PROMETHEUS PRESS/PALAEONTOLOGICAL NETWORK FOUNDATION (TERUEL)
Journal of Taphonomy
2003 Available online at www.journaltaphonomy.com
VOLUME 1 (ISSUE 4)

Taphonomy of Freshwater Turtles: Decay and Disarticulation in Controlled Experiments

Leonard R. Brand*, Michael Hussey, John Taylor
Department of Natural Sciences, Loma Linda University, Loma Linda, CA 92350, U.S.A.

Journal of Taphonomy 1 (4) (2003), 233-245.
Manuscript received 11 December 2003, revised manuscript accepted 18 June 2004.

We conducted an experimental study of the timing and nature of taphonomic processes in turtles that allowed a comparison among different environments. We documented decay and disarticulation of freshly-killed aquatic turtles in controlled settings, including freshwater and seawater aquaria, and outdoor terrestrial settings protected from scavengers. The study area was in hot and dry southern California, with scattered winter rains. We transferred some specimens after 53 days from the terrestrial environment to one of two other environments - freshwater, or an outdoor terrestrial cage - simulating increased rainfall. In water, turtle flesh decayed by bacterial action in three and a half to five months, but insect larvae removed the flesh from terrestrial carcasses within two weeks, leaving dry, desiccated carcasses. Turtles disarticulated most rapidly in water, followed by the high rainfall treatment, then dry terrestrial. The sequence of disarticulation of different bones from the body varied considerably, especially in the terrestrial treatment, but there were some consistent trends. Heads and necks, tails, and limbs tended to disarticulate early in the process. Next the carapace, and lastly, the plastron, disarticulated. Minor weathering occurred on the inside surface of some shell bones in the terrestrial environment. These data provide a basis for estimating maximum length of exposure of fossil turtles before burial and for comparison of turtle taphonomy with taphonomy of other small vertebrates.

Keywords: TAPHONOMY, TURTLE, TESTUDINES, DECAY, DISARTICULATION, BIOSTRATINOMY, EXPERIMENTAL TAPHONOMY

Introduction

Taphonomic research in modern environments is an important aid for interpreting fossil assemblages (Behrensmeyer and Kidwell 1985; Allison 1991). Documented patterns and rates of decay and disarticulation in modern environments, and how they vary among taxa, can suggest estimates of the time between death and burial of partially or fully articulated fossil specimens. They also indicate the variation in time for osteological elements to disarticulate. Also, if taphonomic processes show well-defined qualitative differences in different modern environments this information can provide clues to the taphonomic history of fossils.

* E-mail: *lbrand@ns.llu.edu*

*Table 1. Sample size (N), mean and range body mass for turtles (Trachemys scripta) used in each treatment. Weights in grams. * Carcasses were transferred from the terrestrial setting to a wet cage (high rainfall) or freswater after 53 days.*

	Treatment	N	Mean	Range
Room temp.	1- Freshwater	10	649	567-794
	2- Seawater	10	473	470-476
Ambient temp.	3- Freshwater	4	716	452-965
	5- Terrestrial	6	666	512-906
	6- Terrestrial, then high rainfall*	2	580	566-593
	7- Terrestrial, then freswater*	2	666	593-738

Taphonomic studies must use consistent experimental designs, so that different studies can be compared (Allison 1991).

The timing and sequence of carcass decay and disarticulation has been studied for a variety of modern vertebrate taxa in a number of settings, but few of these studies included turtles. Weigelt (1927) observed turtles killed during a freeze in Texas. Disarticulation of marine turtle carapaces in the intertidal sands of the Indian Ocean was studied by Meyer (1991). Bourn and Coe (1979) studied tortoise taphonomy on Aldabra, and Dodd (1995) documented disarticulation of 80 tortoises and aquatic turtles in Florida.

These studies provide data on sequences of decay and disarticulation of various taxa in a variety of environments. In addition to observations in natural environments, data on taphonomic processes in controlled conditions are also useful, because they allow direct comparison of the effects of specific treatments or conditions. Brand et al. (2003) conducted experiments under controlled conditions designed to reflect natural environments. This research differed from previous research on small vertebrate taphonomy in several ways. Decay and disarticulation of turtles was studied as part of the following research: 1) Four classes of small vertebrates were studied (amphibians, reptiles, birds, and mammals), in different size categories, under the same experimental conditions, so that the data from all taxonomic and size groups could be compared. 2) Freshwater, seawater, dry terrestrial, and wet terrestrial conditions were used, with other parameters being the same, so that the different treatments were similar. 3) Large sample sizes in some treatments allowed evaluation of individual variation in the disarticulation process, under similar conditions. 4) These experiments excluded macro-scavengers (larger than insects) to provide a modern analogue of decay and disarticulation processes without the complicating effects of scavenging.

