Caretta caretta*) nests. *Gopherus agassizii* excavated burrows up to 70 cm long and laid rigid-shelled eggs 10–12 cm below the burrow floor. The 19 cm × 12 cm depressions consisted of hard consolidated sand surrounded by a 3–4-cm-high rim and contained 2–5 hatched eggs in a single layer. These hatched egg bottoms represent ~25% of the original egg, and five of 27 contained fully developed dead neonates. Desiccated membrane separated from the egg interior forming pockets that filled with eggshell and sand. Of 106 and 79 eggshell fragments in the hatched egg and surrounding sand, 48% and 23% occurred concave up, respectively. However, the combined numbers of eggshell fragments inside the eggs and in the immediately surrounding sand approximates the 60:40 ratios at in situ avian nests. Therefore, this ratio may provide reliable evidence for hatching sites regardless of the incubation strategy employed by the adult. *Caretta caretta* nests differed from those of tortoises in their greater depth (~50 cm) and occurrence in moist, cohesive sand. Clutches contained over 100 pliable-shelled eggs that tore and collapsed upon hatching, without brittle fracture. Failed eggs in two clutches showed five development stages, indicating that the deaths occurred over an extended time period. With the exception of predation, the *G. agassizii* and *C. caretta* nests showed no significant eggshell or hatched eggs above the egg chamber.

INTRODUCTION

Dinosaur reproductive biology is often inferred from nesting strategies employed by extant amniotes such as birds, alligators, and turtles (e.g., Erben et al. 1979; Seymour 1979; Coombs 1989; Cousin et al. 1994; Horner 1994, 2000; Carpenter 1999; Varricchio et al. 1997; Deeming 2006; Grellet-Tinner et al. 2006). Although some studies discuss the reproductive biology of various extant taxa (e.g., Coombs 1989; Carpenter 1999; Jackson et al. 2008; Mueller-Töwe et al. 2002), taphonomic studies of modern nesting sites are relatively rare (Horner 1994; Hayward et al. 1997, 2000, 2011; Cruz 2007; Wang et al. 2014). For example, Horner (1994) compares the distribution and size ranges of skeletal remains from dinosaur nesting sites in the Upper Cretaceous Two Medicine Formation to extant avian colonial nesting sites at Lake Bowdoin National Wildlife Refuge in Montana. In addition, several papers report results of experiments related to egg and eggshell fragment transport and examine the ratio of concave-up to concave-down eggshell fragments at modern avian nesting sites for comparison to fossil localities (Hayward et al. 1997, 2011; Oser and Jackson 2014; Wang et al. 2014; Imai 2013). Hayward et al. (2000) use location of openings in eggs (pole versus equator) to distinguish hatched from depredated eggs of ground nesting birds. They also report correlation between nest location, vegetation, and egg depredation. Similarly, Wang et al. (2014) document eggshell distribution and orientation at common tern (*Sterna hirundo*) colonies in Chesapeake Bay, Maryland and suggest several physical characteristics to consider when excavating fossil eggs.

These taphonomic investigations provide important information about the type, condition, and spatial arrangement of bones, eggs, and eggshell

fragments at modern avian nesting localities. Such studies may potentially reveal whether the abundance, location, and condition of biological materials vary in a predictable manner, depending on nesting environment, physiological factors, and behaviors of adults and young. However, a review of the literature reveals a lack of similar taphonomic studies at modern reptilian nesting sites. This is surprising, given that egg burial likely characterized most nonavian dinosaurs (Deeming 2006), and thus reliance on avian models of egg incubation to assess dinosaur nesting sites is questionable in many cases. Here, we document the distribution of biological materials in nests of two chelonians, the Agassiz's desert tortoise (*Gopherus agassizii*) and loggerhead sea turtles (*Caretta caretta*). We discuss the relevance of our observations to inferences about incubation strategies that are based on fossil localities.

AGASSIZ'S DESERT TORTOISE (*GOPHERUS AGASSIZII*)

Biology

Gopherus agassizii inhabits the Mojave and Colorado deserts of California, Nevada, Arizona, and Utah, north and west of the Colorado River (Grover and DeFalco 1995; Ernst and Lovich 2009) (Fig. 1) and was listed as threatened under the Endangered Species Act in 1990. This medium-sized (22 to 32 cm carapace length) terrestrial species displays a highly domed, brown carapace and yellowish plastron (Ernst and Lovich 2009) (Fig. 1B). The legs are short and forelimbs are adapted to digging; the female uses the elephantine hind limbs for egg chamber excavation and positioning of eggs (Grover and DeFalco 1995; Ernst and Lovich

FIG. 1.—Study locality and tortoise species. **A**) Location of tortoise study site. Scale bar = 50 km. **B**) Agassiz's desert tortoise (*Gopherus agassizii*). Carapace is ~ 30 cm in length.

2009). *Gopherus agassizii* spends much of its time in excavated burrows because of the extreme desert temperatures, surfacing during cooler periods of the year and/or day to feed on grasses, young plant shoots, and flowers. *Gopherus agassizii* live 30 to 50 years, with sexual maturity at 15 to 20 years (Ernst and Lovich 2009). The reproductive biology is characterized by egg laying from April to July, with females laying 1–3 clutches with an average of five eggs per clutch (range 1–12) (Ernst and Lovich 2009). Clutch size and egg size are somewhat dependent on size of the female and available forage, with eggs averaging 3.5 cm in diameter (reviewed in Ernst and Lovich 2009). Eggs are subround with a rigid eggshell that consists of tightly interlocking aragonite crystals (Kohring 1999). Incubation requires 70–120 days, with hatchlings emerging from August to October, depending on the geographic region. The young sometimes emerge asynchronously over one to several days (Averill-Murray 2002; Bjurlin and Bissonette 2004; Ernst and Lovich 2009). Primary predators of eggs and hatchlings include kit foxes (*Vulpes macrotis*), coyotes (*Canis latrans*), and ravens (*Corvus corax*) (Woodbury and Hardy 1948; Boarman 2002; Bjurlin and Bissonette 2004).

Nesting Locality and Prior Work

Gopherus agassizii nests in our study are located on land administered by the Bureau of Land Management in the Mojave Desert northeast of Barstow, San Bernardino County, California (Fig. 1A). Prior to the taphonomic study, one of us (AW) identified burrows used by nesting females, assigned an identification number, and recorded the Universal Transverse Mercator (UTM) coordinates using a Global Positioning System. Females were X-rayed to determine the number of eggs present and recaptured daily. They were weighed, looking for a drop in weight roughly equivalent to the anticipated clutch weight. A small cage made of 1 cm² wire mesh was placed immediately above the egg chamber within the burrow in order to capture hatchlings as they emerged from the nest. To deter predation of eggs by canids and other predators, the half-moon-shaped opening of the burrow was also covered by 2.5 cm × 5.0 cm wire mesh screen and staked in position. Incubation of *G. agassizii* eggs within the study area required up to 125 days, and daily monitoring of the nests began after 70 days. The tortoise hatchlings emerged asynchronously in some cases, separated by several days; hatchlings were removed daily from the wire cage above the egg chamber. The taphonomic study was

conducted well after the last hatchling emerged from the nest chamber, in order to avoid harm to potentially viable unhatched eggs.

Taphonomic Methods

Drought conditions in 2012 contributed to a delay in laying and thus hatching within the study area by ~ 2–4 weeks; therefore, the study was conducted later than expected, in early October. We documented eight nests in burrows, which we refer to in the chronological order in which they were studied (i.e., Nest 1, Nest 2). After removal of the wire mesh covering the burrow entrance, cardboard was placed over the wire cage to protect eggshells and other biological materials during removal of the burrow “ceiling” with hand tools. Manually probing the sediments permitted differentiation of the hard compact sand of the burrow floor from the unconsolidated sand that filled the egg chamber. Gentle sweeping with small brushes facilitated removal of sand with minimal disruption to eggs and eggshell material. Hatched eggs and eggshell fragments were counted, mapped, and the orientation of the burrow relative to north noted. We documented the location of eggshell fragments as inside or outside of hatched eggs, as well as their orientation such as concave up, concave down, or vertical. In the latter case, the angle of the eggshell fragment exceeded 45° to a horizontal plane. Concave-up versus concave-down eggshell fragment orientations were compared to 1:1, 60:40, and 20:80 ratios using a chi-square analysis. Due to an error at Nest 1, the number of eggshell fragments inside hatched eggs was not recorded. Additional information noted for the eight nests included substrate characteristics and the number, condition, and approximate developmental stage of nonviable neonates. The excavation was backfilled at each study site and the surface contoured to approximate the original surface.

RESULTS

Gopherus agassizii Burrows and Egg Chambers

Female tortoises excavated nesting burrows in substrates typically composed of friable, medium- to fine-grained sand (Fig. 2A). Burrows extended into the substrate at a relatively shallow angle and sometimes exceeded depths and lengths of 70 cm (Fig. 2B). We consider measurements of most burrows unreliable due to possible disruption of sand during installation of wire cages over the egg chamber. However, Nest 1 provided

FIG. 2.—*Gopherus agassizii* burrow and nest. **A**) Nesting burrow at the base of a creosote bush (*Larrea tridentata*); note sand apron and predator tracks at mouth of the burrow. Cell phone for scale. **B**) Schematic diagram of cross section through the burrow and nest. **C**) Desert tortoise nesting structure showing three of four hatched eggs. **D**) Same as view C with dots showing the irregular outline of hard consolidated sand of the nest rim. Scale bars in views C and D = 3 cm.

the best approximation of the burrow dimensions, measuring 80 cm long by 40 cm wide by 15.5 cm high. The egg chambers at all eight sites occurred ~ 10–12 cm below the burrow floor, and the distances from the burrow entrance to the wire cages covering the chamber varied from ~ 15–70 cm. Only the cage at one site (Nest 6) contained biological remains; these included three small eggshells and a few membrane fragments. Careful removal of unconsolidated sediment from the eight egg chambers revealed irregularly shaped shallow depressions composed of hard consolidated sand. The slightly raised rims sloped away from the center of the nest (Fig. 2C, D). The depressions varied from 15–19 cm long by 8–12 cm wide and the rims stood ~ 3–4 cm high; each depression contained from two to five hatched eggs.

Hatched Eggs

X-rays of the female tortoises associated with the eight nests showed a total of 31 eggs (Table 1, Fig. 3). None of the eight nests yielded intact, failed eggs; however, 2/3 of an egg was present in Nest 6, which may represent a failed and possibly cracked egg. Three additional eggs in Nest 8 were missing at the time of the taphonomic study (discussed below). The chambers, therefore, contained 27 hatched egg bottoms (Fig. 3). These hatched eggs consisted of the lower fourth of the specimen, which varied from ~ 3.0 to 3.5 cm in diameter (Fig. 4A). The closely spaced egg bottoms occurred at a single level in the chamber and displayed irregular, sharply broken edges (Fig. 4A). Membrane within the hatched eggs varied in color and degree of desiccation, even within the same clutch. In some cases, membrane remained tightly attached to the interior of the

hatched egg, whereas with greater desiccation the membrane separated from the egg interior, often carrying broken eggshell fragments along with it. A space typically occurred between the eggshell interior and the desiccated membrane, and this “pocket” sometimes contained sand and eggshell fragments (Fig. 4A). Tightly curled membrane remnants occurred within the hatched egg bottoms and sometimes within the surrounding sand.

