Bonebeds

BONEBEDS

Genesis, Analysis, and Paleobiological Significance

Edited by

Raymond R. Rogers, David A. Eberth,
and Anthony R. Fiorillo

Raymond R. Rogers is professor in and chair of the geology department at Macalester College, St. Paul, Minnesota. **David A. Eberth** is a senior research scientist at the Royal Tyrrell Museum in Drumheller, Alberta, Canada. **Anthony R. Fiorillo** is a faculty member in the Department of Geological Sciences at Southern Methodist University and Curator of Paleontology at the Dallas Museum of Natural History, Dallas, Texas.

CONTENTS

A Conceptual Framework for the Genesis and Analysis of Vertebrate Skeletal Concentrations

Raymond R. Rogers and Susan M. Kidwell

INTRODUCTION

The record of vertebrate skeletal concentration begins with accumulations of agnathan dermal armor preserved in lower Paleozoic rocks (Behre and Johnson, 1933; Denison, 1967; Allulee and Holland, 2005). From these relatively modest beginnings, the record soon expands to include fossil deposits that yield the more diversified skeletal remains (calcified cartilage, endochondral elements, teeth) of marine and freshwater gnathostomes (Elles and Slater, 1906; Wells, 1944; Conkin et al., 1976; Antia, 1979; Adrain and Wilson, 1994). By the Late Devonian, tetrapods had ventured into marginal terrestrial ecosystems (Campbell and Bell, 1978; DiMichelle et al., 1992), and this major ecological foray marked a dramatic increase in the potential diversity of vertebrate taphonomic modes. Relative concentrations of vertebrate skeletal hardparts are found throughout the remainder of the Phanerozoic in a wide spectrum of marine and terrestrial depositional settings (Behrensmeyer et al., 1992; Behrensmeyer, Chapter 2 in this volume; Eberth et al., Chapter 3 in this volume).

Like macroinvertebrate shell beds, which are commonly studied for paleontological, paleoecological, paleoenvironmental, and stratigraphic information (Kidwell 1991a, 1993; Brett and Baird, 1993; Brett, 1995; Abbott, 1998; Kondo et al., 1998; del Rio et al., 2001; Mandic and Piller, 2001), vertebrate skeletal concentrations, or "bonebeds," provide a unique opportunity

to explore an array of paleobiological and geological questions. These questions revolve around an array of fundamental "quality of data" issues, such as the degree of time averaging recorded by skeletal material and its fidelity to the spatial distribution and species or age-class composition of the source community. How do vertebrate paleoecology and behavior translate into bone-rich deposits? What are the genetic links between local sedimentary dynamics (event sedimentation, sediment starvation, erosion) and bonebed formation? To what extent are bonebeds associated with important stratigraphic intervals and discontinuity surfaces, such as well-developed paleosols, marine flooding surfaces, and sequence boundaries, and how faithfully does the nature of the skeletal material record the "time significance" of such features?

Clearly, understanding the diverse mechanisms of vertebrate hardpart concentration—and, needless to say, having the ability to recognize these in the fossil record—is vital to accurate paleoecological and paleoenvironmental reconstructions and is also essential for the development of productive collection strategies. Moreover, the stratigraphic distribution and taphonomic signatures of vertebrate skeletal concentrations have geological significance because of their potential to provide critical insights into sedimentary dynamics, local geochemical conditions, and basin-fill history in both marine and terrestrial settings (e.g., Badgley, 1986; Kidwell, 1986, 1993; Behrensmeyer, 1987, 1988; Bartels et al., 1992; Rogers and Kidwell, 2000; Straight and Eberth, 2002; Rogers, 2005; Eberth et al., 2006; Walsh and Martill, 2006).

Our aims here are first to clarify terminology by providing operational definitions, and then, by focusing on the dynamics of vertebrate hardpart accumulation, to distill a relatively simple intuitive scheme for categorizing bonebeds genetically. Like the benthic marine macroinvertebrate record, some concentrations of vertebrate skeletal elements reflect primarily biological agents or activities, such as gregarious nesting habits (yielding bone-strewn rookeries), predation (yielding bone-rich feces), and bone collecting (e.g., hyena dens and packrat middens), whereas others are the result of predominantly physical phenomena such as erosional exhumation (yielding bone lags) and sediment starvation (yielding time-averaged attritional accumulations). In addition, some concentrations reflect single, ecologically and geologically brief events, such as mass-kill deposits, whereas others have complex formative histories recording the interplay of multiple ecological and/or geological agents and events, generally over longer periods. Genetic scenarios are considered here both from a conceptual standpoint and from empirical observations (both actualistic and

stratigraphic record-based studies), and the characteristic taphonomic signatures of different genetic themes are explored.

OPERATIONAL DEFINITIONS

Here we essentially follow Behrensmeyer's (1991, Chapter 2 in this volume) and Eberth et al.'s (Chapter 3 in this volume) definitions of a "bonebed," which at its most basic is a "relative concentration" of vertebrate hardparts preserved in a localized area or stratigraphically limited sedimentary unit (e.g., a bed, horizon, stratum) and derived from more than one individual. Within this broad characterization, two distinct types of bone concentrations are commonly recognized by vertebrate paleontologists: (1) "macrofossil" bonebeds and (2) "microfossil" bonebeds (see Appendix 2.1 in Chapter 2 of this volume for a comparison of terminology [Behrensmeyer, this volume]).

Macrofossil bonebeds (sensu Eberth et al., Chapter 3 in this volume) are herein considered concentrated deposits of skeletal elements from two or more animals in which most bioclasts (>75%, be they isolated elements or entire skeletons) are >5 cm in maximum dimension. Macrofossil bonebeds are known from many different facies and depositional contexts, and they occur throughout the Phanerozoic history of the Vertebrata. Classic examples include the many Jurassic and Cretaceous dinosaur quarries of the western interior of North America (e.g., Hatcher, 1901; Brown, 1935; Sternberg, 1970; Lawton, 1977; Hunt, 1986; Rogers, 1990; Varricchio, 1995; Ryan et al., 2001; Gates, 2005). Mammalian counterparts also abound and include the spectacularly bone-rich Agate Spring locality and the Poison Ivy Quarry in the Miocene of Nebraska (Peterson, 1906; Matthew, 1923; Voorhies, 1981, 1985, 1992), among many others (e.g., Borsuk-Bialynicka, 1969; Voorhies, 1969; Barnosky, 1985; Voorhies et al., 1987; Fiorillo, 1988; Turnbull and Martill, 1988; Coombs and Coombs, 1997; Smith and Haarhoff, 2004).

Macrofossil bonebeds are also known to preserve aquatic and semi-aquatic animals. Examples include abundant amphibian-dominated assemblages from the Late Paleozoic of Texas and Oklahoma (Case, 1935; Dalquest and Mamay, 1963; Sander, 1987), and extensive fish-dominated bonebeds from Cretaceous deposits in Lebanon (Hückel, 1970), the Eocene Green River Formation of Utah and Wyoming (McGrew, 1975; Grande, 1980; Ferber and Wells, 1995), and elsewhere (e.g., Anderson, 1933; Pedley, 1978; Martill, 1988; Adrain and Wilson, 1994; Johanson, 1998; Davis

and Martill, 1999; Fara et al., 2005). Interestingly, macrofossil bonebeds are seemingly less common in the marine realm—or at least less commonly analyzed and reported by vertebrate paleontologists—than might be expected given the great abundance and diversity of marine vertebrates and the potential for the addition of terrestrially derived skeletal material via bedload delivery and "bloat and float" (see Brongersma-Sanders, 1957; Schäfer, 1962, 1972). Well-documented examples of ancient marine macrofossil bonebeds include ichthyosaur lagerstätten from the Triassic of Nevada and the Jurassic of Europe (Ulrichs et al., 1979; Camp, 1980; Hogler, 1992). Less well documented but more common are shark-tooth beds and ecologically mixed assemblages of marine, estuarine, and terrestrial vertebrates associated with marine unconformities and surfaces of maximum transgression in Cretaceous to Neogene records (e.g., Barnes, 1977; Myrick, 1979; Norris, 1986; Kidwell, 1989; Schröder-Adams et al., 2001).

Microfossil bonebeds, which are commonly termed "vertebrate microsites" or "vertebrate microfossil assemblages" in the literature (McKenna, 1962; Estes, 1964; Sahni, 1972; Korth, 1979; Dodson, 1987; Brinkman, 1990; Eberth, 1990; Peng et al., 2001, among others), are sometimes construed as preserving the abundant remains of animals that have body masses on average 5 kg or less (e.g., Behrensmeyer, 1991). Instead of this overall body size criterion, Eberth et al. (Chapter 3 in this volume; see also Wood et al., 1988) propose that microfossil bonebeds be defined as relative concentrations of fossils where most component elements (>75%) are ≤5 cm in maximum dimension. This would include a variety of skeletal material (including entire carcasses) from small animals (such as frogs, salamanders, small snakes, fish, mammals, etc.) and small skeletal components or skeletal fragments from large animals (such as the teeth of crocodiles, dinosaurs, and sharks). In keeping with the operational definition of a bonebed, microfossil bonebeds should occur in a stratigraphically limited sedimentary unit, should demonstrably include the remains of at least two animals, and should preserve bones and teeth in considerably greater abundance than in surrounding strata (i.e., they should be "relatively enriched" with vertebrate bioclasts). Microfossil bonebeds have been described from many different facies (e.g., Nevo, 1968; Estes et al., 1978; Maas, 1985; Breithaupt and Duvall, 1986; Bell et al., 1989; Eberth, 1990; Henrici and Fiorillo, 1993; Khajuria and Prasad, 1998; Gau and Shubin, 2000; Rogers and Kidwell, 2000; Perea et al., 2001; Ralrick, 2004), and like macrofossil bonebeds, they occur throughout much of the Phanerozoic record in both terrestrial and marine depositional settings. Thoughts

pertaining to the genesis of multitaxic microfossil bonebeds are presented later in this chapter.

Finally, "bone sands" are occasionally encountered in the stratigraphic literature and, as the name implies, consist mostly consist of sand-sized grains (0.0625–2 mm) to granules (2–4 mm) of bone. Particles are generally rounded fragments and are usually not identifiable beyond assignment to Vertebrata, but intact skeletal elements (e.g., teeth, vertebrae, phalanges, scales) and large bone pebbles are occasionally dispersed in the bone-sand matrix. Bone sands can vary in geometry from localized lenses to areally widespread sheets associated with unconformities (e.g., classic Rhaetic bone sand of Reif, 1982; SM-0 of Kidwell, 1989) and are most commonly found intercalated in marine strata.

GENETIC FRAMEWORK OF SKELETAL CONCENTRATION

Vertebrates today inhabit virtually every depositional environment, from the deepest ocean basins to mountain lakes, and they exhibit tremendous variation in life strategies, ecological interactions, and body sizes (Pough et al., 2005). Given their current distribution (global) and diversity ($\sim$50,000 extant species), the array of factors with potential to cause mass mortality or otherwise play a role in the concentration and preservation of vertebrate skeletal debris is staggering, and the possibilities only multiply when vertebrates are considered in an evolutionary context that spans more than 500 million years.

Nevertheless, a few general themes can be exploited in order to construct a genetic framework that is applicable across a broad spectrum of vertebrate occurrences, and we believe that the major formative scenarios explored here will provide general guidelines for the analysis of taphonomic history. This review is not exhaustive, however, and the reader is especially referred to the classic works of Weigelt (1927, 1989), Brongersma-Sanders (1957), and Schäfer (1962, 1972) for additional insights into an array of mortality and preservation scenarios in both terrestrial and marine settings. The reader is also referred to works by Behrensmeyer and Hill (1980), Shipman (1981), Behrensmeyer (1991), Martill (1991), Behrensmeyer and others (1992, 2000), and Lyman (1994) for in-depth considerations of vertebrate taphonomic modes and methodological approaches to the reconstruction of taphonomic history.

