Taphonomic Effects of pH and Temperature on Extant Avian Dinosaur Eggshell

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Avian and non-avian dinosaur eggshell contains clues that are helpful in the reconstruction of ancient habitats and behaviors. Fossilized eggshell often shows signs of corrosion attributed to acid dissolution of the calcium carbonate, but this process has never been quantified in controlled experiments. In work reported here, extant avian dinosaur eggshell fragments were placed in buffered solutions of varying pH and temperature for varying periods of time. Changes in the appearance, mass, surface area, and thickness were described and compared with naturally weathered eggshell. Treatment resulted in corrosion and pitting of the outer surface and corrosion of the mammillary structure of the inner surface. Fragment mass, surface area, and thickness generally decreased in response to decreased pH and to increased temperature and exposure time. A classification scheme for eggshell corrosion is proposed.

INTRODUCTION

Fossil eggs and eggshell serve increasingly important roles in illuminating the lives of ancient animals (Carpenter et al., 1994; Carpenter, 1999; Hayward et al., 2000; Chiappe et al., 2001), and they are distributed widely throughout the world (Carpenter and Alf, 1994). Not only does eggshell yield important taxonomic data (Mikhailov, 1991; Zelenitsky, 1995), it also provides a wealth of information concerning ancient parental behavior and nesting ecology (Horner 1982; 1987; Hayward et. al, 1989; 1991; 1997; 2000). Sometimes eggshell is preserved in great quantities (Horner, 1982; Horner and Gorman, 1988; Sanz et al., 1995; Leggitt, 2000; Chiappe et al., 1998; 2001) making it an especially useful forensic tool in the reconstruction of ancient nesting environments (Erickson, 1978). In other cases eggshell may be rare or absent, despite evidences for nesting activity. The paucity of eggshell in such circumstances also yields paleoecological clues. For example, Carpenter (1982) found numerous baby dinosaur teeth representing 11 taxa from the Late Cretaceous Lance and Hell Creek formations in Wyoming and Montana, yet he found few eggshell fragments. He hypothesized that a reducing (low-Eh) depositional environment, combined with water-logged, acidic soils may have been responsible for dissolving most of the original eggshell but leaving the teeth intact.

Both birds and non-avian theropods construct(ed) brittle eggshell that consists of at least two structural layers of calcite (dinosaurid-prismatic and ornithoid-ratite morphotypes; Mikhailov et al., 1996; Mikhailov, 1997), an inner mammillary layer and an outer spongy layer. The mammillary layer contains many conical mammillae tightly compressed into a single continuous layer. Each mammilla consists of noncrystalline minerals concentrically aggregated around a granular matrix, with a nucleus of matrix centrally located near the base. The spongy layer is very compact with no visible stratification. Numerous microscopic pores are distributed irregularly throughout the shell and connect the inner and outer surfaces (Romanoff and Romanoff, 1949; Mikhailov, 1991). This complex substructure is not necessarily preserved uniformly in fossil samples. For example, the outer spongy layer may exhibit pitting, cratering, and loss of outer surface sculpturing, the mammillary structure of the inner surface may be corroded, matrix dissolution and recrystallization may occur, and shell thickness may be reduced (Hirsch, 1979; 1989; 1994; Hirsch and Bray, 1988; Hirsch and Quinn, 1990; Mikhailov et al., 1996; Bray and Hirsch, 1998; Zelenitsky et al., 2000).

Non-uniformity of eggshell preservation presumably reflects exposure to different environmental factors and/or exposure over different lengths of time. Thus, Carpenter (1982) found that by 60 days, acids produced by decaying plant material in a semi-closed container of water (pH=6.6) dissolved the broken edges of chicken eggshell fragments. Hayward et al. (1991) demonstrated that gull eggshell buried by mildly acidic (pH=6.4) Mount St. Helens ash (Hayward et al., 1982; 1989) experienced rapid dissolution, pitting, formation of cratered dissolution rings, and eventual development of a honeycombed structure within seven years. Beyond these two studies, no published experimental work has examined the effects of environmental factors on eggshell during long-term preservation. By contrast, bone weathering has received considerable attention (e.g., Behrensmeyer, 1978; Gordon and Buikstra, 1981; Lyman and Fox, 1989; Trueman, 1997; Downing and Park, 1998; Cutler et al., 1999; Dauphin et al., 1999). Both bone and eggshell are calcified tissues, but they exhibit different physical and chemical properties. With the increasing use of eggshell in paleoreconstruction, eggshell taphonomy should be examined in its own right.