The decay and disarticulation times and disarticulation sequences for turtles, reported in this paper, can be directly compared with the data on other taxa in our study (Brand et al. 2003), since the observations were made at the same time

and under the same conditions. Our conclusions are based on observations of disarticulation events as evidenced by times when body parts or individual bones separated from each other, and on observations of the decay processes.

Methods

We documented decay and disarticulation of turtles in freshwater and seawater aquaria, and with animals on the ground surface. Two sets of experiments were conducted (Table 1). In the first set (treatments [Trs.] 1 and 2) all carcasses were in aquaria at room temperature; treatment one was in freshwater with treatment two in seawater. In the second (Trs. 3, 5-7), temperature was not controlled. Instead, turtles were exposed to the ambient southern California temperature. The second set of treatments included repetition of the freshwater experiment (Tr. 1) as well as three different, outdoor, terrestrial treatments. Some carcasses remained on dry ground for the duration of the observations (Tr. 5), but other carcasses were transferred to either a wet terrestrial environment (Tr. 6) or a freshwater aquarium (Tr. 7) after 53 days. Treatment 7 simulated death in a terrestrial environment followed by transport into a stream or lake. Treatment 6 simulated an environment with high rainfall. Ideally the Tr. 6 carcasses should have been in the wetter environment during the whole experiment, but observations made during the first part of the study led us to decide that observations in a wetter environment might provide additional insight into taphonomic processes affecting turtles under natural conditions.

Experimental setting

Experiments were conducted both in a storage building on the Loma Linda University farm, and in an outdoor area beside the building. Inside the building, trials were conducted in aquaria, with a filter system to keep the water clear and reduce the buildup of bacteria in the water. A window was kept partly open to allow insects to enter and leave the room, and a small fan in this window helped to move stale air out of the room. A heating and air conditioning system was used during Trs. 1 and 2 to maintain an approximately constant temperature in the room. During Tr. 3 the temperature control systems were not used, the window was open, and the temperature in the room mirrored the outdoor temperature.

The outdoor experiments were conducted in a series of cages outside of the building. For Tr. 6 one cage was fitted with mini garden sprinklers to simulate a wet environment. This “wet cage” was watered twice a week for two hours each time during the early morning. Each two-hour watering session spread approximately 9 cm of water over the area. These experiments excluded predators and scavengers except for insects and, in the outdoor experiments, anything else small enough to go through the 1.3 cm wire mesh. We did not see evidence of mice in the terrestrial cages.

Experimental procedure

All subjects were red-eared sliders, *Trachemys scripta*, with carapace lengths of about 16-18 cm and body mass of 452-965

g (mean 605 g) (Table 1), purchased from animal dealers. Mean shell bone thickness was 1.1-2.7 mm for the distal end of costals, and 2.1-3.6 mm for neurals. We did not know the ages of the turtles. They were euthanized with ether, weighed, immediately placed in the experimental chambers, and observed until disarticulated. In Tr. 5, four turtles were placed plastron up, whereas the other six were carapace up. Notes were taken on each animal's condition, the presence of insect activity, state of decay, any body parts that were disarticulated (not attached to the body), and any other pertinent observations. Disarticulated body parts containing several bones were left in place so that further disarticulation could be documented. Whenever single, disarticulated bones were found they were collected, placed in plastic bags, and labeled with the animal number and date of collection. These dated bags of bones and the notes on disarticulation of larger body parts comprised the principle data for the experiments.

Since it was impossible to collect data without some disturbance to the animals, the disturbance was kept as uniform as possible across all experimental conditions. In the aquaria, the water was stirred with a stick, with the amount of movement approximately equal. The stirring was fairly gentle, in order to avoid breaking apart the carcasses. If animals were lying on the aquarium bottom, they were lifted to determine if any loose bones were present. In the outdoor cages, each animal was lifted off the ground at each data collection, any loose bones were removed, and the animal was put back in its original position.

The observations in the aquaria posed particular problems because the decaying animals made it difficult to keep the water clear enough to collect data, and it was necessary to occasionally change most of the water to clean out the accumulating debris. Our techniques and skill at doing this improved during the course of the experiments, however. During Trs. 1 and 2 some small bones were accidentally lost, and data collection in later treatments was more complete and accurate than in Trs. 1 and 2. Additional details of experimental procedures can be found in Brand et al. (2003).