In keeping with the goal of developing a conceptual framework comparable to those already in existence for the macroinvertebrate fossil

Genetic Framework for
Vertebrate Skeletal Concentration

Biogenic Concentrations   Physical Concentrations

Intrinsic Biogenic Concentrations •••• concentration results from behavior / activity of individuals preserved in assemblage (see Figure 1.2)	**Extrinsic Biogenic Concentrations** •••• concentration results from feeding behavior or collecting activity of other animals (see Figure 1.3)	**Hydraulic Concentrations** •••• concentration results from action of surface flows - water, wind, sediment (see Figure 1.4)	**Sedimentologic Concentrations** •••• concentration reflects dynamics of sedimentary budget - obrution, starvation, erosion (see Figure 1.5)

Post-Concentration Possibilities
(see Figure 1.6)

Direct Permanent Burial   **Reworked and/or Overprinted**   **Dispersed and/or Destroyed**

Figure 1.1. Vertebrate skeletal concentrations are grouped according to their inferred relations to biological and physical agents. Most vertebrate skeletal concentrations can be readily categorized as either biogenic or physical in origin. Biogenic concentrations are by definition produced by biological agents or events, and two general types are differentiated in relation to the formative role of intrinsic and extrinsic agents. Concentrations of vertebrate skeletal elements generated by physical processes are similarly subdivided into two general categories. Hydraulic concentrations result from the actions of transporting flows, whereas sedimentologic concentrations reflect the dynamics of the sedimentary budget. Postconcentration possibilities include (1) direct permanent burial, (2) reworking and/or overprinting, and (3) dispersal and/or destruction.

record (Johnson, 1960; Kidwell, 1986, 1991a; Kidwell et al., 1986), vertebrate skeletal concentrations are grouped here according to their inferred relations to biological and physical agents (Fig. 1.1). Most vertebrate skeletal concentrations can be readily categorized as either biogenic (intrinsic versus extrinsic) or physical (hydraulic versus sedimentologic) in origin, although the potential for mixed formative histories abounds. Mass mortality assemblages that have been reworked, sorted, and reconcentrated by fluvial processes are good examples of such mixed-origin concentrations (e.g., Voorhies, 1969; Wood et al., 1988; Eberth and Ryan, 1992). Contrary to the macroinvertebrate record, diagenetic processes such as compaction and pressure solution are deemed largely inconsequential with regard to

Intrinsic Biogenic Concentrations

perilous behavior
and/or life strategy

environmental hazards
and/or perturbations

death during gestation
death during parturition
gregarious nesting/birthing
death upon spawning
rutting (e.g., locked antlers,
tusks)

stranding/miring
flooding/drowning
wildfire
drought
poisoning/disease
severe short-term weather

Death Assemblage (n≥2)

Figure 1.2. Intrinsic biogenic concentrations develop as a result of activity or behavior of the fossilized organism itself. Concentrations might reflect perilous behavior in life, such as colonial nesting habits, or gregarious behavior in death, such as fatal spawning events. Concentrations might also reflect behaviors forced by unusual environmental hazards or perturbations. The key factor is that concentration results ultimately from the behavior or activity of the animals represented in the death assemblage, and is not the result of direct action by other organisms or physical processes.

the primary concentration of vertebrate hardparts, although diagenesis is certainly a factor in long-term preservation potential, and early diagenetic prefossilization may play a role in the reworking of bones into some erosional lags (see below).

Biogenic Concentrations

Biogenic concentrations of vertebrate hardparts are by definition produced by biological agents or events, and two general types are recognized here (Fig. 1.1). *Intrinsic biogenic concentrations* (Fig. 1.2) result from the "normal" activity or behavior of the vertebrates preserved in the death assemblage. Examples include concentrations that reflect gregarious behavior in life, such as colonial nesting habits, or in death, such as fatal spawning events. In some instances, the key behavior is forced by environmental conditions, specifically unusual hazards or perturbations that elicit behavior that results in a concentrated death assemblage. A prime example is drought, during which gregarious and nongregarious animals alike may modify their behavior so that their carcasses become concentrated in the

Extrinsic Biogenic Concentrations

spatially-focused   post-mortem
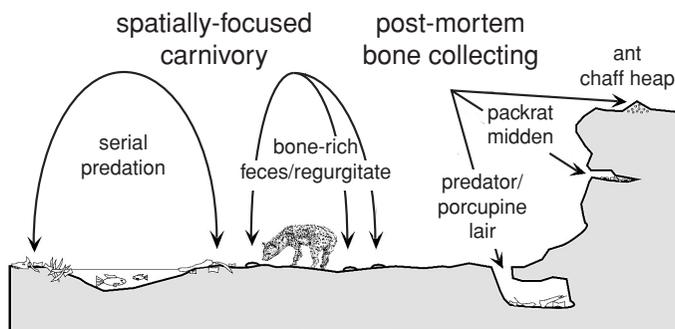carnivory   bone collecting

Figure 1.3. Extrinsic biogenic concentrations of vertebrate hardparts are produced by extrinsic biological agents, most notably predators. Nonpredatory animals such as porcupines and packrats also concentrate vertebrate hardparts due to habitual collecting. More rarely, intimate predator-prey associations are preserved, such as instances of fatal ingestion and dead carnivores with osseous gut contents.

vicinity of persistent food and water resources (Shipman, 1975; Haynes, 1988, 1991; Rogers, 1990; Dudley et al., 2001; among others). The key factor is that the formation of a death assemblage results ultimately from the behavior or activity of the hardpart producers and is not the result of direct action by other organisms or physical processes such as aqueous flows.

Biogenic concentrations of vertebrate hardparts also can be produced by the actions of other animals, acting on the hardpart producers (Fig. 1.3). Good examples of such *extrinsic biogenic concentrations* are predator-generated bone accumulations, such as bone-rich fecal masses and regurgitates (Mayhew, 1977; Dodson and Wexlar, 1979; Hoffman, 1988; Kusmer, 1990; Schmitt and Juell, 1994; Laudet and Selva, 2005; among others). Nonpredatory animals such as porcupines and packrats also concentrate vertebrate hardparts in appreciable quantities due to habitual collecting (e.g., Brain, 1980, 1981; Shipman, 1981; Betancourt et al., 1990). More rarely, intimate predator-prey associations are preserved, such as instances of fatal ingestion (or partial ingestion, see Grande, 1980; Davis and Martill, 1999) and dead carnivores with osseous gut contents (e.g., Eastman, 1911; Romer and Price, 1940; Eaton, 1964; Ostrom, 1978; Colbert, 1989; Charig and Milner, 1997; Chen et al., 1998; Varricchio, 2001; Hu et al., 2005; Nesbitt et al., 2006). This final category is somewhat of a hybrid mode of biogenic concentration (intrinsic plus extrinsic), in that it preserves the remains of the animal that generated the concentration via its typical behavior (the predator) and its ingested prey.

Intrinsic Biogenic Concentrations

Animals are unlikely to engage in activities as part of their regular life strategies that result in mass mortality. However, some vertebrates, by virtue of their reproductive physiology or behavior, are predisposed to localized, multi-individual ($n \geq 2$) mortality. At least three routine life-history events linked to reproduction predictably generate localized concentrations of bones and teeth.

The first reproduction-related scenario is the death of a pregnant viviparous or ovoviviparous female. Death of a pregnant female and one or more fetuses can result from a variety of causes (e.g., disease, breached birth, trauma) and can occur during gestation or during parturition. This scenario can transpire in any environmental context, and the only truly distinctive taphonomic signature is the intimate association of an adult female and a prenatal individual or individuals. Death during pregnancy or aberrant birth is a common phenomenon (e.g., Bergerund, 1971), and spectacular examples are known from the fossil record. For example, numerous specimens of the ichthyosaur *Stenopterygius* from the Early Jurassic Holtzmaden locality of southwestern Germany have been recovered with embryos both within the body cavity and partially expelled through the birth canal (Hauff, 1921; Böttcher, 1990).

A second reproduction-related scenario that can lead to accumulations of vertebrate hardparts relates to nesting in general, and gregarious nesting and birthing habits in particular. Given the definition of a bonebed, a single nest of any egg-laying vertebrate can in theory translate into a skeletal concentration if any combination of two or more embryos (assuming they have developed a mineralized and, thus, preservable skeleton) or hatchlings or nest-attending adults die and remain in close proximity. Death in and around a nest can readily result from intrinsic causes such as sickness or disease, abandonment, trampling/smothering, or siblicide (Burton, 1985; Anderson, 1990, 1995). Predators and inclement weather can also play a role in the buildup of bones in and around nesting sites. Mortality rates can be especially high in colonial nesting grounds, where overcrowding can lead to disease and agonistic behavior. Colonial nesting is especially common among seabirds (Furness and Monaghan, 1987), and aggressive behavior in seabird rookeries can take a particularly heavy toll on unattended chicks (Müller-Schwarze, 1984; Burton, 1985).

Pinnipeds also gather in rookeries in order to undergo synchronized mating and birthing. Mortality rates of seals, sea lions, and walruses in rookeries can be high, especially with regard to juveniles, and death can

result from a variety of causes, including extreme or unusual weather, starvation, disease, and trauma (LeBoeuf and Briggs, 1977; Fay and Kelly, 1980; Johnson and Johnson, 1981; LeBoeuf and Condit, 1983; LeBoeuf and Laws, 1994; Ovsyanikov et al., 1994). Pups separated from their mothers are particularly vulnerable and often are crushed by breeding bulls or bitten by unrelated females in response to attempted suckling (LeBoeuf and Briggs, 1977). Huber et al. (1991) estimated that pup mortality in northern elephant seal colonies ranges from 10% to 40% on an annual basis. Mortality rates among elephant seals, and presumably other pinniped taxa, are density dependent and vary directly with the crowding of beach rookeries (e.g., Reiter et al., 1978).

From a taphonomic perspective, a concentration of vertebrate hardparts associated with a single nest or a colonial rookery should be dominated by a single taxon and by juveniles, which under most circumstances would be the most vulnerable age class (e.g., Emslie, 1995). Age spectra can vary, however, depending on the nature of the mortality event (Forcada et al., 1999; Meng et al., 2004). For example, frenzied episodes of mass mating in pinniped rookeries (e.g., "mobbing" by Hawaiian monk seals) can produce death assemblages that include both juveniles and adult females (Johnson and Johnson, 1981; Banish and Gilmartin, 1992). Bonebeds resulting from this scenario can be autochthonous (e.g., bones still in nest), parautochthonous (bones scattered within rookery), or allocththonous, given the propensity of seabirds and marine pinnipeds to gather in seaside rookeries where storms and marine transgression can readily rework and transport skeletal material. Site fidelity, combined with regular annual mortality, should in principle propagate time-averaged assemblages of skeletal elements. Bone assemblages derived from nesting animals (e.g., birds, nonavian dinosaurs) may be associated with additional evidence of colonial activity, including guano deposits, abundant fragmentary eggshell, remains of prey, and multiple nest structures (Horner and Makela, 1979; Horner, 1982, 1994; Baroni and Orombelli, 1994; Emslie, 1995; Chiappe et al., 1998, 2004; Emslie et al., 1998; McDaniel and Emslie, 2002).

Finally, several species of fish regularly undertake arduous and ultimately fatal journeys to spawning grounds. The classic example is the five species of Pacific salmon in the genus *Oncorhynchus*, which as sexually mature adults leave oceanic habitats and venture upstream into natal river systems to reproduce. This journey can stretch for more than 1000 km, and while in transit the salmon do not feed but rely instead on stores of fat (Curtis, 1949; Maxwell, 1995). Pacific salmon tend to die shortly after spawning, presumably a result of starvation and perhaps accelerated

senescence, and their carcasses accumulate in vast numbers within and downstream from spawning grounds. A death assemblage of fishes linked to a fatal spawning event should be dominated by a single taxon and a single age class (reproductively capable adults) and should exhibit minimal levels of time averaging since spawning is typically synchronized (Wilson, 1996). However, given the generally poor preservation potential of fish carcasses (Schäfer, 1962, 1972; Nriagu, 1983; Smith et al., 1988), especially in slightly acidic freshwater systems, the likelihood of long-term preservation and entry into the fossil record is probably low (but see Wilson [1996]; and note that in the face of these taphonomic challenges, nitrogen isotopic signatures are proving to be extremely useful for reconstructing past fluctuations in salmon abundance [e.g., Finney et al., 2002]).

Biogenic concentrations of bones and teeth also develop when animals experience unusual or unpredictable circumstances in their local environment. Environmental hazards (such as the asphalt pools at Rancho La Brea [Stock, 1972]) and perturbations (such as drought [Shipman, 1975]) are envisioned as contributing factors related to events or behaviors that translate into local accumulations of vertebrate hardparts. A wide variety of environmental conditions can serve to bring or keep animals together prior to or during their death (Berger et al., 2001). The circumstances and taphonomic signatures of a selection of relatively common scenarios are explored here, namely stranding, miring, flooding, wildfire, severe short-term weather, drought, and disease.