This paper reports the first controlled experiments to examine the effects of pH and temperature on corrosion patterns in dinosaur eggshell, and tests the hypothesis that the rate of corrosion increases in response to both decreasing pH and increasing temperature under controlled experimental conditions. It also discusses the implications of the experimental results for interpretations of fossil di-

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nosaur eggshell, and a classification scheme for stages of eggshell corrosion is proposed.

MATERIALS AND METHODS

On July 2, 1994, twelve glaucous-winged gull (*Larus glaucescens*) eggshells were covered by a poultry wire exclosure and allowed to weather on the surface (pH=6.3±0.4) of the glaucous-winged gull colony on Violet Point, Protection Island National Wildlife Refuge, Jefferson County, Washington. A sample fragment was collected from each of these eggshells on August 4, 1995 and August 2, 1996. Additional experimental eggshell fragments were collected from five newly hatched glaucous-winged gull eggshells from the same locality. Fragments were broken to the desired mass (19–21 mg) and diameter (approximately 5 mm) using fine forceps.

Solutions of pH 6.2, 6.6, 7.0, and 7.4 were made by adjusting a 10 mmol solution of PIPES buffer in double-distilled water to the desired pH using HCl and NaOH. All solutions were prepared in 1-l Erlenmeyer flasks at the experimental temperatures for which they were intended (4°C, 25°C, and 35°C). Portions of 100-ml were transferred to lidded, 120-ml specimen containers. Five fragments were subjected to each experimental treatment and only one fragment was placed in each container.

A pilot study was performed to determine the length of time needed under each experimental condition to produce measurable change in eggshell structure, yet not remove all calcium carbonate from the fragments. Because of dramatic increases in eggshell corrosion observed at higher temperatures, time periods were varied for each of the pH levels as follows: at 4°C for 7, 14, 21, 28, 35, and 42 days; at 25°C for 4, 8, 14, 16, 20, and 24 days; at 35°C for 2, 4, 6, 8, 10, and 14 days. All three temperature regimens included a 14-day treatment, which allowed for comparison of various temperature and pH effects over a standard unit of time.

Mass, inner surface area, and fragment thickness were determined for each fragment both before and after experimental treatment. Inner surface area of fragments was determined using a CCD video camera module mounted on a Leica WILD MZ8 stereo microscope. The captured image was digitized using ComputerEyes/RT video frame grabber (Digital Vision, Inc.) and NIH Image software. Fragment thickness was averaged over five randomly selected locations along the radial image. ANOVA and Scheffe's F tests were used to compare treatments at the 0.05 significance level. Freshly hatched, naturally weathered, and experimentally treated eggshell fragments were compared using stereo light and scanning electron microscopy.

RESULTS

Natural Eggshell

In radial section (Fig. 1A), the outer edge of untreated eggshell appeared smooth and undulating, and the mammillary structures defined the profile of the inner surface. The outer surface was glossy, pigmented, mottled, and lacked structural ornamentation (Fig. 1B). Pore openings were located in shallow depressions and were surrounded by networks of shallow channels. The tightly packed mammillae of the inner surface were surrounded by shallow, irregular interstices (Fig. 1C). The presence of craters in the mammillae indicated calcite resorption by the embryo (Hirsch and Quinn, 1990). The mammillary cones were not always clearly defined but could usually be distinguished.

After one year of natural weathering, the outer surfaces of eggshell fragments (Fig. 1E) were visibly altered. Much of the texturing that characterized fresh eggshell was absent. The glossy appearance of the outer surface was subdued, although in radial section (Fig. 1D) the outermost layer appeared to remain partially intact. The depressions containing the pores were shallower and the surrounding network of channels was no longer evident. The inner surfaces (Fig. 1F) had been significantly eroded along the margins of the mammillae. The mammillary structure was still evident, but much of the detail exhibited by fresh eggshell had been obliterated. After two years of weathering, fragments showed similar features to those weathered for one year, except that the outer surfaces exhibited a higher degree of roughness (Fig. 1H), the inner mammillary structures were less distinct, and the interstices surrounding the mammillae had been largely obliterated (Fig. 1I).