Eggshell Orientation.—Due to error in the field, Table 1 lacks information on eggshell orientations inside eggs at Nest 1, thus leaving 23 hatched egg bottoms that are discussed here. Orientations for the 106 eggshell fragments in the egg bottoms for these 7 nests include 48% concave up, 22% concave down, and 30% vertical. In contrast, the orientations of 79 eggshells in the sand immediately surrounding the hatched eggs differed substantially from those within the hatched egg remnants: 23% were concave up, 38% concave down, and 33% vertical (Table 1, Fig. 3). Another 6% are considered of indeterminate orientations, due to possible disruption during removal of sand from the chamber. Excluding ~ 1/3 of the eggshells in the sand that were vertical and of indeterminate orientations, the combined numbers of eggshell fragments inside the egg bottoms and in the immediately surrounding sand yielded 57% concave up and 43% concave down.

Deceased Neonates

Excavation revealed that three of the four eggs identified in X-rays of the female from Nest 5 were hatched; however, three fully developed,

TABLE 1.—Eggshell orientations in all hatched tortoise (*Gopherus agassizii*) eggs compared to sediment surrounding the clutch. Abbreviations: CU = concave up, CD = concave down; V = vertical; UNK = unknown orientation. * Eggshells inside the four eggs were not documented for Nest 1. Fragments in eggs, CU:CD = 69:31; in sand, CU:CD = 38:62; combined eggs and sand, CU:CD = 57:43.

Nest	Eggs in X-rays/ hatched eggs	Eggshells in eggs/sand	CU (%) in eggs/sand	CD (%) in eggs/sand	V (%) in eggs/sand	UNK (%) in eggs/sand	% Total eggshells inside eggs	Comments
1*	4/4	NA/11	– /5(45)	–/3(27)	–/3(28)	–/0(0)	NA	–
2	4/4	10/11	4(40)/2(18)	1(10)/5(45)	5(50)/2(18)	0(0)/2(18)	48	1 deceased neonate
3	2/2	11/3	2(18)/0(0)	8(73)/1(33)	1(9)/0(0)	0(0)/2(67)	79	–
4	4/4	34/7	19(56)/2(29)	5(15)/1(14)	10(29)/4(57)	0(0)/0(0)	83	1 missing neonate
5	4/4	1/6	0(0)/1(17)	1(100)/5(83)	0(0)/0(0)	0(0)/0(0)	14	4 deceased neonates
6	5/4	23/28	18(78)/8(29)	4(17)/13(46)	1(4)/7(25)	0(0)/0(0)	45	2/3 egg, broken
7	4/4	16/12	6(37)/0(0)	2(13)/2(17)	8(50)/9(75)	0(0)/1(8)	57	–
8	4/1	11/1	2(18)/0(0)	2(18)/0(0)	7(64)/1(100)	0(0)/0(0)	92	1/2 egg, no hatchlings
Total	31/27	106/79	51(48)/18(23)	23(22)/30(38)	32(30)/26(33)	0(0)/5(6)	57	

desiccated, and deceased neonates remained within the egg bottom. One neonate faced the wall at a 45° angle, whereas the other two were oriented toward the center of the chamber. Large fragments of eggshell covered portions of the anterior carapaces. Carapace length and width varied from ~ 3.4 cm × 4.0 cm to 4.0 cm × 3.5 cm; sand and small (< 1 cm) eggshell fragments occurred between the carapace and plastron in some cases. Head and forelimb elements remained intact, and those portions that extended beyond the carapace retained the skin covering (Fig. 4B). However, the extremely fragile forelimb elements disarticulated easily, especially the distal phalanges. The posterior portions of the skull and mandible and other skeletal elements covered by the carapace remained articulated but lacked soft tissues including skin (Fig. 4C).

The fourth egg in Nest 5 lay adjacent and slightly separated from the other three. Careful removal of this egg revealed its impression in the consolidated sand of the egg chamber wall. Although the egg appeared intact on first inspection, the side next to the wall was broken, revealing a late stage embryo. The head faced toward the chamber wall, and a narrow, vertical strip of eggshell covered the rostral end of the skull (Fig. 4D). The left forelimb protruded slightly beyond the broken edge of the egg, whereas the right forelimb remained inside. Portions of the forelimbs that extended beyond the carapace retained their skin, whereas other skeletal elements within the carapace lacked all soft tissue. Membrane that had separated from the eggshell interior lay adjacent to the right forelimb and displayed semicircular holes of similar diameter as the forelimb unguals; eggshell next to the right forelimb also exhibited similar holes along the edge (Fig. 4D). Detached membrane immediately above the neonate closely overlaid the carapace, leaving a pocket or space that was partially filled with sand (Fig. 4D). Based on our observations, we interpret this egg as pipped or broken by the embryo, which was in the initial stages of hatching when death occurred.

Nest 2 contained four hatched eggs, one of which also contained a deceased neonate (Table 1). The neonate remained within the hatched egg bottom, oriented with the head facing toward the consolidated sand of the chamber wall; a large eggshell fragment covered ~ 1/4 of the posterior carapace. This neonate closely resembles those in Nest 5, and most of the characteristics described above apply to this individual as well.

Missing Hatchlings and Eggs

The wire cage above Nest 6 yielded only four of the five hatchlings expected from the X-rays of the gravid adult female (Table 1). Removal of sand from the egg chamber exposed a small 6 cm wide by 4 cm high tunnel that branched off the main burrow. Definitive evidence for its origin and significance is lacking. In addition to four hatched eggs, ~ 2/3 of a fifth egg was tightly pressed into the chamber wall. An opening occurred in the upper portion of the egg, and the egg contained a substantial amount of desiccated yolk. Predation seems unlikely because

of the amount of remaining yolk, thus suggesting that the egg was infertile or the embryo failed to develop properly during incubation, possibly because the egg cracked during oviposition. The opening in the top of the egg may have resulted during emergence of other hatchlings.

X-rays of the gravid female associated with Nest 8 confirmed the presence of four eggs, but no hatchlings emerged from the egg chamber (Table 1, Fig. 3). The wire cage that covered the egg chamber showed slight displacement, whereas the wider-gage mesh covering the burrow entrance remained intact, with no obvious evidence of nest predation (e.g., predatory digging). Small accumulations of tortoise eggshell occurred 6 m and 11 m west and northwest of the nest, and these fragments were estimated, respectively, to represent ~ 1/4 and 1/3–1/2 of an intact egg. No other eggshells were observed outside of a wire cage at any other study site. Excavation of the egg chamber revealed a single partial egg that represented ~ 1/3, rather than the typical 1/4 of a hatched egg (Table 1). The broken surface was tightly pressed against the chamber wall and this partial egg contained multiple stacked eggshell fragments with various orientations, whereas only three eggshell fragments occurred in the sand surrounding the egg (Table 1). Although the remaining egg portion somewhat exceeds the size of most specimens, we consider this egg as hatched because of its shape and similar appearance to other hatched eggs. The fate of all four hatchlings from this nest remains unknown. Although speculative, the female tortoise may have deposited the three missing eggs at a different nesting site.

LOGGERHEAD SEA TURTLE (*CARETTA CARETTA*)

Biology

Caretta caretta exhibit adaptations for a marine existence. Their legs are modified to flippers, heads and necks are no longer retractable, and special glands allow excretion of excess salt from their systems. The females come ashore only to lay their eggs (Bishop et al. 2011). Adult *C. caretta* in the southeastern United States average 1 m in length and weigh ~ 113 kg (Fig. 5A). Two *C. caretta* subpopulations inhabit the western North Atlantic: a robust southern subpopulation in middle and south Florida, and a smaller, more endangered northern subpopulation in Georgia, the Carolinas, and Virginia (<http://www.nmfs.noaa.gov/pr/species/turtles/loggerhead.htm>). As late-stage juveniles and mature adults, *C. caretta* migrate along the eastern seaboard's inner continental shelf, foraging for mollusks, crabs, fish, and other food items from the Georgia Banks to Florida. Females reach maturity ~ 20–30 years of age. They nest on the beaches from early May to early August, producing ~ 4–5 clutches at 10–14 day intervals during the nesting season. Nests average ~ 2.3 m long and 2 m wide (Bishop et al. 2011). The female turtle excavates a flask-shaped egg chamber 40–50 cm deep and typically lays over 100 eggs before burying the clutch and immediately returning

FIG. 3.—Flow diagram showing disposition of 31 tortoise eggs identified in X-rays and orientation of eggshell fragments within eggs and surrounding sand. Abbreviations: CU = concave up, CD = concave down; V = vertical; UK = unknown orientation.

FIG. 4.—Hatched tortoise eggs and deceased neonates in Nest 5. **A)** Hatched egg bottom representing $\sim 1/4$ of the original egg; note sharply broken edges. Arrow indicates desiccated and folded membrane. **B)** Desiccated neonate showing large hole in the plastron that allowed yolk absorption of the yolk into the body cavity prior to and after hatching. Forelimbs retain the skin whereas skeletal elements within the carapace lack soft tissue. **C)** Neonate showing skeletal elements within the carapace. **D)** Neonate that died while pipping the egg. Note eggshell covering the rostral end of the beak. Arrow with white outline on left points to sand between the egg interior and membrane. Two solid black arrows indicate semicircular holes in eggshell and membrane. Scale bars in views A–D = 1 cm.

to the ocean (Bishop and Meyer 2011; Bishop et al. 2011). The round, 4 cm pliable-shelled eggs hatch after ~ 60 days of incubation and the hatchlings dig their way upward to the surface of the beach. They usually emerge from the nesting chamber under the cover of darkness and find their way to the ocean. Primary predators of eggs and hatchlings at the study site include raccoons (*Procyon lotor*), feral hogs (*Sus scrofa*), and ghost crabs (*Ocypode quadrata*). Although listed as threatened worldwide, *C. caretta* in the Carolinas and Georgia are a distinct subpopulation and considered endangered by the state of Georgia (Bishop and Meyer 2011).