Weather and water conditions

Weather information during Trs. 3-7 was obtained from local weather stations, in microhabitats similar to the experimental site. Air temperature in the experimental room and water temperature in one aquarium were also recorded each time data were collected. The Southern California weather pattern consists of dry, hot summers and cool winters with occasional rainstorms from fall to spring. Temperature, water and soil characteristics during the experiments are reported in Brand et al. 2003.

Data analysis

The following data were entered into a database: day (number of days since the animal was placed in the experiment) on which each disarticulated bone was removed from the experiment; day on which each larger body part was

Table 2. Recovery rate of turtle bones, as percent of expected number of bones (based on number of bones in each individual, and number of complete carcasses of that type), listed as range of percentages for different treatments.

Bone group	Trs. 1, 2	Trs. 3-7
Skull bones	63	78-86
Ribs and vertebrae	48-50	40-86
Limb & girdle bones	85	89-92
Foot Bones	15-66	24-82
Shell bones	86-100	98-100

disarticulated from the body (e.g. entire leg, scapula plus entire front leg, head, tail, etc), and day on which each animal or significant part thereof sank to the bottom of the aquarium. Differences among taphonomic parameters were examined using Kruskal-Wallis tests in SPSS 8.0 (Norusis 2000).

Results

Recovery rate of bones

In the aquaria some bones were no doubt lost during cleaning operations, and some bones in outdoor cages may have been lost in the soil. The percent of bones recovered (Table 2) was generally lowest in Tr. 1, and increased with improvements in methods of bone recovery and maintaining water quality.

Our results are based on 5,740 turtle bones recovered during the experiments. Shell bones were almost all recovered, whereas foot bones had the lowest percent recovery. Recovery rates in Trs. 3-7 were considered sufficient for calculating disarticulation rate and disarticulation sequence. Data from Trs. 1 and 2 were used only in determining overall disarticulation rate because of the lower recovery rates.

Decay process

Turtles in fresh or seawater floated for 2-10 weeks before sinking (Figure 1). There was no significant difference in floating time between Trs. 1-3 ($N = 24$; $df = 2$; chi square = 4.05; $p = .132$).

The processes following death were quite different among different treatments. In water, the flesh was gradually decayed. In the terrestrial environment, insect larvae quickly devoured the flesh of each animal. Within 19-27 days, only empty shells, dried skin and skeletons remained. The dry desiccated appendages detached from the shell within three to eight weeks; bones within the appendages slowly disarticulated over the next two years (Figure 2).

In Tr. 7 the desiccated turtles, with internal tissues removed by insects, were placed in water on day 53. The skin was softened by the water and the axial skeleton and appendages fell apart rapidly. Disarticulation of the shell was slow, with large individual variation (Figures 2, 3).

Disarticulation time

The shortest disarticulation times occurred in fresh and seawater (Trs. 1-3, 7; Figure 1). Even in Tr. 3, 75% of the disarticulation occurred as fast as in Tr. 1 and 2. Disarticulation time was longest in the