Experimentally Treated Eggshell

Post-treatment appearances of the inner and outer surfaces of eggshell varied widely. The outer surfaces of some fragments appeared to have experienced little, if any, corrosion following treatment, whereas those of other fragments exposed to the same treatment were extensively corroded. Moreover, corrosion did not occur evenly on both surfaces; some fragments appeared to have corroded more on the outer surface, whereas others experienced more corrosion on the inner surface. Corrosion resulted in a rougher outer surface, loss of the network of channels surrounding the pore openings, fusion of mammillae, and pitting (Fig. 1K, N). Fragments placed in acid solutions for the longest periods were honeycombed and experienced complete loss of mammillary structure (Fig. 1M, O). Pigmented protein layers were exposed in some fragments from which most of the calcium carbonate had been removed. This protein was covered with blotches of alternating darker and lighter pigmentation. When wet, this protein material was flexible and easily torn; when dry, it became rigid, brittle, and sometimes curled. Some treated fragments showed small flakes of calcium carbonate peeling off the inner surface. Several fragments that had experienced extensive calcium carbonate dissolution began to curl when they dried.

Loss of mass occurred for all experimental treatments, with greatest losses occurring at higher temperatures and lower pH values. At 4°C (Fig. 2A), final masses of fragments treated by acidic solutions were significantly less than those exposed to neutral and alkaline solutions. At 25°C (Fig. 2B), differences in mass between fragments exposed to acid versus neutral/alkaline pH narrowed in comparison with 4°C data, although losses in solutions with acidic pH were more pronounced. At 35°C (Fig. 2C), no significant difference was observed in fragment masses experiencing acidic and neutral pH solutions, whereas frag-