Nesting Locality and Previous Work

St. Catherines Island represents one of 12 barrier islands fringing the Georgia coast. The island lies ~ 80 km south of Savannah in Liberty County, Georgia (Fig. 5B, C). Bounded on the north and south by St. Catherines Sound and Sapelo Sound, respectively, the island measures ~ 16 km long and 1–3 km wide (Bishop et al. 2011). Three beaches occur on the island: North Beach, Middle Beach, and South Beach. South Beach, the largest of the three, represents the primary sea turtle nesting locality monitored by the St. Catherines Island Sea Turtle Conservation Program

FIG. 5.—Loggerhead sea turtle (*Caretta caretta*) and nest site. **A)** *Caretta caretta*. Carapace is ~ 90 cm in length. **B)** Map of Georgia with star showing locality. **C)** St. Catherines Island. Scale bar = 5 km. **D)** Sea turtle crawlway to nesting site and return to the ocean. Scale bar = 25 cm. **E)** Plan view of egg chamber with G. Bishop for scale.

(Bishop et al. 2011). North Beach and Middle Beach are smaller and the latter less accessible for nest surveys. Of the four threatened or endangered sea turtle species commonly seen in Georgia marine waters, only *C. caretta* typically nest on the island (Brannen and Bishop 1993; Bishop and Marsh 1994; Hayes et al. 1995; Bishop et al. 2000, 2007, 2009, 2011; Linsley et al. 2008; Bishop and Meyer 2011).

Taphonomic Methods

The taphonomic study was conducted in conjunction with regular activities of the St. Catherines Island Sea Turtle Conservation Program, under their permit obtained from the Non-Game Program, Coastal Resources Division, Georgia Department of Natural Resources. The initial studies in late July, 2011 were augmented in August 2013 by additional observations of 30 nests and two depredated nests, one by a raccoon (nest 13-001) and the other by a feral hog. In the latter case, the nest was completely destroyed and therefore no number was assigned.

Daily surveys on North and South Beach revealed adult crawlways, indicating new nesting activity overnight (Fig. 5D). To locate the nest, thin layers of sand were scraped from the surface, revealing the plan-view outline of the egg chamber (Fig. 5E). Differences between the darker infilling sand and lighter-colored substrate aided in their recognition. Nests located below the high tide line and judged likely to suffer inundation by seawater were excavated, and the eggs counted and reburied in an artificial egg chamber nearby, using sand from the original nest.

Hereafter, natural nests are those that remained *in situ* for development, and artificial nests are those that were reburied. Plastic screens placed over the surface of the egg chamber helped protect the nest from predators, while allowing hatchlings to pass through and find their way to the ocean.

Hatched Clutches.—Crawlways and/or emergence craters provided evidence for the emergence of juveniles during the night. During relocation or after hatching events, the nest chamber was carefully excavated by removing the loose sand by hand. In addition to the nest number and incubation date, other data collected at each site included the number of (1) successfully hatched eggs; (2) unhatched, nonviable eggs; (3) potentially viable eggs; (4) dead hatchlings; and (5) live hatchlings that failed to escape the nest. Potentially viable eggs were reburied in the nest chamber, whereas obviously nonviable, unhatched eggs showing evidence of decay were examined for embryonic remains. Embryonic development stage was qualitatively assessed by the size of the carapace, and the embryos categorized as large, medium, or small for comparative purposes. Surviving hatchlings were released to the ocean after dark in order to reduce the risk of predation. After removal of the contents, two egg chambers were filled with expandable polyurethane foam (Great Stuff™ Insulating Foam Sealant, by Dow Chemical Company, Midland, Michigan, United States) to create a cast of the interior. The cast was excavated, examined for flipper marks (Bishop et al. 2011), covered with polyurethane varnish for protection, measured, and photographed.

TABLE 2.—Eggs, embryos, and hatchlings examined from ten excavated *Caretta caretta* nests.

Nest	Clutch count	Hatched eggs	Unhatched eggs	Dead hatchlings	Live hatchlings	Embryos examined	Notes
1	146	119	19	0	2*	5	*1 died later; 2 possibly viable eggs reburied; embryo size variable
2	127	110	8	1	3	0	Unhatched eggs contained only yolk
3	118	96	21	0	0	0	<i>In situ</i> nest
4	107	93	9	0	0	0	2 possibly viable eggs; 1 unhatched egg ¼ of normal
5	129	67	56	0	0	6	
6	90	57	31	1	0	0	
7	106	94	11	0	0	3	Embryos all similar size
8	118	72	44	1	4	0	Relocated; hatched later; cast made
9	82	56	21	0	0	0	Relocated; hatched later; chamber cast made
10	109	47	58	7	27	0	Relocated, hatched later; cast made
Total	1132	811	278	10	36	14	

RESULTS

Caretta caretta Nests

Data recorded for our sea turtle study included clutches from six artificial nests containing eggs previously relocated to sites above the high tide line and one natural nest (Table 2). Three additional nests were also relocated; however, these three clutches hatched after completion of the study and therefore their data are not included here. Relocation of these three clutches permitted casting of two of the three original egg chambers with polyurethane foam and exposure of the sedimentary structures associated with the nests. In addition, two predation sites were documented in 2013. Below, we describe the sedimentary and taphonomic attributes of these nesting sites.

Caretta caretta Nest Morphology

The three natural nests (Nests 8, 9, and 10) relocated during the study occurred on the foreshore area below the high tide level, and the sites included maternal crawlways to and from the ocean (Fig. 5D). Elliptical areas of disrupted sediment, plants, and twigs occurred in the nesting area (covering pit of Bishop et al. 2011) above the egg chamber (Bishop et al. 2009, 2011). Careful removal of the sand that filled the egg chamber revealed clutches of tightly packed eggs ~ 30–40 cm below the surface of the beach (Fig. 6A). The eggs occurred in moist, cohesive fine- to medium-grained quartz sand. Exposure of the sedimentary structures during removal of the polyurethane foam casts of the nests revealed parallel, horizontal laminae that alternated with thin, heavy mineral laminae, typical of backbeach deposits (Bishop et al. 2009, 2011) (Fig. 6B).

The polyurethane foam cast of Nest 8 indicates that the landward portion of the egg chamber extended more deeply into the substrate than the seaward side (Fig. 6C). The narrow cylindrical neck and expanded, bulbous portions of this nest measure 14 cm and 30 cm wide, respectively, with a maximum vertical depth of 28 cm. Narrow (50–60 mm) sinuous ridges occur in the egg chamber at the bottom and deepest portion (Fig. 6C). A pronounced ridge (3–4 cm wide), consistent with a rear flipper mark, curves upward about midway through the chamber, whereas the opposite side of the cast displays a relatively smooth surface. The cast of Nest 10 also shows similar morphology as Nest 8 but with less distinct flipper marks. The diameters of the neck and lower portion of the Nest 10 chamber, and its greatest depth, measure 14 cm, 25 cm, and 38 cm, respectively.

Hatched Eggs

The single *in situ* hatched clutch (Nest 3) displayed a 10 cm round opening in the sand from which the hatchlings emerged. The plastic mesh

remained over the opening and hatchling tracks extended away from the nest in several directions. Raccoon tracks were present around the opening to the egg chamber, and a decomposing hatchling occurred ~ 65–70 cm from the chamber.

Clutches from this natural nest and the nine artificial nests contained a total of 1132 eggs, and of these, 71% hatched successfully. However, only 67% of these eggs produced hatchlings that successfully emerged from the egg chamber, as some perished before exiting the nest (Table 2). The remnants of the pliable eggs remained largely intact but partially collapsed, and the opening from which the hatchlings exited the egg appeared torn or split. These remnants typically represented over 50% of the original egg (Fig. 6D), but smaller egg pieces (sherds) also occurred in the nest. All eggshells remained at the bottom of the chamber, and none were exposed on the beach as a result of the hatchlings digging their way to the surface. No eggshell debris was noted inside the hatched eggs, within the egg chambers, or on the overlying beach surface. Depredated nests documented in 2013 represent an exception to this observation (discussed below).

Of 278 unhatched eggs in the egg chambers, we examined the contents of 89 eggs from five different nests. These five nests contained failed eggs that consisted of just yolk (Nests 2, 4), eggs with yolk and others with late-stage embryos of similar size (Nest 7), and eggs with yolk and others with differently sized late-stage embryos (Nests 1, 5). For example, dead embryos in Nests 1 and 5 represented three different sizes that corresponded inversely with amount of yolk remaining in the egg (Fig. 6E, Table 2); the carapaces of larger individuals were more round than those of smaller embryos. The largest embryo in Nest 5 showed unusual and pronounced asymmetry of the skull, and the egg tooth occurred off center (often referred to as scissor-jaw) and displayed a jugal boss. A nonviable egg in Nest 4 measured only ~ 1.5 cm in diameter, or ~ 1/4 of normal egg size. Some nonviable eggs showed extensive invasion by grass roots. Two possibly viable eggs from Nest 4 were reburied in the egg chamber, and their fates remain unknown. A total of 10 dead hatchlings occurred in four nests and five nests contained 36 live hatchlings, which were released into the ocean (Table 2). In total, Nest 1 contained deceased individuals representing at least five different stages: a hatchling; eggs containing only yolk; and eggs with small, medium, and large embryos.

Nest Predation

Two sea turtle nests were attacked by mammalian predators during the night of oviposition, and disruption of the nests varied according to the type of predator. A feral hog produced substantial disruption of the sand as it dug up the buried clutch, creating a large inverted cone-like crater into the covering pit. The hog consumed all of the eggs, leaving behind only a few eggshell fragments from the depredated eggs (Fig. 7A). In

FIG. 6.—*Caretta caretta* nests, eggs, and embryos. A) Stacked eggs within the egg chamber. Scale bar = 2 cm. B) Side view of excavation around nest area with poured cast still in place, shown by arrows. Arrows indicate edges of the nest cast prior to its excavation. Scale bar = 10 cm. C) Cast of the nest showing flipper marks midway through its depth. Left side was toward the ocean. Scale bar = 5 cm. D) Groups of 10 hatched, partially collapsed sea turtle eggs removed from a nesting chamber. Scale bar = 10 cm. E) Different sized embryos from three failed eggs in the same clutch. Scale bar = 5 cm.

FIG. 7.—Depredated *Caretta caretta* nests. **A)** Predation by feral hog. Arrows point to the few remnants present of eggs that were preyed upon. Scale bar = 50 cm. **B)** Predation by raccoon. Note clustered eggs on edge of the nest. Scale bar = 10 cm.

contrast, raccoon (*Procyon lotor*) predation resulted in less disturbance of the sand at Nest 13-001, which contained 102 eggs. The raccoon dug many exploratory holes into the loose sand of the covering pit before locating the egg mass. Following the egg chamber neck downward, the raccoon lifted 19 eggs out of the egg chamber; many of these exhibited narrow slits that resulted from long, sharp claws slicing the egg. These sliced egg remnants were scattered for several meters around the nesting area. In contrast, eggs removed intact from the chamber were carried to a high point on the side of the nest and consumed, leaving behind the depredated eggs in a cluster (Fig. 7B). Eighty-three eggs remained in the egg chamber, and abundant sliced eggs in the upper part of the clutch leaked albumin and yolk over the underlying intact eggs.