With regard to strandings, Wilkinson and Worthy (1999) report that from 1989 through 1994, a total of 21,228 marine mammals (pinnipeds, cetaceans, sea otters, manatees) came ashore along the coastlines of the United States. Cetaceans, which comprise a significant fraction of this total (6768), are particularly susceptible to mass stranding because they are highly social and thus engage in coordinated group activity that leads on occasion to group mortality. On average, mass strandings of cetaceans number fewer than 15 animals, but some die-offs include hundreds of individuals (Smithers, 1938; Kellogg and Whitmore, 1957; Caldwell et al., 1970; Odell et al., 1980; Geraci and Lounsbury, 1993; Geraci et al., 1999).

The reasons behind cetacean mass strandings are often obscure. Schäfer (1962, 1972) proposed the possibility of "psychically induced" events, with panic or excitement perhaps coursing through a highly organized cetacean pod, ultimately leading to its subaerial demise. Panic attacks could conceivably result from predation pressures, or perhaps "extraordinary meteorological, volcanic, or oceanic events" (Schäfer, 1972,

p. 20). Local coastal effects, such as shore-parallel sand ridges, strong currents, or unusual tidal volumes could presumably also play a role (Schäfer, 1962, 1972; Brabyn and McLean, 1992). Some stranding events could potentially reflect a breakdown in navigation due to the impairment of echolocation in shallow waters, or geomagnetic anomalies (Dudok van Heel, 1966; Klinowska, 1985, 1986; Kirschvink et al., 1986). Resultant bonebeds should preserve a monospecific sample of a social unit (e.g., Camp, 1980; Hogler, 1992). The age spectrum would depend on the demographics of the affected pod. The coastal setting of mortality has great potential for reworking during storms, however, with bones likely to be incorporated into ravinement beds during marine transgression.

Miring as an agent of vertebrate mortality and skeletal concentration is perhaps best illustrated by the classic Rancho La Brea locality in the Pleistocene of southern California. Here, scores of animals big and small became trapped and perished in viscous pools of asphalt over tens of thousands of years (Stock, 1972; Spencer et al., 2003). A miring scenario has also been proposed for several low-diversity accumulations and isolated occurrences of prosauropod dinosaurs preserved in the Late Triassic of central Europe (Sander, 1992; Hungerbühler, 1998). Taphonomic features noted in support of miring include the prevalence of upright postures (including vertically oriented limbs), and a preservational bias in favor of the posterior/ventral body region. Sander (1992) further noted that juvenile prosauropods were absent in the bonebed assemblages and proposed that they may have escaped entrapment due to their smaller size and "lower foot pressure" (but see Berger [1983] for an account of juvenile horses trapped in a quagmire). Contorted strata indicative of extrication efforts (fugichnia) might also accompany carcasses mired in soft sediments.

From a conceptual standpoint, flooding in a terrestrial setting can lead to biogenic accumulations of vertebrate skeletal debris in at least three ways. First, when landscapes are inundated with floodwaters, terrestrial animals tend to move to higher ground, if there is any to be found. If animals succeed in securing an "island refuge," they may find themselves stranded for long periods. If the refuge lacks sufficient carrying capacity, animals may begin to starve. Close quarters may also lead to stress and agonistic behavior. If carnivores are present, predation could conceivably transpire at intensified levels. The resultant death assemblage would potentially include an assortment of animals of variable age classes that were mobile enough to reach high ground before drowning. The death assemblage should be relatively autochthonous with regard to the site of death, but the assemblage may not represent a typical ecological "community"

because the animals arguably assembled under duress. The level of time averaging should be relatively low unless fatal flood events recur at sporadic intervals. Long-term preservation is not a given because burial potential is limited in "high-ground" locations. An apparent exception was described by Kormos (1911: cited in Weigelt, 1927, 1989), who invoked flooding (or perhaps fire) to explain a Pliocene mammal assemblage preserved in karst caves in a limestone crag. Burial potential would also be enhanced if flooding occurred in a large river system near sea level (e.g., Mississippi delta).

Aquatic animals also experience hardship during major flood events, potentially due to changes in aqueous chemistry (Whitfield and Patterson, 1995), or as the result of stranding as floodwaters recede. The latter scenario is particularly lethal to fish, which can become trapped in temporary back swamps and sloughs (Smith et al., 1988; Wilson, 1996; Johanson, 1998). The resultant death assemblage would presumably include fishes of variable age classes that ventured into flooded regions during high-water stage. The death assemblage should be autochthonous to parautochthonous with regard to the actual site of mortality. If fish bones survive scavengers and the rigors of subaerial weathering (Behrensmeyer, 1978; Smith et al., 1988), there is a reasonable chance of burial given their association with low ground on the floodplain.

Rivers and lakes in "high-water" or flood stage can also generate local concentrations of terrestrial vertebrate carcasses, with perhaps the most commonly cited example being the mass drowning of wildebeest during their overland migrations (Talbot and Talbot, 1963; McHugh, 1972; Schaller, 1972, 1973; Sinclair, 1979; Capaldo and Peters, 1995). Rivers need not be in flood stage, however, for mass drowning to occur (Dechant-Boaz, 1982). Apparently the pressure of the advancing herd is a killing agent in and of itself, as it forces animals in the lead to falter and drown as they pile up one upon another in swift-moving currents. The well-known *Centrosaurus* Bonebed (Quarry 143) in the Dinosaur Park Formation of Alberta (Currie and Dodson, 1984; Eberth and Ryan, 1992) has been interpreted to represent a dinosaur analog of the wildebeest stream-crossing scenario (but see Ryan et al. [2001] and Eberth and Getty [2005] for more recent interpretations). At this locality, more than 220 *Centrosaurus* individuals are preserved at the base of a broad, lenticular sandstone body interpreted as an ancient stream channel deposit. Several other fossil bonebeds (e.g., Turnbull and Martill, 1988; Wood et al., 1988) have also been attributed to mass drowning of vertebrates while crossing streams.

Bonebeds originating from fatal river or lake crossings should in principle preserve a monospecific sample comprising the herding taxon (e.g.,

Cole and Houston, 1969; Capaldo and Peters, 1995), although bones of other animals can be present at the accumulation site prior to the event and can also be added to the death assemblage subsequent to the event. If migratory herd structure is "fluid," as in the case of the wildebeest (Talbot and Talbot, 1963), a mixed age-class death assemblage is likely. If a mobile herd is socially organized, with perhaps adult animals leading the social unit, a more selective age spectrum could possibly be generated. With regard to depositional setting, bones should be preserved in fluvial or lacustrine deposits, although some reports (e.g., Turnbull and Martill, 1988) contend that floodwaters may actually transport carcasses out of the active channel belt and onto the adjacent floodplain. Preservation potential is generally good in fluvial and lacustrine settings (Behrensmeyer, 1988; Behrensmeyer et al., 1992).

Wildfires can also cause animals to congregate under duress and can ultimately lead to mass mortality. The likelihood of mass mortality depends to some extent on the abundance and mobility of animals in the path of the fire, and the dynamics of the fire advance (Lawrence, 1966; Singer et al., 1989). Mobile animals will often escape largely unscathed, but slow animals, such as turtles, and relatively immobile animals, such as nest-bound birds and newborns, can suffer dramatic losses. Aspects of the local terrain also play a role, especially with regard to the potential for concentration. If an obstruction is encountered, such as a cliff or a canyon, animals may gather and perish en masse by flames or by asphyxiation. Animals may also seek refuge at local water sources, where they may be overcome by heat or suffocate (Singer et al., 1989). The refuge scenario was invoked by Sander (1987) to explain a diverse assemblage of tetrapods preserved in lacustrine facies of Permian age. Bones derived from assemblages related to fire may show microscopic evidence of burning (Shipman, 1981; Shipman et al., 1984) and may be associated with charcoal deposits (fusain if fossilized [Jones, 1997; Falcon-Lang, 1998, 1999; Zeigler, 2002]). Preservation potential is generally good if animals congregate in or near water sources, which are often sites of sediment accumulation.

A wide range of mass mortality scenarios can be linked to extreme or unusual short-term weather events. Rapid spring thaws of snow pack or ice can lead to catastrophic flooding (see above) and can also leave animals stranded on islands or ice rafts, where starvation and possibly hyperpredation can lead to mass die-offs (Geraci and Lounsbury, 1993; Geraci et al., 1999). Conversely, rapid cooling events and severe winter stress can lead to hypothermia and starvation in both aquatic (Weigelt, 1927, 1989;

Storey and Gudger, 1936; Gunter, 1941, 1947; Brongersma-Sanders, 1957; Waldman, 1971; Economidas and Vogiatzis, 1992; McEachron et al., 1994; Marsh et al., 1999) and terrestrial (Berger, 1983; Borrero, 1990; Jehl, 1996) settings. If the drop in temperature is particularly severe, fatal ice-trapping can occur, as in the case of approximately 300 coots that were immobilized in ice and subsequently died of exposure in a small oxbow lake of the Illinois River in 1985 (Oliver and Graham, 1994). Marine mammals, such as beluga whales and narwhals, can also be trapped in ice by the thousands during unusual freezes (Freeman, 1968; Sergeant and Williams, 1983; Siegstad and Heide-Jørgensen, 1994). More exotic weather-related killing agents such as fog (Lubinski and O'Brien, 2001), large hail and lightning (Kuhk, 1956; NWHC, 1998, 2001), and unusually large oceanic waves (Bodkin et al., 1987) can also result in mass mortality and potentially generate localized concentrations of vertebrate skeletal debris. The long-term preservation potential and taphonomic signatures of a weather-related bone assemblage depend on taxon-specific and site-specific attributes and generally cannot be predicted for this diverse category of killing agents.

Drought is a very significant and recurrent killing agent in modern ecosystems (Tulloch, 1970; Corfield, 1973; Tramer, 1977; Coe, 1978; Haynes, 1988, 1991; Dudley et al., 2001), and numerous examples of drought-related mortality have been inferred from the fossil record (Matthew, 1924; Huene, 1928; Brown, 1935; Case, 1935; Dalquest and Mamay, 1963; Saunders, 1977; Hulbert, 1982; Rogers, 1990, 2005; Schwartz and Gillette, 1994; Fiorillo et al., 2000; Gates, 2005). During a drought, gregarious and nonsocial animals alike necessarily congregate in the vicinity of persistent reserves of food and water. If drought persists and resources are further depleted, fitness diminishes and animals begin to succumb to malnutrition and disease. Their plight may only worsen if drenching rains follow the drought and turn the terrain into a quagmire (Mellink and Martin, 2001). Carcass assemblages numbering in the hundreds may develop, and a variety of clues can be used to identify these drought-related skeletal concentrations in the fossil record (Shipman, 1975; Rogers, 1990; Falcon-Lang, 2003). Potential indicators include a suitable paleoclimate (indication of aridity and/or seasonality), an aqueous depositional setting, and age- and sex-specific mortality profiles (Voorhies, 1969; Hillman and Hillman, 1977; Conybeare and Haynes, 1984). The preservation potential of drought assemblages is good owing to the concentration of animals around water sources and the likelihood of flooding, erosion, and burial subsequent to drought (Weigelt, 1927, 1989; Kurtén, 1953; Shipman, 1975; Gillson, 2006).

Finally, under the general rubric of "sickness and disease," a host of biotoxins, abiotic chemical poisons, viruses, bacterial infections, and parasites can and often do trigger events of vertebrate mass mortality (Gunter et al., 1948; Brongersma-Sanders, 1957; Grindley and Taylor, 1962; Nyman, 1986; Pybus et al., 1986; Wurtsbaugh and Tapia, 1988; Worthylake and Hovingh, 1989; Thompson and Hall, 1993; Leonardos and Sinis, 1997; Berger et al., 1998; Swift et al., 2001; Braun and Pfeiffer, 2002; and see USGS National Wildlife Health Center Quarterly Mortality Reports for a wealth of additional examples). Whether a mortality event linked to sickness or disease translates into a concentration of vertebrate skeletal debris would of course depend on local conditions at the time of death and postmortem events. Likewise, the preservation potential and taphonomic attributes of a given assemblage would depend on the selectivity of the killing agent and local ecological and geological circumstances. Diagnosing sickness or disease in the fossil record, beyond the routine characterization of pathologic bone, is difficult at best, and often impossible (Baker and Brothwell, 1980; Rothschild and Martin, 1993; Hopley, 2001). A few potential examples include (1) lung failure in Miocene mammals, which was attributed to ash inhalation (Voorhies 1992), (2) botulism poisoning of dinosaurs (Varricchio, 1995), (3) red-tide-related poisoning of Pliocene cormorants (Emslie and Morgan, 1994) and (4) toxic cyanobacterial poisoning of Pleistocene mammals (Braun and Pfeiffer, 2002).