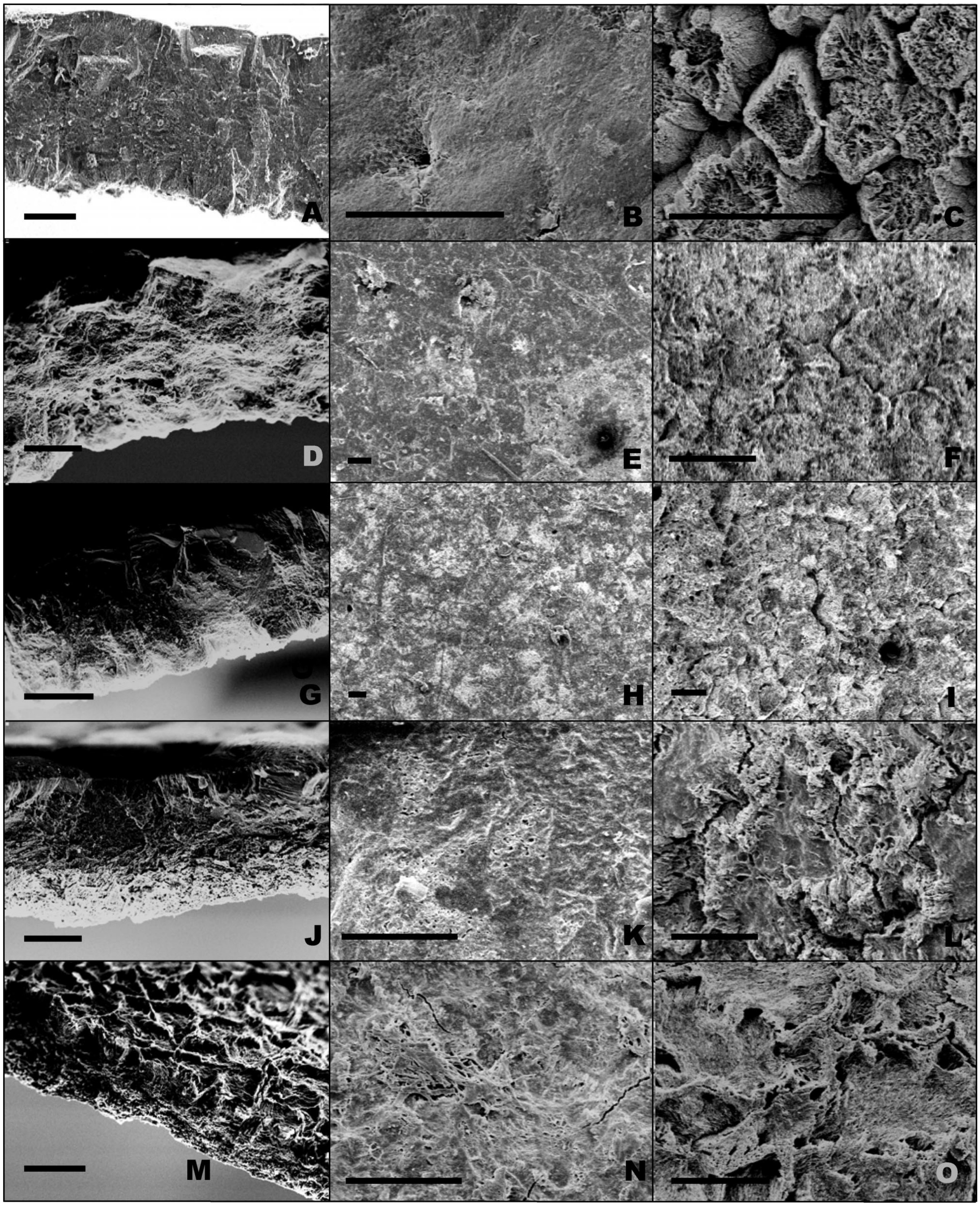

FIGURE 1—Scanning electron micrographs of glaucous-winged gull eggshell. All bars represent 100 μm and all radial views show eggshell with outside surface up. (A–C) Fresh, untreated eggshell. (A) Radial view; note distinct blocky crystalline structure. (B) Outside surface of eggshell with pore and shallow channels. (C) Inner surface of eggshell with distinctly cratered mammillae. (D–F) Eggshell after 1 year of weathering on surface of nesting colony. (D) Radial view, showing little alteration. (E) Outer surface, corroded with loss of channels and more shallow depression surrounding pore. (F) Inner surface, with significant loss of mammillary structure. (G–I) Eggshell after 2 years of weathering on surface of nesting colony. (G) Radial view. (H) Outer surface, with rough appearance. (I) inner surface, with indistinct mammillae. (J–L) Eggshell after 14 days at 25°C in buffered pH 6.6 solution. (J) Radial view, with large number of small pits apparent. (K) Outer surface, with