Smaller predators such as ghost crabs burrowed into the soft sand leading into the egg chamber and fed on the eggs, egg remnants, and hatchlings. They pierced the eggs and young with their pincers and sometimes dragged an occasional eggshell to the surface. Their burrowing activity sometimes facilitates predation by mammalian predators (G. Bishop, personal observations, 2014), presumably by allowing scent to emerge from the chamber; however, this predation by ghost crabs caused minimal disruption of the sediments.

DISCUSSION

Nesting biology differs significantly between *Gopherus agassizii* and *Caretta caretta*. The tortoises (*G. agassizii*) dig shallow, elongate nests in the dry sand of burrow floors in an arid environment (Fig. 2). The clutches contained only 2–5 eggs, and hatchlings sometimes emerged asynchronously over one to several days; whether the eggs hatched asynchronously remains unknown. The hatched eggs were in close proximity to one another at a single level in the substrate. They consisted of a large fragment of the eggshell that corresponded to the egg bottom and represented about $\frac{1}{4}$ of the original egg (Fig. 4A). During hatching, the rigid eggshell broke into small pieces; these fragments, along with pieces of membrane, occurred inside the remnants of the hatched eggs and in the sand that filled the egg chamber (Figs. 3, 4A). Asynchronous escape of hatchlings may have contributed to eggshell fragmentation. All hatched egg bottoms remained within the egg chamber beneath the level of the burrow floor, and none were exposed at the surface as a result of the hatchlings digging their way out of the chamber. However, three small eggshell fragments in Nest 6 apparently adhered to the emerging hatchlings and were present in the wire cages above the chamber.

In contrast, the sea turtles (*C. caretta*) laid clutches of over a hundred pliable eggs (Table 2). The female deposited the eggs one on top of another in flask-shaped egg chambers, and the eggs were substantially deeper in the substrate than the tortoise eggs, surrounded by moist and cohesive sand (Fig. 6B). The hatchlings typically emerged synchronously in a single night, although a few failed to escape the nest. The loosely arranged aragonite crystals of the pliable sea turtle eggs contrast with the rigid, interlocking crystals of tortoise eggshells. Consequently, the eggs differ significantly in appearance after hatching. The sea turtle eggs, both individually and as a collective mass, collapsed after emergence of the hatchlings. The remaining collapsed egg remnants typically represented more than $\frac{1}{2}$ of the original egg (Fig. 6D). The opening from which the hatchling escaped resembled a tear or slit, lacking the sharply broken edges that characterized the tortoise eggs (Figs. 4A, 6D). No eggshell fragments comparable to those in the tortoise nests occurred inside the hatched sea turtle eggs, in the sand that filled the egg chambers, or on the surface of the beach above the egg chambers. Further, the lack of significant sand inside nearly all sea turtle eggs examined suggests that the partial collapse of the hatched eggs, as well as the moist and more cohesive sand texture, resulted in little or no sediment entering the egg as the hatchlings emerged.

Neonate Remains

Neonates that failed to escape from the tortoise and sea turtle nests also differed in several ways. Deceased tortoise neonates in Nest 2 and Nest 5 remained in the hatched egg bottoms and retained large eggshell fragments over the carapace. An additional neonate from Nest 5 died in the act of pipping or breaking the egg (Fig. 4D). Interestingly, the deceased tortoise neonates in Nest 5 and Nest 2 showed little variation in size. This similarity of size, lack of remaining yolk, and presence of eggshell covering significant portions of the carapaces suggest that in each case death occurred during or shortly after hatching, rather than at an earlier stage of embryonic development. Death may have resulted as a consequence of drought-related stress, entombment in the indurated sand, starvation related to failure to emerge, or other unknown factors.

Portions of the tortoise skull, limbs, and phalanges that remained inside the carapaces (Nest 2 and Nest 5) lacked skin covering; in contrast, those that extended outside of the carapace typically retained the skin (Fig. 4B, C). The water content of the hatchling's body likely facilitated more rapid bacterial decomposition within the carapace, compared to

elements surrounded by dry sand. Disarticulation of the distal phalanges began almost immediately after the neonates were removed from the hatched egg bottom. Knell (2012) reported a similar disarticulation pattern for extant turtle carcasses.

The relationship of eggshell to skeletal elements also provides information about hatching. The opening of the pipped egg was pressed against the compact sand of the chamber wall, and a narrow fragment of eggshell still covered the rostral portion of the horny beak of a neonate from Nest 5 (Fig. 4D). Circular holes in the membrane and eggshell indicate that the forelimbs were used to break the egg, whereas the presence of eggshell covering the beak indicates that the egg tooth had not been used prior to embryonic death (Fig. 4D). This suggests that both egg tooth and forelimbs are likely used by this species during hatching.

In contrast to asynchronously emerging desert tortoises, the sea turtles emerge synchronously overnight. Failed loggerhead eggs in Nest 1 and Nest 5 contained embryos of different sizes that were inversely proportional to the amount of yolk remaining in the egg. The young from Nest 1 showed at least five different development stages (Fig. 6E). This suggests that neonatal death occurred at different stages of development. In addition, we observed 36 sea turtle hatchlings (3%) that failed to emerge from the egg chambers. These were retrieved and released in the ocean. Without our intervention, some of these hatchlings would likely have died within the nest, thereby increasing neonatal remains within the clutch.

Relevance to Mesozoic Nesting Sites

Although some studies now place turtles within Archosauria (Crawford et al. 2012), the smaller egg size and thinner eggshell of all extant reptile eggs likely places limits on their usefulness as models for dinosaur reproductive biology. Nevertheless, several characteristics are shared between extant reptiles and at least some dinosaurs. These include egg shape, egg arrangement within clutches, substrate burial of eggs, high gas conductance rates, and precocial young (Coombs 1989; Carpenter 1999; Deeming 2006).

In addition to reptile eggs, megapode birds (Megapodiidae) are sometimes mentioned in discussions of nonavian dinosaur incubation strategies because they incubate eggs in vegetation mounds, as proposed for some dinosaurs (e.g., Coombs 1989, Carpenter 1999; Deeming 2006; Jackson et al. 2008). However, we feel that megapodes provide an inadequate analog for several reasons that are discussed in Jackson et al. (2008, p. 239). In addition, vegetation mounds have poor preservation potential in the fossil record because they represent topographic highs that are subject to greater erosion by wind and water than buried clutches. The decay of vegetation through microbial anaerobic metabolism would likely lower ambient pH, leading to more rapid eggshell dissolution, and thus fewer fossils would probably enter the rock record. Finally, megapode eggs in a single mound are laid by multiple females and often dispersed throughout the vegetation, rather than clustered like most reptile and dinosaur eggs. Because they were laid at different times, embryonic development varies among megapode eggs, and thus peak oxygen requirements also differ late in embryonic development (Seymour and Ackerman 1980; Seymour et al. 1986; Booth and Seymour 1987; Jones et al. 1995). The gaseous microenvironment around a single megapode egg would likely differ substantially from conditions surrounding the large clutches of clustered eggs laid by many dinosaurs. Therefore, underground nests of modern reptiles likely provide a more appropriate model for nonavian dinosaur eggs that were incubated in a substrate. Below, we discuss our observations of desert tortoise and *C. caretta* nesting sites and their relevance to previous hypotheses about Mesozoic egg incubation.

Egg Preservation Potential

Despite the increasing number of discoveries in the last 20 years, fossil eggs from rocks older than the Late Cretaceous are rare (Carpenter and

TABLE 3.—Factors that influence nest preservation.

Environment
Nest location (beach, terrestrial, palustrine)
Proximity to water and flooding
Sediment type (e.g., mud, sand)
Vegetation type and amount
Soil pH
Climate (humid, arid)
Eggs and Nests
Eggshell mineralization (pliable or rigid)
Incubation mode (open nest, burial in vegetation or substrate)
Depth of nest in substrate
Egg size and shell thickness
Clutch size
Number of egg levels in clutch
Population density at nesting site
Abundance, type, and behavior of predators
Adult
Carnivore, herbivore
Age and size
Solitary or colonial nests
Presence or absence of parental care
Duration of nest attendance or guarding
Hatchlings
Development mode (precocial, altricial)
Anatomy
Resident time in the nest

Alf 1994). This sparse fossil record may reflect the predominance of pliable eggs in the early Mesozoic, suggesting a significant role for differential preservation of pliable versus rigid-shelled eggs (Hirsch 1983). For example, Bishop et al. (1997) reported a sea turtle nesting trace that includes a covering pit, egg chamber, egg molds, body pit, and adult crawlway from the Cretaceous Fox Hills Formation in Elbert County, Colorado. The sedimentary structures of the nesting trace strongly resembled those of modern *C. caretta* nests on St. Catherines Island. Deeming and Unwin (2004) questioned this identification because of the absence of fossil eggs and eggshells associated with the nesting trace. They suggested that successful nests of turtles and crocodilians are characterized by the presence of eggshell fragments, and that these should also occur at fossil nest sites. However, our study of tortoise and sea turtle nests suggests that the preservation of eggs and eggshell fragments at fossil localities may depend on a variety of factors (Table 3). The most important of these is eggshell mineralization, namely, whether the eggs are of rigid or pliable structure (Hirsch 1983)

All extant birds, alligators, crocodiles, and some geckos and turtles produce rigid-shelled eggs, whereas all sea turtles lay pliable eggs. As documented in our study, the rigid *G. agassizii* eggs exhibited brittle fracturing as a result of hatching; eggshell fragments occurred inside the egg bottoms and in the surrounding sand. Only three fragments in one nest occurred immediately above the egg chamber on the surface of the burrow floor. In contrast, excavation of hatched *C. caretta* nests revealed collapsed remnants of eggs, but no eggshell fragments comparable to the *G. agassizii* eggshell within the chamber or on the surface of the beach. In addition, decomposition of pliable eggs results in rapid disaggregation of the loosely arranged aragonite crystals that compose the eggshell (Hirsch 1983). This increases the crystal surface area and hence exposure to ions in solution, which facilitates eggshell dissolution (Phillot and Parmenter 2007). The solubility of calcium carbonate minerals, including aragonite, is several orders of magnitude higher in seawater than in freshwater because of the influence of the ionic strength created by the various solutes in seawater (Degens 1965). This suggests that the porosity and

TABLE 4.—Eggshell fragment orientations reported in studies of extant and fossil nesting localities and experimental research. Abbreviations: CU = concave up, CD = concave down, UPD = D. Varricchio, unpublished data, 2014. References: (1) this paper; (2) Hayward et al. 2000; (3) Hayward et al. 2011; (4) Wang et al. 2014; (5) Simon 2014.