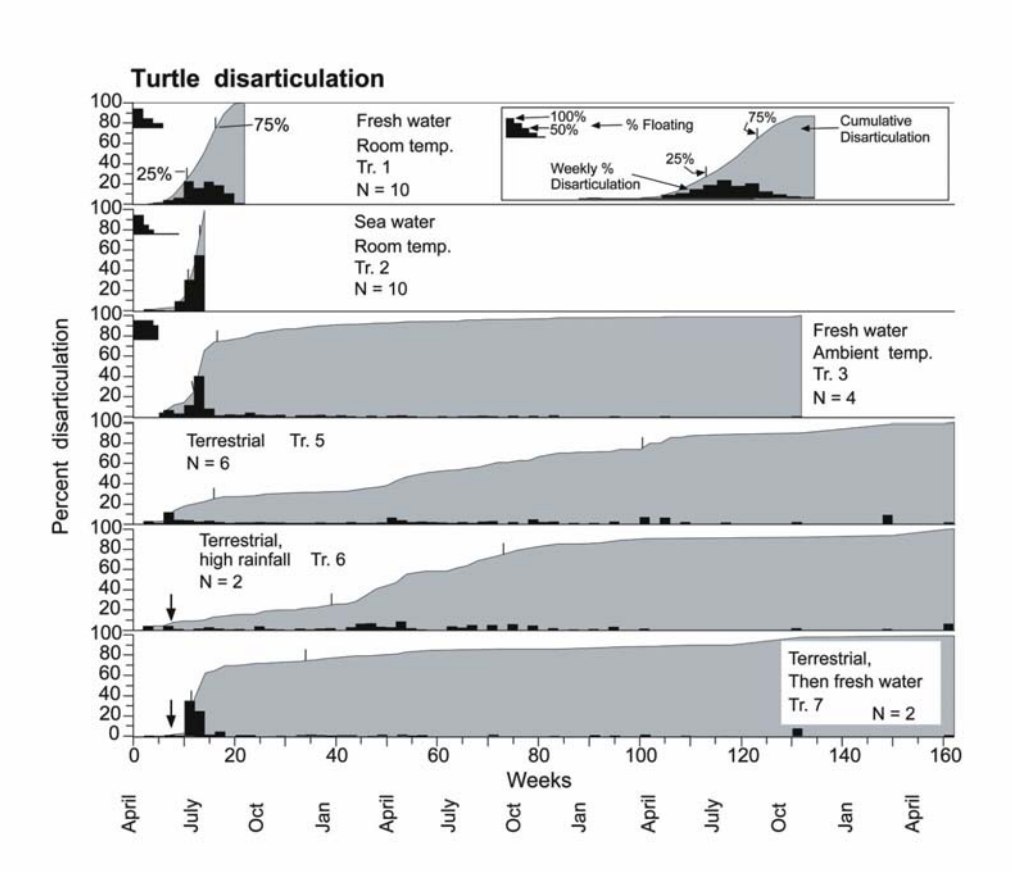

FIGURE 1. Mean disarticulation times for turtles. Black vertical bars indicate percent of bones disarticulated in each two-week interval, and shaded polygons indicate cumulative percent of bones disarticulated, ending at 100% disarticulation. Smaller black bar graphs near top left of each aquatic treatment graph indicates percent of carcasses floating during part or all of each two-week interval. Arrows indicate time at which carcasses in Trs. 6 and 7 were transferred from terrestrial to wet or aquatic treatment. Small vertical bars along top of polygons indicate time at 25% and 75% disarticulation. N = number of turtles.

terrestrial condition (Tr. 5; Figure 1), and this time was affected very little by high rainfall (Tr. 6; Figure 1). Disarticulation times among Tr. 1-7 were significantly different for mean, 25%, and 75% disarticulation (Kruskal-Wallis test; chi square = 11.78-21.34; $df = 5$; $p < .05$). At the end of three years most turtles in terrestrial conditions had portions of shell still articulated (Appendix 1; Figs. 2, 3).