Extrinsic Biogenic Concentrations

Localized accumulations of vertebrate hardparts also result from the activities of other organisms, which can range from scavenging insects to large-bodied, voracious predators. Two general categories of accumulation are recognized, and these essentially relate to whether the bone assemblage reflects (1) spatially focused predatory activity or (2) purposeful postmortem bone collecting (Fig. 1.3).

One example of a predatory concentration is the direct ingestion of multiple prey items, which, depending on the intensity of gastric processing, can yield a bone-rich, multi-individual fecal mass or regurgitate. Numerous studies have explored the end results of avian, mammalian, and crocodilian digestion as it relates to the taphonomy of bones and teeth (e.g., Mayhew, 1977; Dodson and Wexlar, 1979; Fisher, 1981; Andrews and Nesbit Evans, 1983; Hoffman, 1988; Andrews, 1990; Kusmer, 1990; Denys et al., 1992; Denys and Mahboubi, 1992; Schmitt and Juell, 1994;

Terry, 2004; Laudet and Selva, 2005; among others), and the findings indicate that differentiating the feces and regurgitate of various bone-ingesting species is possible, even in the fossil record. For example, Mayhew (1977) compared the taphonomic characteristics of modern mammalian remains in pellets of diurnal and nocturnal birds of prey and identified characteristic breakage patterns and distinctive corrosion effects. These criteria were then applied to a Pleistocene fossil locality in order to identify the concentrating agent, which turned out to be a diurnal avian predator. Along these same lines, Schmitt and Juell (1994) and Denys et al. (1992) argued that skeletal representation, bone-fragment size, macroscopic and microscopic attributes of bone surfaces, and chemical composition could be used to distinguish bone assemblages of canid origin (specifically coyote and sand fox) from those of avian or human derivation. A multivariate analysis of new and published datasets demonstrates that small-mammal assemblages concentrated by owls are in fact consistently distinguishable from concentrations produced by diurnal raptors and mammalian predators on the basis of degree of fragmentation and skeletal-element representation (Terry, 2005). Distinctive taphonomic characteristics of digested bones and teeth, combined with the distinct morphologic characteristics of regurgitated pellets or fecal deposits, thus facilitate recognition of such accumulations (a coprocoenosis sensu Mellet [1974]) in the fossil record.

Another predatory scenario results from serial predation, which according to Haynes (1988, p. 219) "refers to regular and habitual killing of prey animals in the same loci, which are favoured by predators because of features of the terrain or localized abundance of prey." Haynes (1988) provided two examples of concentrations generated by serial predation. The first was a "cumulative bone site" in Wood Buffalo National Park in northern Alberta, Canada. The locus of bone accumulation was a small slough (~30 × 30 m in size) situated in an open grassland setting punctuated by small stands of trees. The bones of five bison—two adult males, two adult females, and one subadult—were found scattered around the edge of the slough. The monotaxic accumulation of bison elements was attributed to wolf predation that transpired over the span of a few years. Haynes' second example was from a water hole in Hwange National Park, Zimbabwe. This site contained the remains of at least 77 individuals, representing 14 vertebrate taxa (Haynes, 1988, p. 228), and was attributed to lion and hyena predation over a span of several years. Haynes (1988) argued that bone accumulations produced by serial predation are not straightforward to identify, and that distinguishing them from mass-death assemblages

might be especially difficult. Criteria that might be useful in the fossil record include (1) evidence of time averaging, although mass-death sites can also show variable stages of bone weathering (Haynes, 1988), (2) indication of bone processing by carnivores, (3) a preponderance of potential prey animals, and (4) perhaps a depositional setting consistent with potential prey localization (e.g., stream margins, water holes).

The second category of extrinsic biogenic concentration reflects the intentional collection (and transport) by organisms of dead skeletal material. The habitual retrieval of bones and carcasses to cache sites or lairs for feeding or gnawing is a well-documented phenomenon. Carnivorous mammals notorious in this regard include hyenas, wolves, leopards, and a variety of mustelids (Yeager, 1943; Vander Wall, 1990). The bone-collecting habits of the hyenas have been particularly well studied (e.g., Buckland, 1823; Kruuk, 1972; Potts, 1986; Skinner et al., 1986; Horwitz and Smith, 1988; Skinner and van Aarde, 1991; Kerbis-Peterhans and Horwitz, 1992; Lam, 1992). The characteristic features of bone assemblages accrued by hyena include extensive evidence of crushing and gnawing (focused particularly on protruding features), an unusual abundance of bone chips (reflecting bone-crushing tendencies), and relatively rare evidence of distinct puncture marks. Avian taxa such as hawks and owls also regularly transport vertebrate prey, and they sometimes store their remains in multi-individual larders. Owls in particular make frequent use of prey stockpiles (Pitelka et al., 1955; Cope and Barber, 1978; Vander Wall, 1990), and the thick accumulations of pellets that develop under roost sites are effectively middens, combining the effects of serial predation with homing behavior and regurgitation of undigested remains (bones, teeth, and hair from small mammal prey).

Nonpredatory animals such as porcupines also collect bones, presumably to chew for dietary reasons (Ca^{2+} uptake) and to keep ever-growing incisors in check. Bones collected by the African porcupine (*Hystrix africaeaustralis*) tend to show particularly heavy damage from gnawing (Brain, 1980, 1981) and may exhibit scoop-shaped excavations in the cancellous interiors of broken long bones in association with characteristic gnaw marks (Maguire et al., 1980). Packrats (*Neotoma* spp.) also transport and collect bones, although their motives are more difficult to ascertain. According to Elias (1990, p. 356), packrats "bring objects to their den site for a variety of reasons, including food, curiosity, and protection," and Hockett (1989) reported that relatively few bones recovered from a midden in the Nevada desert displayed gnaw marks that could be attributed to the resident packrat. The relatively small bones that are collected by packrats are found in association with an array of other small

collected objects (e.g., shells, seeds, twigs), and would potentially be encased in the crystallized urine (amberat) of the packrat (Van Devender and Mead, 1978; Mead et al., 1983; Betancourt et al., 1990; Cole, 1990; Elias, 1990).

The curious category of ant-generated bone assemblages occupies the minuscule end of the bone-collecting spectrum. Shipman and Walker (1980) described the characteristics of modern bones collected by East African harvester ants (*Messor barbarus*), which apparently retrieve small bones from surrounding terrain to their chaff heaps in order to feed on adhering soft tissue (Shipman, 1981). Shipman and Walker (1980) found that ant-generated assemblages were superficially similar to owl pellet assemblages but could potentially be distinguished by a greater diversity of sampled taxa (predators are presumably more selective than scavenging ants), and preponderance of robust elements. A similar phenomenon occurs when ants encounter preexisting concentrations of fossil bones during excavation of their subterranean tunnels (Clark et al., 1967; RRR, pers. observ. 1993).

Finally, throughout much of their history, humans have interacted with vertebrates both as predators and as scavengers, producing extrinsic biogenic bone concentrations at sites of mass or serial killing (bison jump-offs, mammoth mires), consumption (middens), and tool making (postmortem utilization). A large anthropological and archeological literature is devoted to the phenomenology and recognition of "bonebeds" of these types (e.g., Frison, 1974; Graham et al., 1981; Grayson, 1984; Frison and Todd, 1986; Haynes, 1991; Holliday et al., 1994; Meltzer et al., 2002), and thus we do not discuss it here in further detail. Generally speaking, however, these present some of the same challenges as in diagnosing nonhominid biogenic concentrations. This includes the observation that humans were not necessarily agents of concentration, even where they are associated with bones via artifacts, and instead could have been agents of (minor) dispersion, for example removal of elements from drought-aggregated bison (e.g., Gadbury et al., 2000; Mandel and Hofman, 2003).

Physical Processes of Concentration

Concentrations of vertebrate skeletal elements generated by physical processes are best conceptualized if vertebrates and their skeletal elements are viewed as sedimentary particles, or "bioclasts" (e.g., Behrensmeyer, 1975; Shipman, 1981). Like inorganic sedimentary particles, the behavior

of vertebrate bioclasts in fluid flows is primarily a function of size, shape, and density, with bioclasts being entrained, transported, and deposited with moderate predictability. Whether accumulations of vertebrate hardparts develop as a result of physical hydraulic processes depends upon numerous factors, including the energy and persistence of the hydraulic medium, the threshold velocity of bioclasts relative to inorganic matrix, and the abundance of bioclastic material delivered to the system. A critical aspect of the concentration equation relates to the budget of nonbioclastic material (host matrix). If the system is starved of such sediment in relation to biological input, an attritional accumulation of vertebrate bioclasts could potentially accrue. If this sediment is supplied but reworked and winnowed from the system more readily than bioclasts, a residual hydraulic lag of relatively dense skeletal elements may result. If bioclast transport occurs at lower velocity than does the matrix, then a relative concentration of transported bioclasts could theoretically result "downstream," assuming the existence of some trap (but see discussion below). If an unusual amount of sediment is delivered to the system abruptly, an "obrution" event concentration of vertebrate bioclasts may be generated (sensu Seilacher et al., 1985; Brett, 1990). The key factor in all of these scenarios is that the *final concentration* of vertebrate skeletal components is predominantly the result of physical factors—either hydraulic processes or sedimentary budgets, rather than biological phenomena (Figs. 1.4 and 1.5).

Fluvial Hydraulic Accumulations

In a study of vertebrate preservation in fluvial settings, Behrensmeyer (1988, p. 191) distinguished between assemblages that accumulated under the influence of "sustained active flow" (channel-lag assemblages) and those that accumulated after a channel is abandoned by flow (channel-fill assemblages). Bones and teeth preserved in channel-lag assemblages are generally considered parautochthonous to allochthonous. Component elements may exhibit a variety of taphonomic features generated by the multitude of biological and physical processes that can act upon vertebrate hardparts both before and during their interaction with fluvial processes. Bones may exhibit abraded edges and processes, indicating sustained interaction with abrasive sediment driven by currents, or may appear fresh and angular (Behrensmeyer, 1982, 1987, 1988). Accumulations may also show size and shape sorting and preferred orientations relative to prevailing currents (Voorhies, 1969; Behrensmeyer, 1975; Korth, 1979;
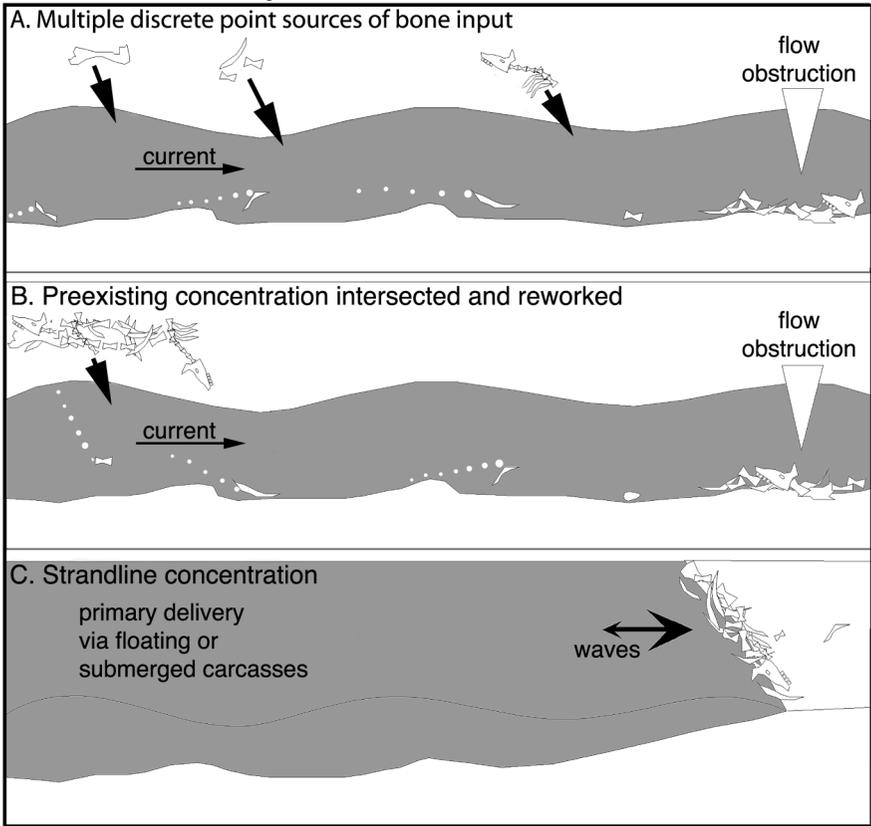
Hydraulic Concentrations

A. Multiple discrete point sources of bone input

flow obstruction

current

B. Preexisting concentration intersected and reworked

flow obstruction

current

C. Strandline concentration

primary delivery
via floating or
submerged carcasses

waves

Figure 1.4. Hydraulic concentrations of carcasses, parts of carcasses, or disarticulated bones and/or teeth form by the action of surface flows (wind, water, sediment) or wave activity. Transport of bioclastic material to the site of concentration is an integral part of this formative scenario. Numerous factors determine whether relative accumulations of vertebrate hardparts develop in these settings, including the energy and persistence of the hydraulic agent, the amount of bioclastic material delivered to the system, and the presence of trapping mechanisms (e.g., log jams).