CU:CD	Description	References
Tortoise Nests		
69:31	Inside eggs	1
38:62	Within surrounding sediment	1
57:43	In eggs and sediment combined	1
Avian Colonial Nesting Sites		
63:37	Gull colony surface	2
66:34	Avian hatching site	2
68:32	Tern colony, surface	4
42:58	Tern colony, subsurface	4
79:21	Eagle predation site	3
67:33	Gull cannibal midden	2
Experimental Research		
20:80	Natural and experimental fluvial flow	2
50:50	Simulated turbidity flow	2
42:58	Chick hatching & trampling, arena	3
66:34	Chick trampling, arena	3
Dinosaur Nesting Sites		
60:40	Devils Coulee site, Alberta, Canada	2
56:44	Jackknife Creek site, Idaho, U.S.A.	5
60:40	Augusta site, Montana, U.S.A.	2
50:50	<i>Troodon</i> nesting site, Montana, U.S.A.	UPD

permeability of beach sand and inundation of failed clutches by seawater would facilitate dissolution of mineral and rapid microbial decomposition of the organic components of the eggshell matrix. The physical characteristics of sea turtle eggs (or any pliable egg), therefore, likely preclude their preservation in the fossil record except under exceptional conditions (Hirsch 1983). Thus, the absence of eggshell associated with a trace fossil nest, particularly from a marine environment, does not invalidate interpretations based on sedimentologic characteristics.

Eggshell Distribution

The presence of eggshell fragments inside versus outside of fossil eggs is sometimes used to infer the type of incubation and hatching strategy employed by extinct animals. Mueller-Töwe et al. (2002, p. 158) propose that eggshell fragments that occur inside hatched eggs, rather than in surrounding sediments, provide strong evidence for underground incubation and hatching. They apply this reasoning to spherical dinosaur eggs from China that contain eggshell fragments identified in computed tomography (CT) scans. However, these fossil eggs came from various museum collections and lack taphonomic and sedimentologic data. Therefore, they were unable to compare the number and orientation of eggshells inside the fossil eggs to those present in the surrounding rock. To our knowledge, no study of fossil eggs provides quantitative data for eggshells that occurred inside the egg, compared to those in the surrounding matrix.

In our study of both *G. agassizii* and *C. caretta* nests, successful hatching failed to produce significant biological material above the egg chamber. Only predation resulted in exposure of partial eggs at the ground surface. In the *G. agassizii* nests, 106 eggshell fragments were present inside the *in situ* remnants of the eggs; however, the surrounding sand also contained a substantial number, namely 79 fragments. When individual nests are examined, the number of eggshells inside and outside of the egg bottoms varied substantially (Table 1). At least some of this variation relates to factors such as the missing eggs in Nest 8 and the presence of four deceased neonates in Nest 5. In the latter case, large portions of eggshell covered the carapaces, thereby contributing fewer

fragments to the hatched eggs and surrounding sand. Nevertheless, this variation in eggshell distribution in the *G. agassizii* clutches suggests that assessment of multiple fossil clutches from the same locality will likely provide more accurate information than that obtained from excavation of a single whole or partial clutch.

Eggshell Orientation

Documented ratios of concave-up (CU) to concave-down (CD) orientations of eggshell fragments on modern avian nesting colonies provide valuable information for the recognition of egg predation, trampling, and the presence of *in situ* nesting sites (Table 4). Hayward et al. (2011) noted that eggshell orientation within gull nests, chicken hatching sites, and predation sites was marked by a predominance of concave-up eggshells (Table 4). Wang et al. (2014) also found a similar proportion of concave-up eggshells (68%) on the surface of tern nests on an island in Chesapeake Bay after the nesting season. In contrast, a subsurface assemblage at a tern colony show a marked decrease in concave-up eggshells, with 42% CU and 58% CD (Wang et al. 2014), a value similar to that obtained through experiments with chick trampling (Hayward et al. 2011). In contrast, hydraulically transported assemblages produce very skewed assemblages with usually under 20% of the eggshell oriented concave up (Hayward et al. 2011; Imai 2013).

The percentages of concave-up to concave-down eggshells obtained from these studies of modern avian sites are sometimes applied to Mesozoic localities in order to understand the origin of fossil eggshell assemblages (e.g., Hayward et al. 2000; Oser and Jackson 2014). However, evidence suggests that, in contrast to birds, most dinosaurs incubated eggs within a substrate (Deeming 2006); unfortunately, no comparable taphonomic data exists for extant reptile clutches for comparison. Further, surficial processes such as fluvial transport of eggs and eggshells are unlikely to impact dinosaur clutches that were buried and hatched underground, unless the eggs were subsequently exhumed by erosion or predation. Nevertheless, measured CU:CD ratios at some dinosaur nesting sites match surprisingly well with avian models for *in situ* nesting localities where reported ratios are ~ 60:40 (Hayward et al. 2011).

The combined CU:CD orientation ratio for all *G. agassizii* nests in our study was 57:43 (n = 122), similar to the ratios of *in situ* avian nests and the dinosaur localities (Table 4). This total does not include the remaining egg bottoms, which would further raise the concave-up value. However some caveats need to be considered in regard to this number. First, this sample is not statistically distinguishable from a 50:50 ratio nor a 60:40 ratio as evaluated with a chi-square test, but it is statistically significant when compared to orientation of transported avian eggshell fragments noted above. Furthermore, sample size and CU:CD ratios varied widely across the individual tortoise nests. Eggshell fragment counts ranged from 4 to 43, while the percent of CU eggshell varied from 14% to 78%. Additionally, orientation also differed depending on the location of the eggshell fragments. Eggshells within the egg bottoms showed a CU:CD ratio of 69:31 (n = 73) (Table 4). In contrast, fragments in the sand immediately surrounding the hatched tortoise eggs exhibited CU:CD ratio of 38:62 (n = 48) (Table 4, Fig. 3). A higher proportion of CD eggshells in this latter fraction might suggest that fluvial transport had occurred, which was clearly not the case in our study. Because tortoise carapaces cause extensive eggshell damage during hatching, this orientation likely reflected fragmentation of the upper, predominantly concave-down 75% of the eggs. Taken separately, these two fractions in the egg bottoms and surrounding sediment are both significantly different from 50:50 and 20:80 ratios (i.e., transported material; Hayward et al. 2011; Imai 2013) as evaluated by a chi-square test, with the eggshells from the surrounding sediment also differing from 60:40. Thus, in assessing fossil assemblages for eggshell orientation and location, one needs a large sample size (e.g., n > 100) representative of the entire locality. Finally,

FIG. 8.—Schematic diagram of fossil egg showing changes in membrane over time. A) Hatched egg with intact membrane and infilling of sand and eggshell fragments. B) Membrane separates from egg interior. C) Broken eggshell lodged between membrane and egg interior. D) Preservation of vertical and subvertical eggshell fragments lacking membrane in sediment infill. Arrows in views A–C indicate infilling sediment; arrows in view D show direction of eggshell transport. Scale bars in views A–C = 5 cm.

our observed ratios for buried tortoise clutches resemble those at dinosaur nesting sites that are interpreted as nontransported eggshell assemblages (Table 4 and references therein).

The Influence of Membrane on Eggshell Orientation

Computed tomography (CT) of fossil eggs sometimes shows isolated eggshell fragments suspended vertically or subvertically within the sediment filling the hatched egg (Mueller-Töwe et al. 2002, plate 4b, h; plate 6e, f; plate 7g). Our observations of hatched tortoise eggs provide possible insight into the potential processes of preservation for this orientation.

Tortoise eggs consist of an outer inorganic layer of aragonite and an inner protein membrane (Packard and DeMarco 1991). Asynchronous emergence of some hatchlings may have resulted in varying degrees of membrane separation and desiccation within a single clutch. Pockets that formed between the membrane and egg interior as the membrane dried often contained sand and eggshell fragments (Figs. 4A, D). We propose the following sequence of events to explain the vertically oriented eggshell documented in dinosaur eggs (Fig. 8). Initially, the membrane adhered tightly to the egg's inner surface (Fig. 8A). As desiccation proceeded, the membrane dried and separated from the egg interior (Figs. 4A, 8B, C). Some broken eggshell fragments around the opening adhered to the

membrane as the latter separated from the egg. As the pocket filled with sand, eggshell fragments eventually detached and fell into this space as the membrane dried or were trapped within this infilling material (Figs. 4A, 8C). Eventually, complete degradation of the membrane left the eggshell fragments suspended in the sediment fill (Fig. 8D). The same process also likely resulted in eggshell fragments falling to the bottom of the egg in various orientations. Eggshell fragment piles similar to this occur opposite the “hatching window” in some dinosaur eggs (Cousin et al. 1994; Mueller-Töwe et al. 2002). These eggshell fragments, however, may have fallen to the bottom of the egg days or even months after emergence of the hatchlings, and not necessarily as a result of the hatchling's escape from the egg.

Egg Tooth and Hatching Mode

Mueller-Töwe et al. (2002) suggested that some dinosaurs possessed an egg tooth, based on the large, regularly shaped opening in the upper surface of many dinosaur eggs from China. They suggested that species with an egg tooth are likely to produce less damage to the egg during hatching than those without this structure. However, our study suggests that the hatching behavior and bauplan of the animal may have had a greater impact on the condition of the egg than the presence or absence of an egg tooth.

Like many modern amniotes (e.g., crocodilians, avians, squamates), the desert tortoise possesses an egg tooth (Miller 1955). However, all eggs from the hatched clutches show irregular and sharply broken edges around the remaining portion of the egg, rather than a neatly perforated opening (Fig. 4A). Further, the embryo that died in the process of pipping the egg (Nest 5) retained a narrow strip of eggshell that covered the beak. Eggshell and membrane adjacent to the forelimbs exhibited circular puncture holes that corresponded closely to the diameter of the unguals (Fig. 4D). This suggests that at this early stage of hatching, the neonate used the forelimbs to break the egg, rather than the egg tooth. The use of both the egg tooth and forelimbs may characterize many extant and extinct amniotes.

The broad carapace of tortoise embryos also produced extensive damage, with the remaining portion of the egg bottom accounting for only ~ 25% of the original egg (Fig. 4A). In contrast, a taphonomic study of American crocodile nests (F. Jackson, personal observation, 2009) showed that hatched, rigid-shelled eggs typically displayed relatively small openings, coincident with the narrow and elongate hatchling body shape, with ~ 70% of the original egg remaining intact after hatching. This estimate concurs with that previously reported for hatched crocodile and gharial eggs (Mueller-Töwe et al. 2002 and references therein). The extent to which crocodilian adults assisted with hatching in these examples remains unknown. Similar differences in posthatching egg preservation may characterize dinosaur eggs as well; for example, eggs of armored dinosaurs such as ankylosaurs may show significantly more damage after hatching than those of nonavian theropods with more elongate bauplans. Hatchling bauplan, rather than the presence or absence of an egg tooth, likely played a greater role in the posthatching condition of many fossil eggs. Finally, distinguishing damage that results from hatching from the effects of lithostatic compaction and recent weathering proves difficult in many fossil egg specimens.