Separation of the thin epidermal scutes from shell bones occurred

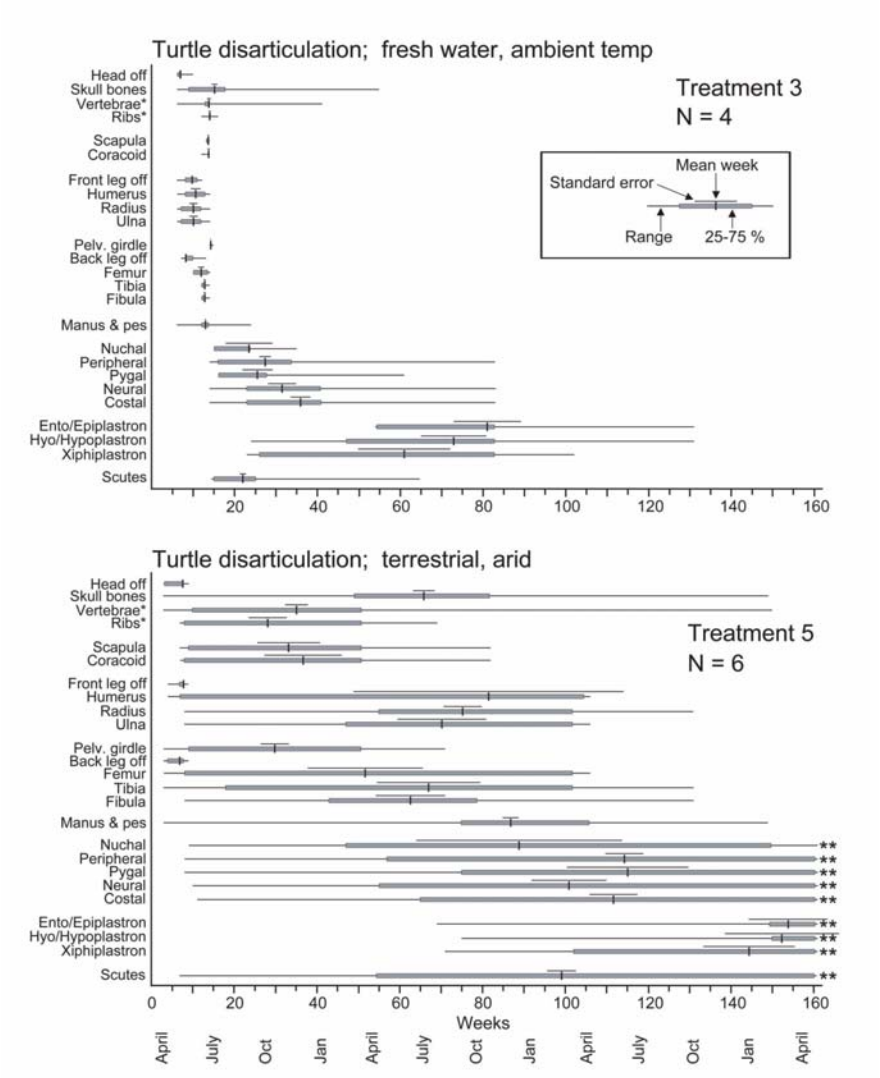

FIGURE 2. Disarticulation sequence for turtles in Trs. 3 and 5. Based on all disarticulation events, which includes separation of individual bones from body, and also separation of larger body parts (entire leg, e.g.) from the body. Graphs show week of mean disarticulation event for each category, standard error of the mean, quartiles (week in which 25% and 75% of disarticulation events had occurred), and ranges. In Tr. 3, some grouping of bones was done, because of the small variance between bones. N = number of turtles. * Ribs = small sacral ribs, not fused to carapace; vertebrae = cervical and caudal vertebrae and ventral half of each trunk vertebrae, which commonly separated from the dorsal portion. ** indicates that some bones were still articulated when the experiment was ended after 3 years.

concurrently with the disarticulation of the shell bones (Figure 2). There was great variation in the timing of this process, especially in the terrestrial environment.

Disarticulation sequence

Under all experimental conditions, heads with necks, legs, and tails separated from the body early in the process. The skeletal elements within these body parts then disarticulated from each other. The shell took the longest to disarticulate, beginning with the carapace. The plastron was almost always the last portion of shell to disarticulate (Figures 2, 3). In the terrestrial environment the disarticulation took longer, with greater variability (Figure 2).

The breakup of the shell usually began with sections of peripheral bones separating from the costals. Then breaks occurred across the carapace and the carapace began to separate from the plastron. The breakup of the plastron began posteriorly and progressed anteriorly. The disarticulation of the shell always occurred by separation of complete bones from each other at the sutures, not by breaking of bones. Disarticulation was hastened in the part of the shell, carapace or plastron, in contact with the ground (Figure 3).

There was considerable individual variation in shell disarticulation times (Figs. 2, 3). In the terrestrial experiment, disarticulation was affected by precipitation, with more bones disarticulating during the winter rainy season than in the dry season.

When terrestrial specimens were placed in water after 53 days in terrestrial conditions, the appendages disarticulated quickly (Tr. 7; Figure 3), although on average it took longer for the shells to disarticulate than in Tr. 3.

Weathering

In these experiments, turtle shell bones were exposed to potential weathering more than non-shell bones. No weathering was seen on turtle shells that remained in water (weathering stage 0; Behrensmeyer 1978), with no exposure to direct sunlight, even at the end of three years (Figure 4B). In the terrestrial environment (Tr. 5) most appendicular bones disarticulated and were collected before significant exposure to the weather.

After turtle shells lay on the ground for 60-75 weeks, 7% of the carapace bones and 40% of the plastron bones had weathered to stage 1 (Figure 4A). At the end of three years 8% of the carapace bones and 79% of the plastron bones were at weathering stage 1, and 6% of the carapace bones and 21% of the plastron bones had reached stage 2.