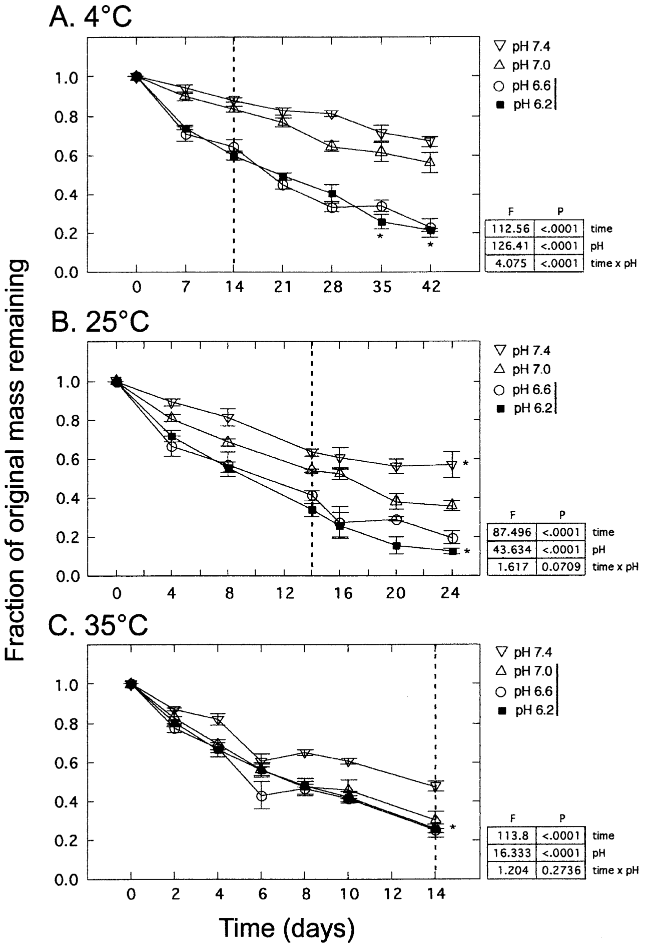

FIGURE 2—Fraction of eggshell mass remaining over time for each experimental treatment. Data represent means ± standard errors. Shell-mass means for experiments at pH values linked by the same vertical line in the legend are not significantly different at the 0.05 level (Scheffe's F test). The vertical dotted lines at 14 days indicate a comparable time among the three temperature regimens. Means are based on five replicates, except those with four, which are indicated by asterisks (*).

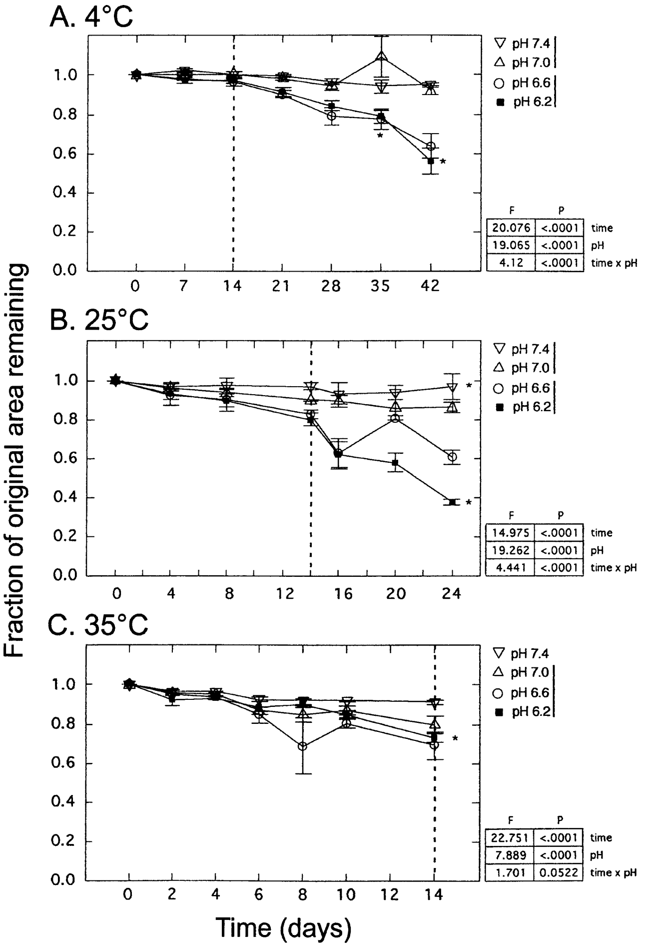

FIGURE 3—Fraction of eggshell surface area remaining after experimental treatment. Data represent means ± standard errors. Surface-area means for experiments at pH values linked by the same vertical line in the legend are not significantly different at the 0.05 level (Scheffe's F test). The vertical dotted lines at 14 days indicate a comparable time among the three temperature regimens. Means are based on five replicates, except those with four, which are indicated by asterisks (*).

ments exposed to alkaline solutions retained significantly higher masses. Corrosion in the alkaline solution was significantly less than in solutions of lower pH. Significant differences in fragment mass were not observed between treatments pH 6.2 and 6.6, regardless of temperature.

Higher losses in fragment surface area were observed in response to solutions of neutral and acidic pH as temperature increased, whereas fragment surfaces areas changed little in the alkaline solution. At all temperatures, pairwise comparisons indicated no significant differences between the effects of pH 6.2 and 6.6 on surface area. At 4°C (Fig. 3A), surface area losses were significantly greater for fragments exposed to pH 6.2 and 6.6 than to 7.0 and 7.4. After 35 days at pH 7.0, eggshell fragments appeared to increase in surface area, although this seems to have been due to a flattening of two of the five sample fragments during this treatment. No significant difference was shown for area loss between fragments exposed to pH 7.0 and 7.4 at 4°C and 25°C (Fig. 3A, B), although area loss under these conditions was significantly less than for fragments exposed to acidic conditions. No significant differences in area loss occurred among fragments at 35°C exposed to pH 6.2, 6.6, and 7.0, although fragments exposed to pH 7.4 retained significantly more surface area than others (Fig. 3C).