Adult Anatomy and Nesting Traces

Several studies attempt to relate nest morphology to dinosaur anatomy (e.g., Moratalla and Powell 1994 and references therein; Varricchio et al. 1999; Vila et al. 2010; Fowler and Hall 2011). However, only a few dinosaur nesting localities are attributable to a specific taxon, based on the presence of eggs containing embryonic remains. Further, Mesozoic nesting traces identified by lithologic characteristics are also rare (Horner and Makela 1979; Bishop et al. 1997, 2011; Varricchio et al. 1997, 1999; Chiappe et al. 2004). The Auca Mahuevo titanosaur nesting site in Argentina, however, yielded both eggs containing embryos and nesting traces containing the same egg type (Chiappe et al. 1998, 2004). This allows more accurate correlation of nest shape and maternal size and anatomy. Fowler and Hall (2011) noted similarities of titanosaur limb features and those of modern tortoises that are adapted to digging. These include weakly curved *en echelon*-oriented unguals, graviportal limbs, and significant phalangeal reduction. Based on these morphological similarities, they proposed a comparable function in tortoises and titanosaur sauropods, namely nest excavation. Their study is of particular interest because it focused on the hindlimb morphology of *Gopherus*, the genus that includes *G. agassizii*, Agassiz's desert tortoise whose nests are described here. Despite their substantially smaller size, desert tortoise nests in our study show striking similarity to titanosaur nests preserved in sandstone at the Auca Mahuevo locality (Chiappe et al. 2004). Desert tortoise nests and titanosaur nesting traces are shallow, elongate, and irregular in shape, and the nests display low, distinct rims that slope away from the nest center (Fig. 2C, D; Chiappe et al. 2004: fig. 3). The tortoise nests and titanosaur nesting traces both contained a single layer of eggs, although this may result for the small size of the tortoise clutches in our study, likely due to drought. In addition, some titanosaur clutches in the mudstone facies at Auca Mahuevo are reported to have more than one

egg level (Chiappe et al. 2005). The sandstone nesting traces at Auca Mahuevo, however, may provide a more reliable indication of egg distribution because ancient Vertisol development in the fine-grained overbank sediments significantly altered the arrangement and distribution of some titanosaur eggs and clutches (Jackson et al. 2013).

This resemblance of tortoise and titanosaur nests likely reflects similar limb morphology, as suggested by Fowler and Hall (2011). Further, the hard compact sand making up the chamber walls, floor, and raised rim of the tortoise nest (compared to the loose fill of the egg chamber) may indicate that early compaction of sediment may have increase preservation potential of the Auca Mahuevo nesting traces.

In contrast to the tortoise clutches, however, Auca Mahuevo titanosaur eggs were hypothesized to have incubated egg clutches in open nests, based on two lines of evidence: (1) six nesting traces preserved in sandstone (Chiappe et al. 2004), and (2) analysis of water-vapor conductance of the eggs (Jackson et al. 2008). Chiappe et al. (2004) documented five nests from a single crevasse-splay sand body, dispersed over a distance of ~ 400 m; a sixth nest occurred in a channel sandstone in a different stratum. All six nests contained fine-grain mudstone, suggesting that the nests and eggs were exposed at least at the time the fine-grain sediments were deposited. In addition, the Auca Mahuevo titanosaur eggs exhibit low water-vapor conductance compared to most dinosaur eggs, with a conductance rate (CR) $2.1\times$ greater than expected for an avian egg of similar mass (Jackson et al. 2008). This 2.1 value was considered consistent with the open nest hypothesis that was based on the sedimentology of the nesting traces (Jackson et al. 2008). However, these conductance values are similar to those of megapodes that buried their eggs in vegetation mounds (CR = $1.7\times$) or birds nesting under wet, but open conditions (e.g., loons, grebes; CR = $2.9\text{--}4.2\times$) (Jackson et al. 2008: table 4). Thus, the sauropod value is somewhat ambiguous because it falls between the low values typical of eggs incubated in an open nest and the much higher values in eggs associated with buried incubation (Deeming 2006; Tanaka and Zelenitsky 2014).

This interpretation of an open nest was not without dissent (Grellet-Tinner et al. 2012), and earlier papers speculated that Auca Mahuevo titanosaur eggs were incubated in high-humidity conditions consistent with vegetation in the nest (e.g., Grellet-Tinner et al. 2004, 2006). Grellet-Tinner et al. (2012) report a substantially higher gas conductance for Auca Mahuevo titanosaur eggs compared to Jackson et al. (2008). They attribute this difference to an $8\times$ higher pore density that they obtained from their single eggshell sample. However, Grellet-Tinner et al. (2012) do not mention several key factors necessary for accurate assessment of conductance. These include the total area of the eggshell sampled and how pore density was determined (tangential thin sections or from the egg surface), nor do they provide tangential views that permit comparison to the low pore density shown in Jackson et al. (2008: fig. 4B). Finally, the single eggshell analyzed in Grellet-Tinner et al. (2012) came from egg bed 4 at Auca Mahuevo, whereas those analyzed by Jackson et al. (2008) came from egg bed 3, a stratigraphic difference that may encompass thousands of years and different soil and climate regimes.

To our knowledge, water-vapor conductance rates are not available for desert tortoise eggs. Nevertheless, the similarity between the desert tortoise and sauropod nesting traces suggests a possible alternative interpretation of the sauropod nests, including shallow excavations with minimal sediment cover (e.g., 10–12 cm), similar to the tortoise nests in our study. The low conductance values of the titanosaur eggs may reflect the arid to semiarid climatic and soil conditions present at the Auca Mahuevo locality in the Late Cretaceous, as evidenced by the extensive development of Vertisols (Jackson et al. 2013). Some type of covering would presumably aid in deterring predation and water loss from the eggs; however, it remains difficult to explain the presence of fine-grained sediment deposited from suspension settling of mud that filled the six nests and covered the eggs (Chiappe et al. 2004). Future study of water-

vapor conductance rates in desert tortoise eggs may provide insight about incubation at shallow depths in arid conditions, and its potential effect on eggshell microstructure, pore abundance and distribution, and water-vapor conductance rates. Finally, shallow irregular-shaped nests are documented at many dinosaur localities, and a single layer of eggs appears typical of this group (Mikhailov 1997; Reisz et al. 2012). Therefore, the deep, flask-shaped nest containing stacked eggs produced by sea turtles may not provide an adequate model for substrate burial of most dinosaur eggs.

Synchronous and Asynchronous Development

Weishampel et al. (2008) describe four partial, weathered eggs containing well-preserved oviraptorid embryos from the Nemegt Formation in Mongolia. They suggest that size disparity among these oviraptorids may have been a consequence of asynchrony of egg laying and embryonic development. However, evidence from our study suggests an alternate possibility.

Sea turtle eggs are fertilized in a short period of time, laid simultaneously, and thermal conditions in the deep nests are relatively uniform; therefore, the eggs develop at very similar rates (Houghton and Hays 2001). As a consequence, the hatchlings emerge *en masse* and move up through the chamber sand together during a single night; a few stragglers may require longer or fail altogether to exit the chamber (Houghton and Hays 2001; Bishop et al. 2011). The dead embryos in two of three *C. caretta* clutches on St. Catherines Island exhibited variation of size that was inversely related to the amount of yolk remaining in the eggs (Fig. 6E). Yolk supplies the developing embryo with a large proportion of its nutrients, and rapid lipid utilization occurs during the later stages of embryonic development, corresponding with maximal growth (Noble 1991). Different sizes of embryos and yolk sacs within the same loggerhead clutch strongly suggest that their deaths occurred at different times during incubation. In the fossil record, this could mistakenly be interpreted as asynchronous embryonic development that ended as a result of a catastrophic death event.

Extant Taxa as Analogs

Discussions about dinosaur egg incubation often include comparison to the reproductive biology of extant taxa (e.g., Coombs 1989; Varricchio et al. 1997; Carpenter 1999; Mueller-Töwe et al. 2002; Grellet-Tinner et al. 2006; Jackson et al. 2008). In many cases, reference to animals at more inclusive taxonomic levels (i.e., birds, alligators, turtles) are appropriate. However, some studies refer to crocodiles and alligators collectively as “crocodiles” (e.g., Carpenter 1999); or “crocodilians” (e.g., Hirsch 1994; Horner 2000; Grellet-Tinner et al. 2006), without distinguishing between the nesting strategies that may characterize the two groups. For example, Kohring (1992) speculated about the origin of eggshells on a single bedding plane from the lower Miocene of Germany, suggesting the assemblage resulted from local transport at a “crocodilian” nesting site after a heavy rain. However, alligators incubate eggs in vegetation mounds and some crocodiles lay eggs in holes (Magnusson et al. 1989). This difference would profoundly impact the potential for fluvial transport of eggshells and their preservation in the rock record. Similarly, dinosaur nesting sites are sometimes compared to the nesting ecology of “turtles” or “chelonians” (e.g., Mueller-Töwe et al. 2002; Deeming and Unwin 2004; Grellet-Tinner et al. 2006), without specifying the type of turtle. Such terms could include any member of the superorder Chelonia, which exhibit a wide range of eggshell mineralization and nesting ecology. Given the differences in the reproductive biology of *G. agassizii* and *C. caretta* in our study, we suggest that more specific taxonomic identification of modern species will prove more useful in discussions of dinosaur nesting site taphonomy.