Shipman, 1981). The degree of articulation and element association is generally low, especially for microfossil bonebeds (e.g., Rogers and Kidwell, 2000).

Fluvial transport and dispersal of vertebrate skeletal debris have received a great deal of attention (e.g., Dodson, 1971; Wolff, 1973; Lawton, 1977; Badgley, 1986; Behrensmeyer, 1988; Hook and Ferm, 1988), and numerous experiments have been conducted to learn how to recognize these phenomena (e.g., Voorhies, 1969; Dodson, 1973; Behrensmeyer,
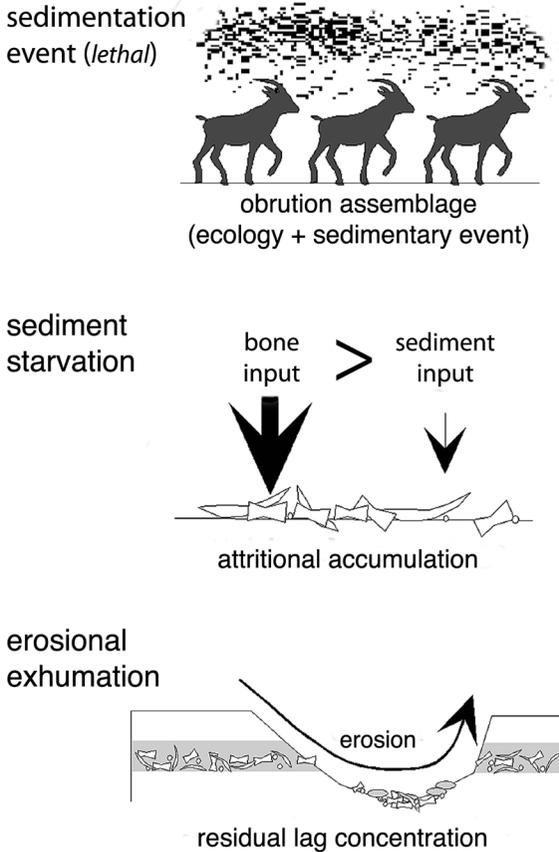
Sedimentologic Concentrations

sedimentation
event (*lethal*)

obrution assemblage
(ecology + sedimentary event)

sediment
starvation

bone
input > sediment
input

attritional accumulation

erosional
exhumation

erosion

residual lag concentration

Figure 1.5. Sedimentologic concentrations, like hydraulic concentrations, are intimately linked to hydraulic processes. The key difference lies in their direct genetic link to the siliciclastic sedimentary budget, be it positive, zero, or negative. An obrution assemblage forms in response to, and is permanently buried by, a single unusual circumstance of sediment deposition. The obrution category is a composite mode of concentration that hinges upon both ecology (living animals initially congregate) and sedimentary geology (obrution triggers mortality and captures the concentration). An attritional assemblage of vertebrate hardparts initially forms during an episode of sediment starvation, with conditions of low sedimentary dilution fostering concentrations of vertebrate material by passive means. Residual lag concentrations form when erosion preferentially removes siliciclastic sedimentary matrix, leaving behind a hydraulic (transport-resistant) lag of larger and/or denser skeletal material exhumed from previous deposits.

1975; Korth, 1979; Hanson, 1980; Frison and Todd, 1986; Argast et al., 1987; Aslan and Behrensmeyer, 1996; Blob 1997; Trapani, 1998). For example, based on his seminal flume studies, Voorhies (1969) introduced the concept of fluvial transport groups (later referred to as "Voorhies groups" by Behrensmeyer, 1975), which reflect the transport potential and sorting

behavior of disarticulated vertebrate elements (specifically those of sheep and coyote) with increasing current velocity. Using these guides, Voorhies (1969) interpreted the Pliocene Verdigre Quarry bone assemblage of Nebraska as hydraulic in origin. He argued that a preexisting assemblage of disarticulated and variably weathered bones and teeth had been concentrated during "a single flood of major proportions" at the base of an "off-channel sediment-trap."

Subsequent studies have extended the analysis to other vertebrate groups. Dodson (1973) focused on the flume behavior of disarticulated elements and component parts (e.g., skulls) of frogs, toads, and mice and identified the sequence of movement in unidirectional currents. He demonstrated that the bones of small vertebrates (microvertebrates) were particularly susceptible to transport (rather than "hiding" in the benthic boundary layer), and also identified the possibility of floating bones, which would of course have great dispersal potential in fluvial systems.

Behrensmeyer (1975) examined the consequences of bone size, shape, and density on transport potential for numerous different mammals. In addition to theoretical considerations of dispersal, she conducted experiments on bone settling velocities and was thus able to estimate the hydraulic equivalence of modern and fossil bones and their associated sedimentary matrix. Behrensmeyer (1975) also addressed the significant and often overlooked details of bottom morphology, current profile, and burial potential as they relate to bone transport and dispersal.

In a more recent analysis of hydrodynamic dispersal potentials, Blob (1997) returned to the question of Voorhies groups for nonmammalian material, specifically the soft-shelled turtle *Apalone spinifera*. He found that turtle elements generally fall into three groups that disperse in a relatively predictable fashion. However, the initial orientations of turtle elements on the flume bed played a significant role in their dispersal potential, and, contrary to expectation, threshold velocities for the entrainment of turtle elements correlated poorly with bone density. Thus, he cautioned against the uncritical application of mammalian hydrodynamic sorting patterns to the analyses of nonmammalian assemblages.

In one of very few actualistic studies of bones in natural fluvial systems, Aslan and Behrensmeyer (1996) surveyed a 2 km stretch of the East Fork River in western Wyoming to relocate 311 experimental bones and teeth placed in the river between 1974 and 1983 (Hanson, 1980; Behrensmeyer, 1982, 1991). One hundred and forty-two bones of the original experimental sample were relocated, and observations were taken on 372 additional naturally occurring bones between 1974 and 1987. Most of the experimental bones had been transported less than 1000 m from their point

of origin, and virtually all showed minor evidence of abrasion. Interestingly, there was no correlation between degree of abrasion and distance of transport. Perhaps most important to the present discussion, however, was their discovery that both natural and experimental bones accumulated along the inside bends of sinuous channels with prominent point bars (Aslan and Behrensmeyer, 1996). They attributed these accumulations to flow resistance in sinuous channel bends, which is approximately twice as great as in straight reaches (Lisle, 1976; Dietrich, 1983). Aslan and Behrensmeyer (1996) did not, however, encounter multi-individual concentrations of naturally occurring bones on point bars in their study transect (Behrensmeyer, pers. comm., 2000).

In general, the dynamics of bone concentration under active flow in modern fluvial channels is poorly understood, at least in relation to our working knowledge of bone transport, bone degradation (abrasion and rounding), and bone burial in the same setting (but see Brady et al., 2005). This is unfortunate, because fossil bones and teeth are common in fluvial deposits (e.g., Korth, 1979; Behrensmeyer, 1987, 1988; Koster, 1987), and numerous channel-hosted concentrations of fossil bones have been reported in the literature (e.g., Lawton, 1977; Eberth, 1990; Fiorillo, 1991; Badgley et al., 1995; Rogers and Kidwell, 2000). Some of these ancient fluvial bone assemblages have been linked to mass-death events, and in these cases the concentrations of hardparts are envisioned as parautochthonous deposits derived from a nearby multi-individual source (e.g., Voorhies, 1969; Eberth and Ryan, 1992; Ryan et al., 2001). Others, however, have been interpreted as attritional accumulations that developed over time as bones and teeth of numerous animals were hydraulically transported within the fluvial system. Two trapping mechanisms are commonly invoked to explain these attritional accumulations: in-channel obstructions such as trees or large carcasses (Fiorillo, 1991; Le Rock, 2000), and drops in hydraulic competence associated with sinuous or otherwise compromised channel stretches (e.g., Lawton, 1977).

While the attritional scenarios outlined above are arguably possible, we find it conceptually difficult to accept the proposition that disarticulated bones and teeth of numerous animals delivered from widely separated point sources at different times would travel downstream through complex and hydraulically unstable channel belts and collectively accumulate on a regular basis (Fig. 1.4A). In fact, we find it much more likely that bones and teeth would tend to disperse over time as a function of differential transport. Moreover, as pointed out above, vertebrate elements released from point sources along the East Fork River tended to travel less than 1000 m from their origination point, despite years of residence time

Raymond R. Rogers and Susan M. Kidwell

in the active channel (Aslan and Behrensmeyer, 1996). This suggests that bones and teeth derived from background mortality along the stretch of a river should, given time, diffuse downstream, resulting in dispersed occurrences relative to their respective sites of origin and individual sorting behaviors.

It strikes us as more likely that many, if not most, multi-individual concentrations of disarticulated vertebrate skeletal elements preserved in ancient fluvial channels were derived from a preexisting concentrated source (Fig. 1.4B). Eberth (1990) alluded to this possibility in an analysis of vertebrate microsites in the Judith River Formation of Alberta. He proposed that preexisting "floodplain concentrates" of vertebrate microfossils were the likely source for the numerous paleochannel-hosted microvertebrate assemblages in the Dinosaur Park Formation of Alberta. Badgley et al. (1998) also addressed the potential of preexisting sources and proposed that localized concentrations of vertebrate microfossils in fluvial facies of the Middle Miocene Ghinji Formation of Pakistan are the product of initial biological accumulation (probably linked to predator activity) with subsequent reworking, transport, and redeposition in fluvial channels. Rogers and Kidwell (2000) focused on the significant role of preexisting sources in their analysis of vertebrate skeletal concentrations and discontinuity surfaces in terrestrial and marine facies in the Cretaceous Two Medicine and Judith River Formations of Montana. They identified sites on the floodplain where physicochemically resistant vertebrate hardparts accumulated to concentrated levels via attritional processes (see below), and provided physical stratigraphic and taphonomic evidence for the fluvial reworking of preexisting floodplain concentrations into channel-hosted microvertebrate assemblages (see also Rogers, 1995). More information on the erosional exhumation and reconcentration of bone in both fluvial and shallow marine settings is presented below.

Strandline Hydraulic Accumulations

Vertebrate remains also accumulate hydraulically along strandlines, where they are subject to wave activity (Fig. 1.4C). Weigelt (1927, 1989) described the formation of strandline assemblages and provided examples from the fossil record. In most cases, bones and teeth are delivered to the strand via floating carcasses, which become anchored and may disarticulate in the swash zone. Onshore and longshore transport may also deliver isolated skeletal elements to the strand. Entire carcasses and individual skeletal components are usually driven by wave activity to lie tangential to the shoreline. However, if an element is irregular in shape such

that one end serves as a pivot point, it may orient perpendicular to the shoreline. Vertebrate remains along strandlines are commonly associated with plant debris, especially along bodies of freshwater, such as the classic Smithers Lake locality of Weigelt (1927, 1989). Here, vertebrate carcasses accumulated amidst vast quantities of plant debris during a rare winter storm (a "norther"). In most cases, a multi-individual accumulation of skeletal debris along a strandline reflects a precursor event of heightened mortality.