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numerous small pits and rough texture. (L) Inner surface, with deepening of indistinct mammillary craters. (M–O) Eggshell after 24 days at 25°C in buffered pH 6.6 solution. (M) Radial view, with honeycomb structure due to extensive corrosion. (N) Outer surface, with extensive pitting and very rough surface texture. (O) Inner surface, with complete loss of mammillae, extensive pitting, and honeycomb structure.

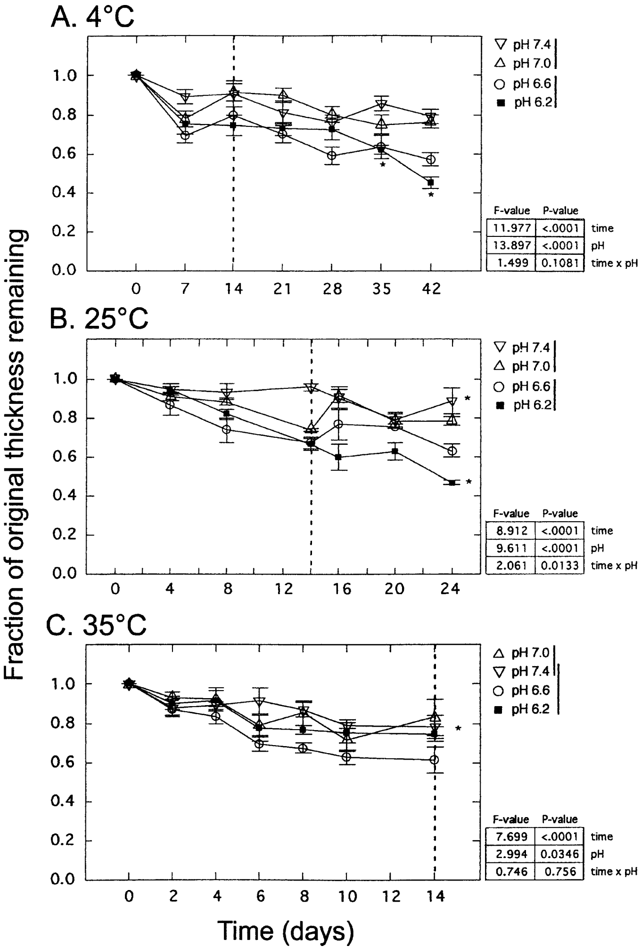

FIGURE 4—Fraction of eggshell thickness remaining after experimental treatment. Data represent means ± standard errors. Thickness means for experiments at pH values linked by the same vertical line in the legend are not significantly different at the 0.05 level (Scheffe's F test). The vertical dotted lines at 14 days indicate a comparable time among the three temperature regimens. Means are based on five replicates, except those with four, which are indicated by asterisks (*). Note that for purposes of reporting the results of Scheffe's test, the legend for 35°C displays a reversed order for pHs 7.0 and 7.4.