Weathering was only seen on the inside surface of shell. In the early stages, the outside surface was covered by epidermal scutes, but in the terrestrial experiment half of the scutes had come off from the bones by week 83 (25% by week 54, and 75% by week 161). After that, the outside surface seems to have been exposed as much to weathering influences as the inside surfaces. The differences between the weathering of carapace and plastron bones was not due to differences in exposure, as four of the turtle shells were ventral (plastron) side up, and six were dorsal (carapace) side up. The cracking and

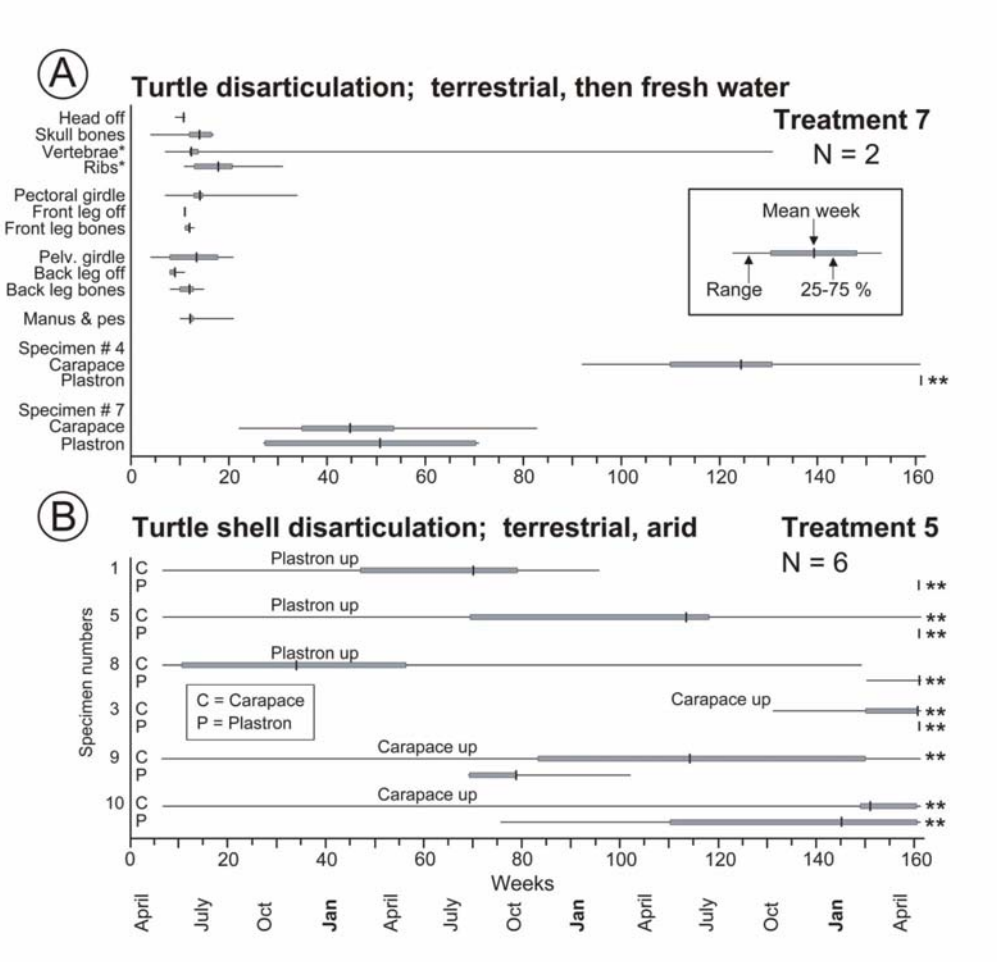

FIGURE 3. A - disarticulation sequence for turtles in Tr. 7, begun in terrestrial and then transferred on day 53 into freshwater. B - Comparison of disarticulation time for carapaces and plastrons for the six specimens in Tr. 5. See figure 2 for explanation.

flaking on these small turtle bones was on a small scale in comparison with those seen on large mammals (Behrensmeyer 1978). Most cracks were 0.5-3 cm long.