Leggitt and Buchheim (1997) compared a modern strandline bone assemblage composed of thousands of disarticulated bird elements (predominantly derived from pelicans and cormorants that died of infectious disease) with an assemblage of *Presbyornis* bones from Eocene Fossil Lake (Wyoming) and found similar taphonomic features. Most striking was the strong alignment of elongate elements (humerus, radius, ulna, tibiotarsus, tarsometatarsus) with respective shorelines. In a study of much older vertebrate remains, Rogers et al. (2001) attributed an enigmatic concretion-hosted assemblage of partially articulated tetrapods in the Triassic of Argentina to a strandline scenario. Tetrapod fossils from the Los Chañares locality exhibit telltale evidence of strandline accumulation, including distribution in a narrow linear swath, and alignment of skeletal debris, including spectacular examples of parallel-arrayed carcasses.

Sedimentary Budgets and Vertebrate Skeletal Accumulation

Empirical data from the marine stratigraphic record demonstrate a strong association between benthic macroinvertebrate concentrations and discontinuity surfaces of many types, as well as congruence between taphonomic attributes and the inferred duration of the associated hiatus (Kidwell, 1989, 1991a, 1991b, 1993; Fürsich and Oschmann, 1993; Brett, 1995; Naish and Kamp, 1997; Abbott, 1998; Gillespie et al., 1998; Kondo et al., 1998; del Rio et al., 2001; Fernandez-Lopez et al., 2002; Fürsich and Pandey, 2003; Mandic et al., 2004; Cantalamessa et al., 2005; Parras and Casadio, 2005). It is thus reasonable to suspect that spatial and temporal variation in erosion, sedimentary omission, and deposition—that is, patterns in the accumulation of inorganic sediment, as opposed to active manipulation of hardparts—might also exert a strong influence on the distribution and quality of vertebrate fossil assemblages in marine and continental systems (see Rogers and Kidwell, 2000). Accumulations of vertebrate hardparts that ultimately result from budgets of sedimentation are herein categorized as sedimentologic concentrations (Fig. 1.5).

Sedimentologic concentrations overlap with the hydraulic concentrations described in the preceding section in that they too are intimately linked to hydraulic parameters (waves, currents, etc.), because these influence the capacity and competence of inorganic sediment removal and delivery, not simply bioclast mobility. The sedimentologic category, however, focuses on the nonbioclastic sedimentary budget, be it positive (aggradational), negative (erosional, degradational), or zero (starvation, dynamic or total bypassing). In the following analysis, we focus on mechanisms of sedimentologic concentration that operate in sedimentary basins that are fundamentally sinks for sediment and thus accumulating stratigraphic records, as opposed to regions undergoing widespread erosion or chemical degradation, such as karst terrains. In-depth considerations of bone concentrations that accumulate in caves and fissures can be found in works by Fraser and Walkden (1983), Brain (1980, 1981), Andrews (1990), and Benton et al. (1997), among others.

Theoretically, vertebrate hardparts may accumulate to concentrated levels during episodes of sediment starvation. Nondepositional hiatuses create conditions of low sedimentary dilution for the "rain" of skeletal material produced by contemporaneous vertebrate populations (Behrensmeyer and Chapman, 1993) and thus should foster relative concentrations of vertebrate material by passive means. The longer the sedimentary hiatus, the greater the potential quantity (and ecological mixture) of hardparts supplied, and thus the richer and laterally more continuous the ultimate skeletal concentration may be. On the other hand, conditions of low or zero net sedimentation also increase the period that any cohort of skeletal material is subject to destructive postmortem processes operating at or near the depositional interface. Thus, the advantages of lowered sedimentary dilution might be outweighed by taphonomic culling.

The stratigraphic record of marine settings does contain "time-rich" hiatal concentrations of vertebrate skeletal hardparts, generated during stratigraphically significant hiatuses in sedimentation and associated with significant discontinuities, such as parasequence-bounding flooding surfaces, transgressive surfaces, midcycle surfaces of maximum transgression, and third- or fourth-order sequence boundaries (e.g., most articles cited above for macroinvertebrate concentrations, plus Conkin et al., 1976, 1999; Sykes, 1977; Kidwell, 1989, 1993; Macquaker, 1994; Turner et al., 2001; Walsh and Naish, 2002; Allulee and Holland, 2005). Hiatal conditions can reflect a variety of short-term sedimentary dynamics and develop in an array of paleogeographic and historical contexts (e.g., sediment starvation of submarine paleohighs, distal portions of basins, and transgressive

shelves; sediment bypassing of shallow-water environments at grade; erosional truncation associated with rapid transgression and baselevel lowering; Kidwell 1991a, b). Depending on the conditions, vertebrate material may be associated with either scarce or abundant shelly remains from macrobenthos and ranges in condition from articulated specimens of marine reptiles and mammals (most common in the context of anoxia and reduced sedimentation during maximum transgression, but see Brand et al. [2004]) to highly comminuted, abraded and polished teeth and fragmental bones from marine taxa (associated with erosional reworking of marine strata). All of these marine hiatal concentrations, however, are thinner than coeval, less fossiliferous strata, and they typically bear tangible evidence of prolonged low net sedimentation, such as ecological condensation and admixtures of hardparts with diverse taphonomic or diagenetic histories. In the marine realm, it thus appears that the production of new elements during the hiatus, both vertebrate and macroinvertebrate, compensates for the destructive aspects of hiatuses (e.g., retarded permanent burial, repeated small-scale burial-exhumation cycles, possible elevated attack from other taphonomic agents during bioclast residence at or near the sediment-water interface).

Taphonomically comparable hiatal skeletal concentrations are less common in the terrestrial record, and this is not entirely unexpected, given the generally dispersed nature of vertebrate populations and the harsh conditions that can accompany bone exposure on the land surface and pedogenesis during early burial (Behrensmeyer, 1978; Behrensmeyer and Chapman, 1993). These conditions include trampling, scavenging, weathering (UV exposure, oxidation, fungal and microbial attack, freeze-thaw), destructive soil processes (e.g., organic leaching of bases, wet/dry alteration of oxidation states), and exhumation-burial cycles (e.g., via bedform migration within channels).

Despite these negative factors in the accumulation process, some excellent examples of passive, hiatal concentrations of vertebrate hardparts are known from terrestrial systems. Paleosols are one plausible setting for an "attritional" accumulation. Soil formation takes time, and the duration of the hiatus is the key to accumulation: long-term landscape stability provides the opportunity for vertebrate skeletal debris to gradually accumulate in significant abundance, even from low-density living populations. If skeletal input from the local community exceeds the rate of recycling, bones and teeth may build up to concentrated levels. That said, actualistic data derived from land surface assemblages in the Amboseli Basin of Kenya indicate that even after 10,000 years of attritional input, bone densities

would likely still be less than one bone per square meter (Behrensmeyer, 1982).

In a taphonomic study of the Eocene Willwood Formation of Wyoming, Bown and Kraus (1981) identified a specific type of paleosol that was apparently quite conducive to the concentration of vertebrate bioclasts. These authors described numerous concentrations of vertebrate fossils in bluish to greenish gray tabular mudstones that overlie variegated red, purple, and orange mudstones. This repetitive couplet was interpreted as A and B horizons, respectively, of podzolic spodosols (aquods: saturated soils). In the formative scenario, vertebrate elements "accumulated gradually as litter" on alluvial soil surfaces and became incorporated into A horizons presumably through incremental sedimentation and bioturbation. Bown and Kraus (1981) noted a preponderance of teeth and jaws in the Willwood paleosol accumulations, along with an abundance of small and compact postcranial elements such as vertebral centra, carpal and tarsal bones, phalanges, calcanea, and astragali. These relatively durable skeletal elements would presumably be most resistant to physical and chemical degradation at the ground surface and in soil matrices.

Floodbasin ponds and lakes provide another locale for the attritional accumulation of vertebrate bioclasts. Aquatic ecosystems typically support diverse communities of vertebrate animals, including abundant fish, crocodilians, and amphibians. They also tend to attract terrestrial animals to their shores and shallows for purposes of feeding, drinking, and wallowing. Over time, many generations of aquatic, semiaquatic , and terrestrial animals may perish in and around ponds and lakes for a plethora of reasons (senescence, disease, predation), and their skeletal hardparts may in turn contribute to cumulative death assemblages. Whether skeletal elements accrue to concentrated levels would depend on numerous factors, including the density and fecundity of vertebrate populations, and the intensity of biological recycling. The chemical nature of lake and pore waters would also play a role, with high pH and low Eh conditions being most conducive to long-term preservation. A final consideration is the rate at which sediment infills the aquatic basin. Under ideal circumstances for fossilization, sedimentary dilution is minimal (primarily organic), and the aquatic basin persists long enough for skeletal debris to accumulate to appreciable levels.

Rogers (1995) identified 21 microfossil bonebeds that presumably accumulated via such attritional processes within shallow lacustrine basins in the Upper Cretaceous Judith River and Two Medicine Formations of Montana. These subaqueous microfossil bonebeds are characterized by

high-diversity assemblages of predominantly small fossils (<5 cm in maximum dimension) representing both aquatic (fish, amphibians, crocodilians, mollusks) and terrestrial (dinosaurs, mammals) animals (e.g., Sahni, 1972; Rogers, 1995). Beds that yield these vertebrate microfossil assemblages are generally tabular, organic rich, and laterally extensive, and skeletal debris can often be traced for tens to hundreds of meters along available exposures. Skeletal hardparts are abundant but typically disseminated throughout these bone-rich horizons (as opposed to densely concentrated in pockets or along bed contacts), and are also thoroughly disarticulated and dissociated, so that it is virtually impossible to conclude confidently that any two skeletal elements are from the same individual. Elements resistant to physical and chemical degradation, such as teeth, scales, scutes, and small dense bones such as vertebral centra and phalanges predominate. Most skeletal elements show only minimal effects of weathering, although the occasional bone does show advanced stages of surface degradation. Rare bones show surface pitting and etching suggestive of chemical dissolution. Ganoid scales and teeth devoid of ganoine and enamel, respectively, are occasionally recovered. This final condition is consistent with processing in crocodilian digestive tracts (Fisher, 1981).

From a taphonomic perspective, attritional accumulations of vertebrate skeletal hardparts, regardless of their sedimentary context, should be time averaged to a greater or lesser degree, depending on the duration of the hiatus, but should date to the period of the hiatus itself (i.e., be a true hiatal concentration, sensu Kidwell [1991], rather than including lag material reworked from older deposits). Local pockets of fossils might preserve census assemblages (e.g., mass mortalities from drowning or other ecologically brief mortality events within a lake), but in general the material should be time averaged. The longer the hiatus, the greater the opportunity for amassing ecologically heterogeneous assemblages (i.e., mixing of noncontemporaneous communities or community states, rather than simply mixing of generations from single communities). The assemblage is more or less autochthonous, with the accumulating bioclasts derived from attritional mortality in the local vertebrate community. The preservational quality of bones and teeth in the assemblage would likely be variable, as elements are added over time. The degree of articulation and element association will generally be low. Associated sediments may show evidence of the hiatus beyond the presence of concentrated vertebrate bioclasts. For example, in the marine realm attritional accumulations are sometimes associated with firmgrounds or hardgrounds and authigenic mineralization. In terrestrial settings, a prolonged hiatus might be marked by an anomalously mature paleosol profile.

Erosion (negative net sedimentation) can preferentially remove siliciclastic sedimentary matrix and leave behind a true lag of larger and/or denser skeletal material exhumed from previous deposits. This erosion-based scenario can occur anywhere that energy impinges upon sediment or lithified strata with a preexisting vertebrate component. Likely locales for the formation of vertebrate lag concentrations include channels (especially cutbanks) within fluvial systems and a variety of high-energy shallow marine settings, especially shorelines and various intertidal and subtidal channels (Wells, 1944; Behrensmeyer, 1982, 1988; Reif, 1982; Smith and Kitching, 1997; Rogers and Kidwell, 2000). Theoretically, the more deeply that erosion cuts into older sediment or strata, the greater the volume of previously deposited vertebrate material that can be intersected and concentrated into lag form. However, in this formative scenario, any cohort of skeletal material would probably undergo a larger number of reworking events than it would during purely aggradational conditions. Thus, erosion itself represents an additional agent of skeletal breakdown and potential transport out of the local system, and exhumation may have little net positive effect on hardpart supply. On the other hand, if the exhumed material is particularly resilient (e.g., teeth), or is in a prefossilized state (permineralized, see below, and see Smith and Kitching [1997]), then it may endure the rigors of erosion and accumulate in lag form.