CONCLUSIONS

Taphonomic studies of desert tortoise (*G. agassizii*) and loggerhead sea turtle (*C. caretta*) nesting sites are useful for understanding processes that may influence preservation of biological materials at fossil localities. Conclusions drawn from this study include the following:

1. Although smaller in size, the shallow excavation and the arrangement of the rigid-shelled eggs laid by *G. agassizii* resemble the nests of many dinosaurs. Dinosaur egg clutches also commonly consist of a single layer of irregularly arranged eggs (Mikhailov 1997; Reisz et al. 2012). Further, the nesting trace produced by *G. agassizii* exhibits a similar form to that of titanosaur sauropod dinosaurs from Argentina, thus supporting a similar function of the limbs, namely nest excavation as proposed by Fowler and Hall (2011).
2. The egg opening from which the tortoise hatchlings emerged displayed an irregular outline with sharply broken edges. Although *G. agassizii* possesses an egg tooth, the destruction of the upper 75% of the egg likely results from the broad carapace and use of forelimbs (in addition to the egg tooth) during hatching. This suggests that hatchling anatomy and behavior likely influenced the physical appearance of many hatched Mesozoic eggs as well. Further, an irregular opening cannot be used to rule out the presence of an egg tooth in extinct taxa, without consideration of the hatchling bauplan.
3. Desiccation of eggshell membrane in the rigid-shelled tortoise eggs allowed sand and eggshell fragments to fill the spaces between the membrane and the egg interior. This process may account for the presence of vertically oriented eggshells in sediment that fills fossil eggs. In addition, eggshell fragments that were attached to membrane fell into the egg bottom as the membrane dried, assuming different orientations. Thus, eggshell fragments may enter a hatched egg days or even months after hatching, rather than simultaneously with emergence of the hatchling.
4. The tortoise bauplan and hatching process may strongly influence the distribution and orientation of eggshell fragments in the nest. Hatching of *G. agassizii* egg clutches resulted in fragmentation of the upper 3/4 of the egg, and a substantial number of eggshell fragments were distributed within the hatched egg bottom, as well as within the surrounding sand.
5. Combined CU:CD data from all the tortoise clutches produced a 57:43 ratio. This distribution compares favorably with those documented on avian colonies and the few documented dinosaur localities. To a statistically significant degree, these ratios may be useful for distinguishing *in situ* from transported eggshell fragments at fossil localities, regardless of whether nesting was underground or at the surface. However, caution is required when interpreting fossil nesting localities because of the lack of taphonomic studies of extant reptilian nesting sites.
6. *Caretta caretta* laid eggs *en masse* and young emerged nearly synchronously. We observed dead young displaying varying developmental states within the same nest. Therefore, caution is required when hypothesizing the synchronicity or asynchronicity of hatchling development in dinosaur taxa, based upon the size and age of preserved embryos.
7. Some chelonian eggs and nests, such as those of *C. caretta*, are difficult to compare to those of dinosaurs because of the turtle’s pliable eggshell, stacked egg arrangement, and greater depth of the egg chamber. The sea turtle eggs tear and collapse upon hatching, rather than displaying evidence of the brittle fracture typical of rigid-shelled tortoise eggs. Further, these pliable eggs have poor preservation potential because of the loose arrangement of the aragonite crystals that facilitates eggshell dissolution in seawater.

8. Only nest predation resulted in exposure of significant biological material at the ground surface above the egg chambers. Further, the amount of disruption to the sea turtle nests depended on the size and behavior of the predator. Because most dinosaur eggs were buried in a substrate, the discovery of disrupted clutches and potentially transported eggs and eggshells suggests that this resulted from exhumation of the nest due to predation, scavenging after hatching, or erosion.
9. Given the differences in egg shape, degree of mineralization, clutch size, and other physical features of extant eggs, as well as adult nesting strategies and behaviors, we recommend identification of the specific extant species in order to facilitate more accurate comparison to extinct taxa.

ACKNOWLEDGMENTS

Research was supported by National Science Foundation grant #0847777 (EAR) to D. Varricchio. We acknowledge the support of the Bureau of Land Management, Department of the Army, and St. Catherines Island Sea Turtle Conservation Program of The St. Catherines Island Foundation, Inc., which is supported through the Edward John Noble Foundation, Inc. We thank Clarence Everly, Directorate of Public Works-Environmental at the National Training Center, Fort Irwin, California, for logistical support while in the Mojave Desert and funding to A. Walde for the study that located the nests. We thank J. Bonde and R. Saumure for providing contacts for the project, M. Knell and D. Lawver for help in the field at sea turtle nests, and G. See and C. Jones for assistance with field work at tortoise nest sites. Finally, we thank D. Lawver for his helpful discussions of turtles.

REFERENCES

AVERILL-MURRAY, R.C., 2002, Reproduction of *Gopherus agassizii* in the Sonoran Desert, Arizona: Chelonian Conservation and Biology, v. 4, p. 295–301.

BISHOP, G.A., 2007, The St. Catherines Island Sea Turtle Program, updated January 1, 2012, <http://www.scistp.org>. Checked April 2014.

BISHOP, G.A., AND MARSH, N.A., 1994, The 1992 St. Catherines Sea Turtle Program: Nest validation by beach stratigraphy, in Schroeder, B.A., and Witherington, B.E., eds., Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation: NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum NMFS-SEFSC 341, p. 22–24.

BISHOP, G.A., AND MEYER, B.K., 2011, Chapter 14. Sea turtle habitat deterioration on St. Catherines Island: defining the modern transgression, in Bishop, G.A., Rollins, H.B., and Thomas, D.H., eds., Geoarchaeology of St. Catherines Island, Georgia: American Museum of Natural History, Anthropological Papers 94, p. 272–295.

BISHOP, G.A., MARSH, N.B., BARRON, J., PIRKLE, F.L., AND SMITH, R.S.U., 1997, A Cretaceous sea turtle nest, Fox Hills Formation, Elbert Co., CO: Geological Society of America, Abstracts with Programs, v. 29, p. 104.

BISHOP, G.A., MARSH, N.B., AND PIRKLE F.L., 2000, Fossilized Cretaceous sea turtle nest from Colorado, in Kalb, H.J. and Wibbels, T., eds., Proceedings of the Nineteenth Annual Symposium (1999) on Sea Turtle Biology and Conservation: United States Department of Commerce. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum. NMFS-SEFSC-443, p. 291.

BISHOP, G.A., HAYES, R.H., MEYER, B.K., ROLLINS, H.E., RICH, F.J., THOMAS, D.H., AND VANCE, R.K., 2007, Transgressive barrier island features of St. Catherines Island, Georgia, in Rich, F.J., ed., Fieldtrips of the 2007 Annual Meeting, Southeastern Section, Geological Society of America: Statesboro, Georgia Southern University, p. 39–85.

BISHOP, G.A., VANCE, R.K., RICH, F.J., MEYER, B.K., DAVIS, E.J., HAYES, R.H., AND MARSH, N.A., 2009, Evolution of geology field education for K–12 teachers from field education for geology majors at Georgia Southern University: historical perspectives and modern approaches, in Whitmyer, S.J., Mogt, D.W., and Pyle, E.J., eds., Field Geology Education: Historical Perspectives and Modern Approaches: Geological Society of America, Special Paper 461, p. 223–251.

BISHOP, G.A., PIRKLE, F.L., MEYER, B.K., AND PIRKLE, W.A., 2011, The foundation for sea turtle geoarchaeology and zooarchaeology: morphology of recent and ancient sea turtle nests, St. Catherines Island, Georgia, and Cretaceous Fox Hills Sandstone, Elbert County, Colorado, in Bishop, G.A., Rollins, H.B., and Thomas, D.H., eds., Geoarchaeology of St. Catherines Island, Georgia: American Museum of Natural History Anthropological Papers, 94, p. 247–269.

BURLIN, C.D., AND BISSONETTE, J.A., 2004, Survival during early life stages of the desert tortoise (*Gopherus agassizii*) in the south-central Mohave Desert: Journal of Herpetology, v. 38, p. 527–535.

BOARMAN, W.I., 2002, Reducing predation by common ravens on desert tortoises in the Mojave and Colorado Deserts: United States Geological Society, Western Ecological Research Center, Sacramento, California, 33 p.

BOOTH, D., AND SEYMOUR, R., 1987, Effect of eggshell thinning on water vapor conductance of Mallee fowl eggs: Condor, v. 89, p. 453–459.

BRANNEN, N.A., AND BISHOP, G.A., 1993, Nesting traces of the loggerhead sea turtle (*Caretta caretta*), St. Catherines Island, Georgia: implications for the fossil record, in Farrell, K.M., Hoffman, C.W., and Henry, V.J., Jr., eds., Geomorphology and Facies Relationships of Quaternary Barrier Island Complexes near St. Marys, Georgia: Georgia Geological Society, p. 30–36.

CARPENTER, K., 1999, Eggs, Nests and Baby Dinosaurs: A Look at Dinosaur Reproduction: Bloomington, Indiana, Indiana University Press, 312 p.

CARPENTER, K., AND ALF, K., 1994, Global distribution of dinosaur eggs, nests, and babies, in Carpenter, K., Hirsch, K., and Horner, J., eds., Dinosaur Eggs and Babies: Cambridge, UK, Cambridge University Press, p. 15–30.

CHIAPPE, L.M., CORIA, R.A., DINGUS, L., JACKSON, F., CHINSAMY, A., AND FOX, M., 1998, Sauropod dinosaur embryos from the Late Cretaceous of Patagonia: Nature, v. 396, p. 258–261.

CHIAPPE, L., SCHMITT, J., JACKSON, F., GARRIDO, A., DINGUS, L., AND GRELLET-TINNER, G., 2004, Nest structure for sauropods: sedimentary criteria for recognition of dinosaur nesting traces: PALAIOS, v. 19, p. 89–95.

CHIAPPE, L., JACKSON, F., CORIA, R., AND DINGUS, L., 2005, Nesting titanosaurs from Auca Mahuevo and adjacent site (Late Cretaceous; Patagonia, Argentina): understanding sauropod reproductive behavior, in Curry Rogers, K., and Wilson, J.A., eds., The Sauropods: Evolution and Paleobiology: Berkeley, California, University of California Press, p. 348.

COOMBS, W.P., JR., 1989, Modern analogs for dinosaur nesting and parental behavior, in Farlow, J.O., ed., Paleobiology of the Dinosaurs Special Paper 238: Boulder, Colorado, Geological Society of America, p. 21–53.

COUSIN, R.G., BRETON, G., FOURNIER, R., AND WATTÉ, J.P., 1994, Dinosaur egg-laying and nesting in France, in Carpenter, K., Hirsch, K., and Horner, J., eds., Dinosaur Eggs and Babies: Cambridge, UK, Cambridge University Press, p. 56–74.

CRAWFORD, N.G., FAIRCLOTH, B.C., MCCORMACK, J.E., BRUMFIELD, R.T., WINKER, K., AND GLENN, T.C., 2012, More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs: Biology Letters, v. 8, p. 783–786.

CRUZ, I., 2007, Avian taphonomy: observations at two Magellanic penguin (*Spheniscus magellanicus*) breeding colonies and their implications for the fossil record: Journal of Archaeological Science, v. 34, p. 1252–1261.

DEEMING, D., 2006, Ultrastructural and functional morphology of eggshells supports the idea that dinosaur eggs were incubated buried in a substrate: Palaeontology, v. 49, p. 171–185.

DEEMING, D.C., AND UNWIN, D.M., 2004, Reptilian incubation: evolution and the fossil record, in Deeming D.C., ed., Reptilian Incubation: Environment, Evolution and Behaviour: Nottingham, UK, Nottingham University Press, p. 1–14.

DEGENS, E.T., 1965, Geochemistry of Sediments: A Brief Survey: Englewood Cliffs, New Jersey, Prentice-Hall, 342 p.

ERBEN, H.K., HOEFS, J., AND WEDEPOHL, K.H., 1979, Paleobiological and isotopic studies of eggshells from a declining dinosaur species: Paleobiology, v. 5, p. 380–414.

ERNST, C.H., AND LOVICH, J.E., 2009, Turtles of the United States and Canada, 2nd Edition: Baltimore, Johns Hopkins University Press, 827 p.