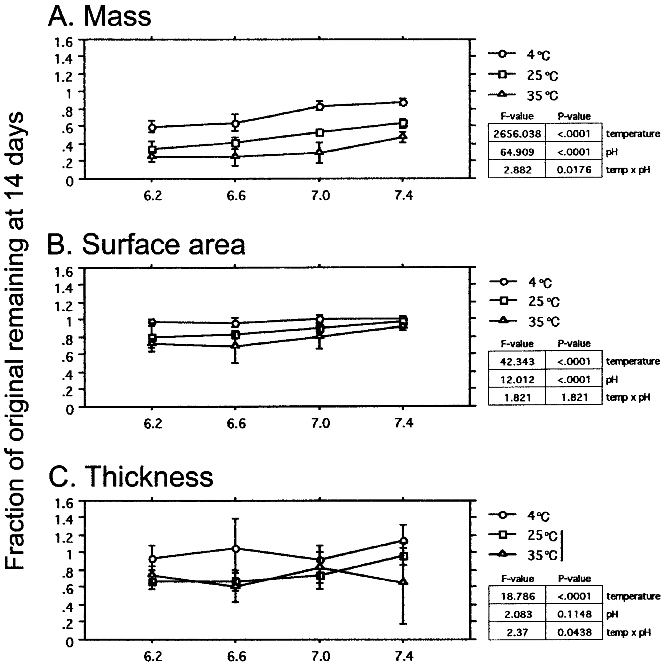

FIGURE 5—Fraction of eggshell remaining after subjection to 14 days under various experimental treatments. Data represent means ± standard errors. Temperature values linked by a vertical solid line in the legend are not significantly different at the 0.05 significance level (Scheffe's F test). (A) Fraction of mass remaining. (B) Fraction of area remaining. (C) Fraction of thickness remaining.

Fragment thickness decreased in response to more acidic solutions (Fig. 4A–C). In all cases, pairwise comparisons indicated no significant differences between thicknesses of fragments exposed to pH 6.2 and 6.6, or between those exposed to pH 7.0 and 7.4, although fragments exposed to alkaline and neutral solutions retained significantly more thickness than those exposed to acid solutions.

A comparison of the various temperature and pH effects at the end of the 14-day period showed that fragment mass and area for all four pH regimes decreased as temperature increased (Fig. 5A, B). Fragment thickness exhibited more variability, with fragments treated at 4°C and 35°C showing no obvious trends. Fragments exposed to 25°C showed reduced rates of corrosion as pH increased and temperature decreased (Fig. 5C).

DISCUSSION

Despite the paucity of experimental work on eggshell weathering, numerous authors have described corrosion features in fossilized eggshell (e.g., Hirsch, 1979; 1989; 1994; Hirsch and Bray, 1988; Mikhailov et al., 1996; Bray and Hirsch, 1998; Zelenitsky et al., 2000). Also, Hirsch and Quinn (1990), Zelenitsky (1995), and Mikhailov et al. (1996) noted that dissolution and recrystallization of weathered non-avian dinosaur eggshell obliterated surface features, making taxonomic classification difficult or impossible.

Mineralized eggshell is primarily calcite ($CaCO_3$), a compound that exhibits low solubility in cold water (0.0014 g/100 ml) and only slightly increased solubility in hot water (0.0018 g/100 ml; Weast, 1974). Corrosion occurred, however, in all aqueous solutions, even those with an alkaline pH. Thus, preservation of eggshell seems unlikely in water-saturated environments. This conclusion is consistent with paleoecological reconstructions of fossil nesting sites. For example, Horner and Makela (1979) and Horner (1982; 1987) reported that hadrosaur nests were found in colonies in arid upland habitats. Other dinosaur nesting habitats included the moderate maritime climate of *Hypacrocaurus* nest sites found in the Two Medicine Formation, Montana (Wolfe and Upchurch, 1987; Horner and Currie, 1994); the semiarid environment of hypsilophodontid nest sites at Proctor Lake in central Texas (Winkler and Murry, 1989); and an area in central Asia subject to temperature extremes that contained a small theropod nest (Barron and Washington, 1982; Kurzanov and Mikhailov, 1989; Paul, 1994). Studies of fossil dinosaur nest sites indicate that temperatures in nests could reach upward to 70°C (Paul, 1994). Under moist condi-

TABLE 1—Proposed classification scheme for eggshell corrosion.

Stage 0—Fresh, non-corroded eggshell. Outer surface ornamentation, if any, intact; pores well-defined and open to outside surface within shallow depressions (Fig. 1B). Inner surface mammillae distinct; rims and craters of mammillae with complex, sharply defined features (Fig. 1C).

Stage 1—Minor corrosion. Outer surface exhibits rougher texture than fresh eggshell; significant loss of surface ornamentation (Fig. 1E). Inner mammillary structure still evident, but rims of individual mammillae eroded (Fig. 1F).

Stage 2—Moderate corrosion. Outer surface rough with ornamentation nearly obliterated; numerous corrosion pits present (Fig. 1K). Inner surface mammillae indistinct and appear fused (Fig. 1I).