In a test of the association between vertebrate skeletal concentrations and erosional surfaces in the Upper Cretaceous Two Medicine and Judith River Formations of Montana, Rogers and Kidwell (2000) found no clear correlation between the abundance of vertebrate skeletal material and the inferred duration of the associated hiatus. The most significant erosional discontinuity in the section (the 80 Ma sequence boundary in the Two Medicine Formation) was virtually barren with regard to vertebrate skeletal debris, whereas erosion surfaces of lesser extent and duration, ranging from marine flooding surfaces to scours within individual fluvial channels, were frequently mantled by diverse skeletal concentrations. Also, the distribution of vertebrate lag concentrations closely tracked the abundance of vertebrate material in underlying and laterally disposed facies, providing evidence that skeletal material was supplied primarily through local erosional reworking with little subsequent lateral dispersion. For example, a prominent flooding surface in the marine portion of the Montana study interval truncates several meters of underlying shoreface strata along its most fossiliferous segment, and the shark teeth, fish and marine reptile bones, and scattered chert pebbles that mantle the surface can also be found, albeit in less concentrated form, in underlying beds. Additional evidence for exhumation consists of reworked steinkerns of

burrows, which are found in abundance on the aforementioned ravinement surface and are of the shoreface ichnogenera commonly found in underlying beds. The taphonomy of the skeletal debris concentrated on the marine ravinement surface is also consistent with physical reworking, in that the majority of the vertebrate elements exhibit evidence of breakage and abrasion. Analogous examples are concentrations of fish plates along burrowed flooding surfaces within the Ordovician Harding Sandstone (Allulee and Holland, 2005), and concentrations of turtle scutes, plant material, and fragments of allochthonous iguanodon, pterosaurs, and snakes in small intertidal channels associated with transgression (Neraudeau et al., 2003).

Rogers and Kidwell (2000) also provided evidence for the exhumation and concentration of vertebrate skeletal debris in the nonmarine portion of their study interval, where the recurrent skeletal lags that mantle fluvial erosion surfaces closely track the abundance of skeletal debris in surrounding floodplain facies. In fact, compelling evidence suggests that most, if not all, channel-hosted vertebrate skeletal lags (microfossil bonebeds) include material reworked from preexisting floodplain concentrations, specifically the lacustrine microfossil bonebeds of attritional origin described above. The reworked channel-lag assemblages contain the same array of taxa and the same assortment of elements as the lacustrine assemblages—teeth, vertebrae, phalanges, scutes, and scales—but some elements are polished. Polish is an enigmatic bone-modification feature (Morlan, 1984; Behrensmeyer et al., 1989), and its origin is less than clear. It can presumably be imparted to permineralized ("prefossilized") material upon exhumation and physical abrasion, and an initial period of burial and diagenesis would seem to enhance the likelihood that abrasion will result in polishing rather than rounding alone. The presence of polished bones in the vertebrate concentrations that drape fluvial scours suggests that at least a portion of the skeletal fraction was reworked in a prefossilized condition.

Erosion-generated vertebrate skeletal concentrations should be time averaged to a variable degree, depending on the depth of incision and the age profile of bioclasts preserved in underlying and laterally disposed strata (see Manning [1990] for an extreme example of erosion-related time averaging). In a purely exhumational scenario, the resultant lag concentration will be entirely older than the hiatal episode that formed the surface. However, skeletal debris can be added to the assemblage both during and after planation or incision. The more severe the downcutting, the greater the potential age differential between material in the lag and the hiatus that concentrated it, and the lower the relevance of its taxonomic

composition to paleoenvironmental conditions during the hiatus. Data presented in Rogers and Kidwell (2000) suggest that residual lag concentrations of vertebrate skeletal debris should tend to be autochthonous to parautochthonous in a spatial sense, due to the apparent strong dependence of lag development on preexisting local sources of skeletal material. However, this does not imply autochthony or parautochthony in any ecological sense, because bioclasts can be preserved in a completely different sedimentary context than their in-life habitat.

Taphonomic artifacts of exhumation might include abrasion and rounding (although this modification feature is not necessarily diagnostic), polish (Rogers and Kidwell, 2000), angular as opposed to spiral breakage patterns (Morlan 1984), variable diagenetic signatures (Trueman and Benton, 1997; Trueman, Chapter 7 in this volume), and environmentally mixed assemblages. Sedimentological features consistent with exhumation include stratigraphic evidence of incision and exotic sedimentary matrices embedded within or adhering to exhumed skeletal debris. Care must be exercised with regard to this final potential indicator, however, because fine clays and silt particles moving within a fluvial system may infiltrate bones as draft fills, and contrast markedly with the coarser-grained fraction represented in the bedload.

Obrution: Ecology and Sedimentology Combined

The third end-member in the sedimentological bonebed spectrum is the obrution assemblage (sensu Seilacher et al., 1985; Brett, 1990; Bruton, 2001), which in our model is a concentration of vertebrate hardparts that initially formed as a carcass assemblage in response to, and permanently buried by, a single and generally unusual circumstance of sediment deposition. The scenario that most readily comes to mind is that of gregarious animals engulfed by a catastrophic sedimentation event, such as an ash fall, slip-face avalanche, or slump/bank collapse. In this category of bone concentration, the stage is certainly set by group activity (e.g., communal habitation, herding, predator-prey interaction), but geology effectively sets taphonomy in motion by triggering the event of concentrated mortality and permanently burying the result. The obrution scenario is thus a special category of concentration that hinges upon both ecology and sedimentary geology.

Fossorial animals should be particularly susceptible to this mode of mortality because their burrows would serve as sediment sinks, and their aestivation chambers could potentially become permanent tombs if the surface were blanketed by an anomalously thick bed of sediment.

However, there are relatively few reports of mortality horizons comprised of clustered aestivation chambers (e.g., Olson, 1939; Carlson, 1968; Olson and Bolles, 1975; Wood, 1988), and even fewer documented examples of multiple individuals entombed in subterranean dwelling chambers (Voorhies, 1975; Hunt et al., 1983; Abdala et al., 2006). A notable exception was provided by Smith (1993), who described pairs of articulated therapsid skeletons preserved in burrow casts in the Upper Permian Beaufort Group of the Karoo Basin in South Africa. Smith postulated that rare occurrences of intertwined skeletons of the genus *Diictidon* were buried alive when crevasse-splay sands plugged their burrows. Potts (1989) and Potts and others (1999) described a similar occurrence in Pleistocene deposits of the Olorgelailie Formation of Kenya, where four intact hyena skeletons were discovered in an ancient burrow system in association with the scattered bones of other animals.

Catastrophic sedimentation can entomb assemblages of gregarious but nonburrowing animals. One dramatic example is the abundant articulated skeletons of theropod, ankylosaurian, and protoceratopsian dinosaurs, lizards, and mammals entombed within structureless beds of sandstone at the Upper Cretaceous Ukhaa Tolgod locality of the Gobi Desert, Mongolia (Dashzeveg et al., 1995). In a recent analysis of this spectacular locality, Loope et al. (1998, 1999) implicated lethal sandslides triggered by heavy rainfall as the depositional events that both captured and entombed the Late Cretaceous biota in a sand dune landscape. Another classic example of vertebrate mass mortality linked to catastrophic sedimentation is the Poison Ivy Quarry of Nebraska (Voorhies, 1985, 1992). Here, many tens of individuals of the gregarious rhinoceros *Teleoceras* are buried alongside horses, camels, and other animals mostly in articulated and three-dimensional condition, owing apparently to a catastrophic volcanic eruption that blanketed the Miocene landscape with a thick ash. This pyroclastic event apparently killed and buried many or all of the smaller animals almost immediately, while larger animals such as *Teleoceras* died shortly after the onset of the event due to related complications. All specimens in the Poison Ivy Quarry are entombed within either primary or reworked volcanic ash that was blown into a local hollow very shortly after death.

Concentrations of vertebrate skeletal debris that enter the fossil record in response to unusual sedimentation events should show minimal evidence of time averaging, because all individuals in the assemblage presumably perished and were buried simultaneously (e.g., Finch et al., 1972; but see Voorhies, 1985, 1992, for a slight variation on this theme). Under most circumstances the assemblage should also be authochthonous,

although some depositional events may transport carcasses a short distance prior to final burial. The preservational quality of specimens should be excellent (e.g., Chiappe et al., 1998; Grellet-Tinner, 2005) unless entombed materials are degraded diagenetically. The degree of articulation and element association should generally be high. The animals represented arguably should be prone to gregarious behavior or at least be likely to interact (e.g., predator-prey associations). Finally, the vertebrate assemblage should be within or immediately beneath a thick or otherwise anomalous sedimentation unit, such as an ash bed or debris flow deposit. Whether this event bed is readily discernible would of course depend on the nature of surrounding sediments, and the extent of postdepositional modification (e.g., bioturbation and pedogenesis).

CAVEATS AND COMPLICATIONS

The general mechanisms of bone concentration presented here are based on conceptual arguments and empirical observations, and the formative scenarios conform to expected and observed physical and biological parameters—they are intended to be intuitively reasonable. More importantly, every category of biogenic and physical concentration distinguished in our genetic framework can be linked to modern or fossil record-based examples (Table 1.1). Arguably, our conceptual framework of skeletal concentration will accommodate many, if not most, of the carcass/bone concentrations found on modern landscapes (or under the sea) and in the fossil record.

However, we recognize that relative concentrations of vertebrate skeletal debris can develop under circumstances that might not readily relate to our scheme. For example, complex circumstances that simultaneously superpose two or more formative scenarios could arise, such as bone collectors (e.g., packrats, hyenas) trapped and entombed within their bone-laden lair by an event of obrution (e.g., Potts, 1989; Potts et al., 1999). Events can also transpire after initial concentration that obfuscate or compound the original signal. Figure 1.6 outlines a selection of hypothetical pathways that could follow after an intrinsic biogenic concentration is generated. One outcome (path A) leads to permanent burial. In this "simple case" scenario, the sample can be somewhat degraded by taphonomic processes prior to final burial, but the mortality and accumulation signal remain relatively uncomplicated. A compound concentration (path B) might develop if the mass mortality event transpires under conditions of sediment starvation, and the resulting bone assemblage

Table 1.1. Modern and ancient examples of group/focused mortality and bone concentrating scenarios.

Group/Focused Mortality	Modern Example	Potential Ancient Example
Reproduction related	Bergerund, 1971; Burton, 1985; Anderson, 1990; Maxwell, 1995	Jordan, 1920; Horner, 1982, 1994; Böttcher, 1990; Baroni and Orombelli, 1994; Wilson, 1996; Chiappe et al., 1998
Stranding	Wilkinson and Worthy, 1999; Kellogg and Whitmore, 1957; Geraci et al., 1999	Camp, 1980; Hogler, 1992
Miring	Chamberlin, 1971; Berger, 1983; Mellink and Martin, 2001	Coope and Lister, 1987; Haynes, 1991; Sander, 1992; Hungerbühler, 1998; Spencer et al., 2003
Flooding/drowning	Whitfield and Patterson, 1995; Johanson, 1998; Varricchio et al., 2005	Kormos, 1911; Parrish, 1978; Hunt et al., 1983; Turnbull and Martill, 1988; Wood et al., 1988; Kahlke and Gaudzinski, 2005
Wildfire	Lawrence, 1966; Nelson, 1973, p. 139; Singer et al., 1989	Sander, 1987; Falcon-Lang, 1998; Zeigler, 2002; Zeigler et al., 2005
Extreme or unusual weather (rapid thaws, rapid cooling, severe storms)	Geraci et al., 1999; Berger, 1983; Borrero, 1990; Oliver and Graham, 1994; Jehl, 1996; Sergeant and Williams, 1983; Siegstad and Heide-Jørgensen, 1994	Voorhies, 1969; Waldman, 1971; Parrish, 1978; Ferber and Wells, 1995
Drought	Tulloch, 1970, Corfield, 1973; Tramer, 1977; Coe, 1978; Conybeare and Haynes, 1984; Haynes, 1988; Dudley et al., 2001; Mellink and Martin, 2001	Matthew, 1924; Huene, 1928; Brown, 1935; Case, 1935; Dalquest and Mamay, 1963; Saunders, 1977; Hulbert, 1982; Rogers, 1990, 2005; Schwartz and Gillette, 1994, Fiorillo et al., 2000
Sickness, disease, poisoning	Gunter et al., 1948; Grindley and Taylor, 1962; Brongersma-Sanders et al., 1980; Nyman, 1986; Pybus et al., 1986; Wurtsbaugh and Tapia, 1988; Worthylake and Hovingh, 1989; Thompson and Hall, 1993; Leonardos and Sinis, 1997; Berger et al., 1998	Martill, 1988; Bell et al., 1989; Leckie et al., 1992; Henrici and Fiorillo, 1993; Emslie and Morgan, 1994; Varricchio, 1995; Emslie et al., 1996; Smith, 2000; Braun and Pfeiffer, 2002