FOWLER, D.W., AND HALL, L.E., 2011, Scratch-digging sauropods, revisited: Historical Biology, v. 23, p. 27–40.

GRELLET-TINNER, G., CHIAPPE, L., AND CORIA, R., 2004, Eggs of titanosaurid sauropods from the Upper Cretaceous of Auca Mahuevo (Argentina): Canadian Journal of Earth Science, v. 41, p. 949–960.

GRELLET-TINNER, G., CHIAPPE, L., NORELL, M., AND BOTTJER, D., 2006, Dinosaur eggs and nesting behaviors: a paleobiological investigation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 232, p. 294–321.

GRELLET-TINNER, G., FIORELLI, L.E., AND SALVADOR, R.B., 2012, Water vapor conductance of the Lower Cretaceous dinosaurian eggs from Sanagasta, La Rioja, Argentina: Paleobiological and paleoecological implications for South American faveololithid and megalolithid eggs: PALAIOS, v. 27, p. 35–47.

GROVER, M.C., AND DEFALCO, L.A., 1995, Desert tortoise (*Gopherus agassizii*): status-of-knowledge outline with references: Forrest Service General Technical Report INT-GTR-316, 134 p.

HAYES, R.H., MARSH, N.B., AND BISHOP, G.A., 1995, Sea turtle nest depredation by a feral hog: a learned behavior, in Keinath, J.A., Baranard, D.E., Musick, J.A., and Bell, B.A., eds., Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation: NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum NMFS-SEFSC 387, p. 129–134.

HAYWARD, J.L., FOLSON, S.D., TAMBRINI, A.A., AND COWLES, D.L., 1997, Experiments on the taphonomy of amniote eggs in marine environments: PALAIOS, v. 12, p. 482–488.

HAYWARD J.L., ZELENITSKY, D.K., SMITH, D.L., ZAFT, D.M., AND CLAYBURN, J.K., 2000, Eggshell taphonomy at modern gull colonies and a dinosaur clutch site: PALAIOS, v. 15, p. 343–355.

HAYWARD, J.L., DICKSON, K.M., GAMBLE S.R., OWEN, A.W., AND OWEN, K.C., 2011, Eggshell taphonomy: environmental effects on fragment orientation: Historical Biology, v. 23, p. 5–13.

HIRSCH, K.F., 1983, Contemporary and fossil chelonian eggshells: Copeia, v. 2, p. 382–397.

HIRSCH, K.F., 1994, The fossil record of vertebrate eggs, in Donovan, S.K., ed., The Palaeobiology of Trace Fossils: Baltimore, Johns Hopkins University Press, p. 269–294.

- HORNER, J.R., 1994, Comparative taphonomy of some dinosaur and extant bird colonial nesting grounds, in Carpenter, K., Hirsch, K., and Horner, J., eds., *Dinosaur Eggs and Babies*: Cambridge, UK, Cambridge University Press, p. 116–123.
- HORNER, J.R., 2000, Dinosaur reproduction and parenting: *Annual Review of Earth and Planetary Sciences*, v. 28, p. 19–45.
- HORNER, J.R., AND MAKELA, R., 1979, Nest of juveniles provides evidence of family structure among dinosaurs: *Nature*, v. 282, p. 296–298.
- HOUGHTON, J.D.R., AND HAYS, G.C., 2001, Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings: *Naturwissenschaften*, v. 88, p. 133–136.
- IMAI, T., 2013, Sedimentological analyses of eggshell transport and deposition: implication and application to eggshell taphonomy: Unpublished M.S. thesis, Montana State University, Bozeman, 62 p.
- JACKSON, F., VARRICCHIO, D., JACKSON, R., VILA, B., AND CHIAPPE, L., 2008, Comparison of water vapor conductance of a titanosaur egg from Argentina, with a *Megaloolithus siruguei* egg from Spain: *Paleobiology*, v. 34, p. 229–246.
- JACKSON, F., SCHMITT, J., AND OSER, S., 2013, Influence of Vertisol development on sauropod egg taphonomy and distribution at the Auca Mahuevo locality, Patagonia, Argentina: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 386, p. 300–307.
- JONES, D.N., DEKKER, R.W.R.J., AND ROSELAAR, C.S., 1995, *The Megapodes*: Oxford, UK, Oxford University Press, 262 p.
- KNEEL, M.J., 2012, Taphonomic and biostratigraphic analysis of fossil freshwater turtles in the Upper Cretaceous (Campanian) Kaiparowits Formation of southern Utah, USA: Unpublished Ph.D. dissertation, Montana State University, Bozeman, 243 p.
- KOHRING, R., 1992, Fossil crocodilian eggshells from the Lower Freshwater Molasse (early Miocene) of Ulm (Ulm-Westtangente, Baden-Württemberg): *Stuttgarter Beiträge zur Naturkunde, series B*, v. 187, p. 1–10.
- KOHRING, R., 1999, Strukturen, biostratigraphie, systematische und phylogenetische Relevanz von Eischalen amnioter Wirbeltier: *Courier Forschungsinstitut Senckenberg*, v. 210, p. 1–307.
- LINSLEY, D., BISHOP, G.A., AND ROLLINS, H.B., 2008, Stratigraphy and geologic history of St. Catherines Island, in Thomas, D.E., ed., *Native American Landscapes of St. Catherines Island, Georgia: The Theoretical Framework*: American Museum of Natural History, Anthropological Papers, Number 88, 1136 p.
- MAGNUSSON, W.E., VLIET, K.A., POOLEY, A.C., AND WHITAKER, R., 1989, Reproduction, in Ross, C.A., and Garnett, S., eds., *Crocodyles and Alligators*: New York, Facts on File, Inc., p. 118–135.
- MIKHAILOV, K., 1997, Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification: *Special Papers in Paleontology*, v. 56, p. 1–80.
- MILLER, L., 1955, Further observations on the desert tortoise, *Gopherus agassizii*, of California: *Copeia*, v. 2, p. 113–118.
- MORATALLA, J.J., AND POWELL, J., 1994, Dinosaur nesting patterns, in Carpenter, K., Hirsch, K.F., and Horner, J.R., eds., *Dinosaur Eggs and Babies*: New York, Cambridge University Press, p. 137–150.
- MUELLER-TÖWE, I., SANDER, P.M., SCHULLER, H., AND THIES, D., 2002, Hatching and infilling of dinosaur eggs as revealed by computed tomography: *Palaeontographica*, v. 267, p. 168.
- NOBLE, R.C., 1991, Comparative composition and utilisation of yolk lipid by embryonic birds and reptiles, in Deeming, D.C., and Ferguson, M.W.J., eds., *Egg Incubation: Its Effect on Embryonic Development in Birds and Reptiles*: New York, Cambridge University Press, p. 17–28.
- OSER, S., AND JACKSON, F., 2014, Sediment and eggshell interactions: using abrasion to assess transport in fossil eggshell accumulations: *Historical Biology*, v. 26, p. 165–172.
- PACKARD, M.J., AND DEMARCO, V.G., 1991, Eggshell structure and formation in eggs of oviparous reptiles, in Deeming, D.C., and Ferguson, M.W.J., eds., *Egg Incubation: Its Effect on Embryonic Development in Birds and Reptiles*: New York, Cambridge University Press, p. 53–70.
- PHILLOT, A.D., AND PARMENTER, C.J., 2007, Deterioration of green sea turtle (*Chelonia mydas*) eggs after known embryo mortality: *Chelonian Conservation and Biology*, v. 6, p. 262–266.
- REISZ, R.R., EVANS, D.C., ROBERTS, E.M., SUES, H.-D., AND YATES, A.M., 2012, Oldest known dinosaurian nesting site and reproductive biology of the Early Jurassic sauropodomorph *Massospondylus*: *Proceedings of the National Academy of Science*, v. 109, p. 2428–2433.
- SEYMOUR, R., 1979, Dinosaur eggs: gas conductance through the shell, water loss during incubation and clutch size: *Paleobiology*, v. 5, p. 1–11.
- SEYMOUR, R., AND ACKERMAN, R., 1980, Adaptions to underground nesting in birds and reptiles: *Integrative and Comparative Biology*, v. 20, p. 437–447.
- SEYMOUR, R., VLECK, D., AND VLECK, C., 1986, Gas exchange in the incubation mounds of megapode birds: *Journal of Comparative Physiology*, v. 156, p. 773–782.
- SIMON, D.J., 2014, Giant dinosaur (theropod) eggs of the oogenus *Macroelongatoolithus* (Elongatoolithidae) from southeastern Idaho: taxonomic, paleobiogeographic and reproductive implications: Unpublished M.S. thesis, Montana State University, Bozeman, 113 p.
- TANAKA, K., AND ZELENITSKY, D.K., 2014, Relationships between nest humidity and nest types in living archosaurs: *Historical Biology*, v. 26, p. 122–131.
- TURNER, R.M., 1982, Mohave Desert scrub: *Desert Plants*, v. 4, p. 157–179.
- VARRICCHIO, D., JACKSON, F., BORKOWSKI, J., AND HORNER, J., 1997, Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits: *Nature*, v. 385, p. 247–250.
- VARRICCHIO, D., JACKSON, F., AND TRUEMAN, C., 1999, A nesting trace with eggs for the Cretaceous theropod dinosaur *Troodon formosus*: *Journal of Vertebrate Paleontology*, v. 19, p. 91–100.
- VILA, B., JACKSON, F., AND GALOBBART, A., 2010, First data on dinosaur eggs and clutches from Pinyes locality (Upper Cretaceous, Southern Pyrenees): *Ameghiniana* (Argentina), v. 47, p. 79–87.
- WALDE, A.D., WALDE, A.M., DELANEY, D.K., AND PATER, L.L., 2009, Burrows of desert tortoises (*Gopherus agassizii*) as thermal refugia for horned larks (*Eremophila alpestris*) in the Mojave Desert: *Southwestern Naturalist*, v. 54, 375–381.
- WANG, P.L., JACKSON, F.D., AND VARRICCHIO, D.J., 2014, Nest taphonomy of common terns (*Sterna hirundo*) on Poplar Island, Chesapeake Bay, Maryland: *Historical Biology*, v. 26, p. 155–164.
- WEISHAMPEL, D., FASTOVSKY, D., WATABE, M., VARRICCHIO, D., JACKSON, F., TSOGTBATAAR, K., AND BARSBOLD, R., 2008, New oviraptorid embryos from Bugintsav, Nemegt Formation (Late Cretaceous), Mongolia, with insights into their habitat and growth: *Journal of Vertebrate Paleontology*, v. 28, p. 1110–1119.
- WOODBURY, A.M., AND HARDY, R., 1948, Studies of the desert tortoise, *Gopherus agassizii*: *Ecological Monographs*, v. 18, p. 145–200.

Received 25 May 2014; accepted 12 December 2014.