Stage 3—Extensive corrosion. Outer surface significantly corroded with loss of major structural features; corrosion craters may be evident (Fig. 1N; also see Hayward et al., 1991, fig. 1L). Mammillary structure of inner surface absent, or nearly so (Fig. 1O). Entire eggshell exhibits a Swiss cheese or honeycomb appearance (Fig. 1M–O; also see Hayward et al., 1991, fig. 1G–I, O).

Stage 4—Final stage. All structural details lost. Eggshell thin due to extensive loss of calcium carbonate; remaining eggshell may be curled due to drying of protein framework; outer surface may now be concave and inner surface convex. Fossilization at this stage unlikely.

tions, such high temperatures would not favor eggshell preservation, even in alkaline sediments.

In experiments reported here, eggshell that underwent moderate corrosion looked similar to naturally weathered eggshell found at the surface of the Protection Island, Washington gull colony. Both experienced some loss of surface texture on the outer surfaces, and mammillary structure of the inner surfaces lost some detail. Eggshell buried beneath Mount St. Helens ash for one year also exhibited this pattern. Experimental eggshell that underwent more extensive corrosion was comparable to gull eggshell buried for seven years beneath acidic (pH=6.4) volcanic ash (Hayward et al., 1991, Fig. 1D–I, O). In both cases, all structural features of the inner and outer surfaces had been removed. The outer surfaces were extensively pitted, and the inner surfaces had lost all evidence of mammillary structure.

Bone, like eggshell, consists primarily of calcium compounds deposited within a protein framework. Mineralized bone, however, is predominantly hydroxyapatite, a complex form of calcium phosphate that contains some carbonate and the elements Sr, Mg, Na, H, F, and Cl (Trueman, 1997). Bone persists under more acidic conditions than calcium carbonate structures, such as eggshell (Retallack, 2001). Not surprisingly, bone-weathering processes are similar to those for eggshell. For example, Downing and Park (1998) detailed some complexities of the diagenesis of buried bones and noted the importance of Eh and pH; Gordon and Buikstra (1981) found that decreasing pH accounted for 84% of variation of adult human bone preservation in seven burial mounds in Illinois; and Retallack (1984) concluded that as sediment pH increased, preservation of calcareous material such as teeth, bones, snail shells, and phytoliths is favored.

Behrensmeyer (1978) defined six bone weathering stages based on macroscopic features of large mammal bones and found that rates of weathering differed by habitat. She also suggested that bone weathering stages might provide information on time of exposure. Lyman and Fox (1989) argued, however, that extent of bone weathering does not in any simple way reflect the passage of exposure time. Similarly, Dauphin et al. (1999) found no correlation between geologic age and extent of preservation of fossil rodent bones in Pleistocene beds of the Olduvai Gorge, Tanzania.

Results presented here suggest that the rate of eggshell corrosion depends on an interaction of pH, temperature, moisture, and time. Eggshell deposited for only a few days in a moist, acidic habitat may exhibit the same degree of corrosion as eggshell deposited for months or years in an alkaline habitat. Thus, as with bones, it seems unlikely that the degree of eggshell corrosion has potential for providing a temporal framework for exposure. Nonetheless, a scheme for categorizing eggshell based on stage of corrosion could provide a useful tool for eggshell classification that, in combination with sediment analysis, could be used to interpret paleoenvironmental conditions. Such a scheme is proposed in Table 1.

In conclusion, increased temperature and acidity in moist surroundings lead to rapid corrosion of dinosaur eggshell. Even cool, moist, alkaline conditions lead to corrosion. Corrosion results in dramatic alterations of surface features, including pitting, flaking, curling, and loss of mammillary structure. Future experiments should examine (1) the effect of varying levels of dissolved calcium carbonate on corrosion rates (Retallack, 1984; 2001), (2) the role of microorganisms in the creation of microhabitats favoring or disfavoring corrosion (Behrensmeyer, 1978; Glover and Kidwell, 1993; Downing and Park, 1998), and (3) the impact of alternately drying and wetting or heating and cooling on eggshell structure (Hare, 1980).

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