Discussion

It could be objected that eliminating scavenging, as in our research, distorts the taphonomic process. However, the purpose

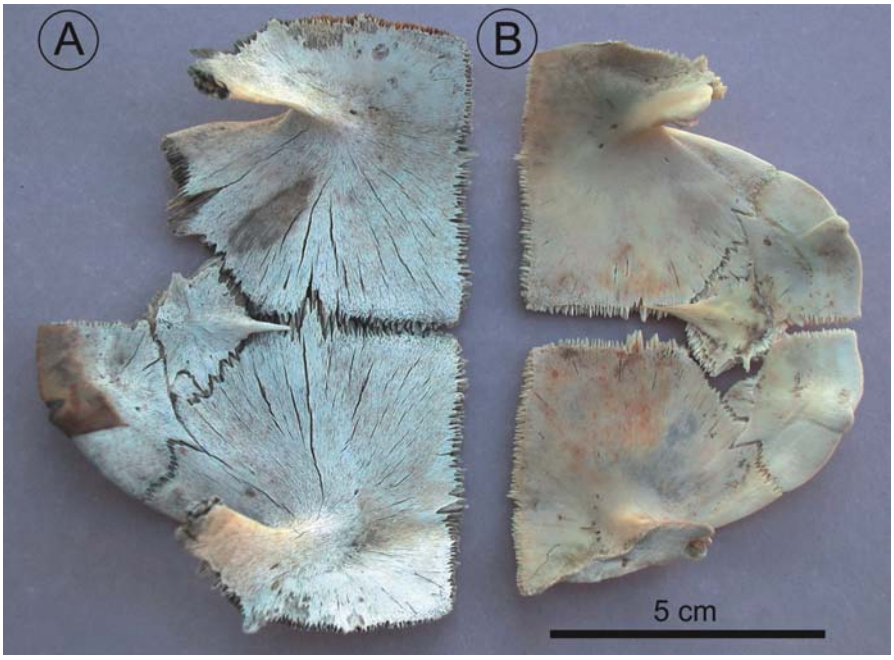

FIGURE 4. Weathering stages of turtle plastron bones after 3 years. A - Stage 1 weathering, from terrestrial environment (Tr. 5). B - Stage 0 weathering, from fresh water (Tr. 3).

of an experimental study under controlled conditions is to isolate and determine the effects of each significant variable that will influence fossilization (Briggs 1995). A full understanding of taphonomic processes is most likely to result from comparative, controlled studies in addition to field observations under natural conditions.

Since scavengers were excluded, disarticulation times in these experiments represent maximum times, and in natural settings the actions of predators and scavengers could be expected to speed up the process considerably. In a natural setting animals floating in streams or lakes may be moved by wind currents or flowing water and deposited on shore, subject to the activities of terrestrial scavengers or to desiccation. It was not feasible to simulate this transport process in the lab.

The presence of water had a significant effect on turtle disarticulation. If turtles are immersed in water, the flesh was degraded by bacterial decay, and most of the skeleton disarticulated within 20 weeks. In a terrestrial environment, the removal of soft tissues by insect larvae left dry skin and bones that remained articulated for much longer times.

Dodd (1995) studied disarticulation

of several species of turtles in Florida in a dry sandhill habitat. The turtles reached stage 9 (carapace completely disarticulated) in 30-40 months, which is approximately the same length of time that it took for our terrestrial turtle carapaces (Tr. 5) to disarticulate.

Differences in the disarticulation times of different skeletal elements offers an explanation for some features of fossil assemblages. For example turtle heads came off early, and their limbs soon followed, but turtle shells were slower to disarticulate. This may be one factor that helps explain large numbers of Eocene fossil turtles with intact shells but few skulls or limbs (Brand et al. 2000). Other factors could produce the same result. For example turtle skulls in most orientations in water are transported at lower velocities than almost all shell bones (Blob 1997). However, turtle limb bones are much more variable in dispersal potential, and it doesn't appear that limbs would be separated from shell bones by differential dispersion (Blob 1997). Also there are unpublished reports that large birds and other scavengers quickly remove heads and limbs from dead turtles. A mass mortality of turtles, as in an Eocene fossil assemblage (Brand et al. 2000) perhaps would reduce the percentage of heads and limbs that scavengers could remove, because of the large numbers of turtles relative to the scavenger population. In a modern lake environment with attritional death of turtles it is probably less likely that turtles will float for an extended time, because of attacks by scavengers.

Animals floating on water will not become a part of the fossil record until they sink or are moved on to the shore, where they can be covered by sediments, and/or are attacked by scavengers and perhaps become part of a microvertebrate accumulation (Mellett 1974). The possibility of turtles floating in quiet water and then sinking may help explain the presence of large numbers of intact turtles in the fine sediment of fluviolacustrine deposits in the Bridger Formation (Brand et al. 2000).

Fossil turtles anatomically comparable to *Trachemys scripta*, with largely intact shells, buried in an aquatic environment, would probably be buried within a maximum of 15-30 weeks or less (Figure 1, 2). In a terrestrial environment shells could have remained essentially intact for over a year (Figure 1, 2). Eocene fossil turtles in the Bridger Formation (Brand et al. 2000) had shells 2-4 times thicker than *Trachemys*, and the length of time for disarticulation of the shell may have been different.

The wide variability in the time of disarticulation of most turtle bones indicates that disarticulation sequence is probably not a useful feature in taphonomic interpretation of fossil assemblages.

Since our turtle study was part of a larger study, our data on turtle disarticulation times, disarticulation sequence and the influence of environment can be directly compared with our experimental data on other small vertebrates (Brand et al. 2003). For example, in the arid terrestrial environment turtle disarticulation began sooner than small mammal or bird disarticulation, but took longer for completion. Turtle shells and small mammal and bird skulls were the slowest small vertebrate body parts to disarticulate in the absence of scavengers.

This experimental regime may correctly model the natural taphonomy for at least some fossil turtle shell assemblages. Vertebrate tooth marks were almost absent on shells of Eocene turtles in the Bridger Formation (Brand et al. 2000), indicating little scavenger influence on taphonomy of these turtle shells. In contrast, the fragmentary nature of most fossil mammal skull material may be the result of scavenger activity (Brand et al. 2003).

Acknowledgements

Euthanasia of turtles was conducted according to a protocol approved by the Loma Linda University animal care committee. Thanks to two anonymous reviewers for their comments on an earlier version of this manuscript.

References

Allison, P. A. (1991). Taphonomy has come of age! *Palaios,* 6:345-346.

Behrensmeyer, A. K. (1978). Taphonomic and ecologic information from bone weathering. *Paleobiology,* 4:150-162.

Behrensmeyer, A. K., and Kidwell, S. M. (1985). Taphonomy's contributions to paleobiology. *Paleobiology,* 11:105-119.

Blob, R. W. (1997). Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates. *Palaios,* 12:151-164.

Bourne, D., and Coe, M. J. (1979). Features of tortoise mortality and decomposition on Aldabra. *Philosophical Transactions of the Royal Society of London, Series B, Biological Science.,* 286:189-193.

Brand, L. R., Goodwin, H. T., Ambrose, P. G., and Buchheim, H. P. (2000). Taphonomy of turtles in the Middle Eocene Bridger Formation, SW Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 162:171-189.

Brand, L. R., Hussey, M. H., and Taylor, J. (2003). Decay and disarticulation of small vertebrates in controlled experiments. *Journal of Taphonomy*, 1 (2):69-95.

Briggs, D. E. G. (1995). Experimental taphonomy. *Palaios*, 10: 539-550.

Dodd, C. K. Jr. (1995). Disarticulation of turtle shells in North-central Florida: how long does a shell remain in the woods? *American Midland Naturalist,* 134:378-387.

Mellett, J. S. (1974). Scatological origin of microvertebrate fossil accumulations. *Science,* 185: 349-350.

Meyer, C. A. (1991). Burial experiments with marine turtle carcasses and their paleoecological significance. *Palaios,* 6:89-96.

Norusis, M. J. (2000). *SPSS 10.0 Guide to Data Analysis.* Prentice Hall, Upper Saddle River, New Jersey.

Weigelt, J. (1927). *Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung*. Verlag von Max Weg, Leipzig. (We used the English translation, *Recent vertebrate carcasses and their paleobiological implications*, published in 1989, by University of Chicago Press)

Appendix 1.

Articulated portions of turtle shells remaining at end of three-year experiment.
Terrestrial environment (Tr. 5), N = 6. Complete plastron + 3 peripherals; two posterior halves of plastron (xiphi- + hypoplastrons); two anterior halves of plastron (hyo- + ento- + epiplastrons); two anterior 1/4 plastrons (hyo- + epi- + entoplastron; one also included a hypoplastron); one fourth of plastron (hyo- + hypoplastron); Posterior 1/3 of carapace; cluster of 5 peripherals + 5 costals + 1 neural + 2 suprapygals; cluster of a nuchal + 1 costal + 3 peripherals; set of 5 costals + 5 neurals; 12 sets of 2-5 peripherals or costals.
Terrestrial high rainfall environment (Tr.

6), N = 2. Right half of plastron (including ento- + epiplastrons); posterior 1/4 of plastron; cluster of 3 costals + 4 peripherals + nuchal; three sets of 4 peripherals or costals.

Terrestrial to aquatic environment (Tr. 7), N = 2. One fourth of plastron (xiphi- + hypoplastron); anterior half of plastron.