|		
Volcanism related	Brongersma-Sanders, 1957; Taber et al., 1982; Kling et al., 1987; Cotel, 1999	Anderson, 1933; Voorhies, 1985, 1992; Rolf et al., 1990; Anderson et al., 1995; Brand et al., 2000; Rogers et al., 2001
Predation	Mellett, 1974; Andrews and Nesbit Evans, 1983; Haynes, 1988; Hoffman, 1988; Schmitt and Juell, 1994; Terry, 2004; Laudet and Selva, 2005	Mayhew, 1977; Grande, 1980; Maas, 1985; Wilson, 1987; Pratt, 1989; Murphey, 1996; Davis and Martill, 1999; Northwood, 2005; Nesbitt et al., 2006
Bone/Carcass Concentration Scenario		
Biogenic carcass or bone collection	Yeager, 1943; Vander Wall, 1990; Kruuk, 1972; Brain, 1980, 1981; Shipman, 1981; Potts, 1986; Skinner et al., 1986; Horwitz and Smith, 1988; Skinner and van Aarde, 1991; Kerbis-Peterhans and Horwitz, 1992	Hunt, 1990; Haynes, 1991; Sundell, 1999; Palmqvist and Arribas, 2001
Fluvial hydraulics	Aslan and Behrensmeyer, 1986; Varricchio et al., 2005	Voorhies, 1969; Lawton, 1977; Fiorillo, 1991; Eberth and Ryan, 1992; Bandyopadhyay et al., 2002
Strandline hydraulics	Weigelt, 1927, 1989; Leggitt and Buchheim, 1997	Weigelt, 1927, 1989; Leggitt and Buchheim, 1997; Rogers et al., 2001; Zonneveld et al., 2001
Hiatus/sediment starvation	Behrensmeyer, 1982, Copenhagen, 1953	Conkin et al., 1976; Bown and Kraus, 1981; Rogers, 1995; Schröder-Adams et al., 2001
Erosion/reworking	Popova, 2004; deflation lags in fossiliferous terrain	Manning, 1990; Smith and Kitching, 1997; Rogers and Kidwell, 2000; Walsh and Martill, 2006
Ecology plus obrution	Hayward et al., 1982	Finch et al., 1972; Voorhies, 1985, 1992; Potts, 1989; Smith, 1993; Chiappe et al., 1998; Loope et al., 1998, 1999; Potts et al., 1999; Grellet-Tinner, 2005
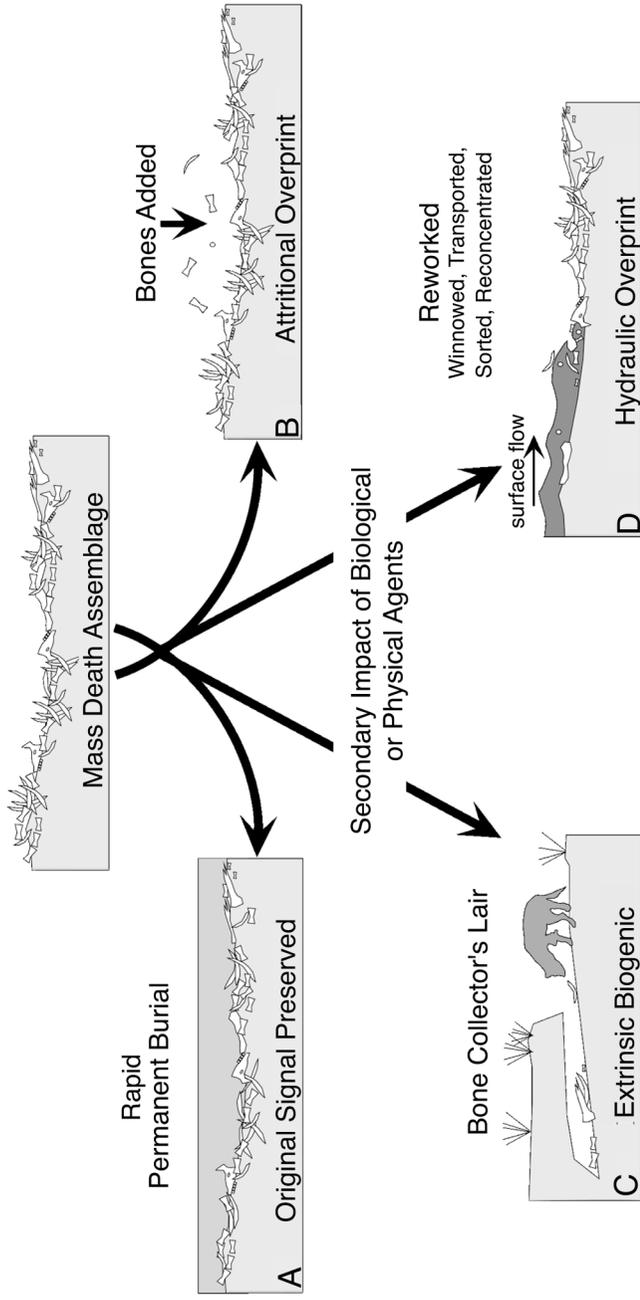
Figure 1.6. Hypothetical pathways that could be followed after a mass-death assemblage is generated. One potential outcome (path A) leads to permanent burial of the unaltered assemblage. A compound concentration (path B) might develop if the mass mortality event transpires under conditions of sediment starvation, and the resulting bone assemblage receives an attritional overprint. A preexisting concentration can also be reworked, transported, sorted, and ultimately reconcentrated by either biological (path C) or physical (path D) agents.

receives an attritional overprint. A preexisting concentration can also be reworked, transported, sorted, and ultimately reconcentrated by either biological (path C) or physical (path D) agents. If a relative concentration of vertebrate skeletal debris exhibits a taphonomic signature that does not readily correspond to one of our major formative categories, it should be viewed as a clear warning to consider a suite of more complex formative scenarios.

Finally, we appreciate the fact that a bonebed, at its most basic expression (remains of two individuals in close association), can form by pure happenstance. Two carcasses can certainly come to rest in close proximity for entirely unrelated, unpredictable, and perhaps ultimately undecipherable reasons. However, it is probably unlikely that this type of chance occurrence is common either in modern settings or in the vertebrate fossil record. The framework for vertebrate skeletal concentration developed here is intended to address a straightforward suite of formative scenarios more pertinent to the central theme of skeletal accumulation. Our scenarios should be viewed as general and recurrent mechanisms or agents of vertebrate hardpart concentration (bonebed generators), and we provide criteria that facilitate their recognition.

SUMMARY AND CONCLUSION

Bonebeds are remarkable features of the vertebrate fossil record. They can embody ancient environmental catastrophes and, thus, reveal some of the most dramatic aspects of past ecosystems. They can also serve as less sensational but equally informative gauges of sedimentary dynamics and biological recycling. Regardless of their particular mode(s) of origin, bonebeds, in their many forms, provide exceptional opportunities to investigate a variety of paleobiological and geological questions.

Here we have proposed a system for the categorization and analysis of bonebeds analogous to the genetic classification scheme proposed by Kidwell et al. (1986) for marine macrobenthic concentrations. Like shell bed counterparts, most vertebrate skeletal concentrations can be readily classed as either biogenic or physical (hydraulic/sedimentologic) in terms of the primary driving process(es), although mixed taphonomic histories are certainly possible (Figs. 1.1 and 1.6).

Two types of biogenic concentrations are recognized in our conceptual treatment. (1) *Intrinsic biogenic concentrations* are the product of the activity or

behavior of the hardpart-producing organism(s) itself and are predictable by products of the vertebrate life cycle. In some instances intrinsic biogenic concentrations reflect behaviors that are forced by environmental conditions, such as unusual hazards or perturbations that result in concentrated death assemblages. (2) *Extrinsic biogenic concentrations* are produced by extraneous biological agents, most notably predators.

Two modes of physical concentration are distinguished in our genetic consideration of bonebeds. (1) *Hydraulic concentrations* of carcasses, parts of carcasses, or disarticulated bones and/or teeth form by the action of surface flows (wind, water, sediment) or wave activity. Transport of bioclastic material to the eventual point of concentration is an integral part of this formative scenario. Two primary settings are fluvial channels (including estuarine channels) and strandlines. Numerous factors determine whether relative accumulations of vertebrate hardparts develop in these settings, including the energy and persistence of the hydraulic agent, the amount of bioclastic material delivered to the system, and the presence of trapping mechanisms (e.g., log jams). Notably, many, if not most, multi-individual concentrations that are preserved in ancient fluvial channels or along ancient shorelines were apparently derived from preexisting concentrated sources.

(2) *Sedimentologic concentrations* are the second major category of physical concentration and are the consequences of largely hydraulically controlled variation in rates of inorganic matrix accumulation, that is concentration of bioclasts via conditions of sediment omission (starvation, bypassing), erosion, or sudden intense deposition. An attritional assemblage of vertebrate hardparts initially forms during an episode of sediment starvation or otherwise zero net sediment accumulation (e.g., bypassing), with conditions of low sedimentary dilution fostering relative concentrations of vertebrate material by passive means. Lag concentrations form when erosion (negative sedimentation) preferentially removes sedimentary matrix, leaving behind a true hydraulic (transport-resistant) lag of larger and/or denser skeletal material exhumed from previous deposits. Finally, an obrution concentration forms in response to, and is permanently buried by, a single, generally unusual circumstance of sediment deposition, such as an ash fall, a slip-face avalanche, or a bank collapse acting upon an ecologically aggregated group of individuals. The obrution category is a composite mode of concentration that hinges upon both ecology (the living animals concentrated themselves) and sedimentary geology (the obrution event triggers mortality and ultimately captures the concentration).

The conceptual framework for vertebrate skeletal concentration developed here is intended to facilitate the classification and study of a wide

variety of bonebeds. Our categories are intentionally broad in scope, with the hope that they will be applicable under most biostratinomic circumstances. Generalizations that pertain to genesis and expected taphonomic signatures (damage states) and bias levels (degrees of time averaging, fidelity to life habitat) are based on natural history studies, actualistic studies, and stratigraphic investigations, and here much work remains to be done—we certainly do not suggest that our community's understanding is now complete. Our goal is to organize the current understanding of bonebeds and to stimulate a broader conception of their origins and significance from a paleobiological perspective. Ideally, the proposed system of categorization and analysis will serve as a workable template for the study of both modern and ancient bonebeds and will thereby promote a better understanding of the spectacular skeletal concentrations that punctuate the long and diverse history of the vertebrates.

REFERENCES

Abbott, S.T. 1998. Transgressive systems tracts and onlap shellbeds from mid-Pleistocene sequences, Wanganui Basin, New Zealand. Journal of Sedimentary Research 68:253–268.

Abdala, F., J.C. Cisneros, and R.M.H. Smith. 2006. Faunal aggregation in the Early Triassic Karoo Basin: Earliest evidence of shelter-sharing behavior among tetrapods? Palaios 21:507–512.

Adrain, J.M., and M.V.H. Wilson. 1994. Early Devonian cephalaspids (Vertebrata: Cornuata) from the southern Mackenzie Mountains, N.W.T., Canada. Journal of Vertebrate Paleontology 14:301–319.

Allulee, J.L., and S.M. Holland. 2005. The sequence stratigraphic and environmental context of primitive vertebrates: Harding Sandstone, Upper Ordovician, Colorado, USA. Palaios 20:518–533.

Anderson, D.J. 1990. Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis. American Naturalist 135:334–350.

Anderson, D.J. 1995. The role of parents in sibilicidal brood reduction of two booby species. The Auk 112:860–869.

Anderson, D.K., J. Damuth, and T.M. Bown. 1995. Rapid morphological change in Miocene marsupials and rodents associated with a volcanic catastrophe in Argentina. Journal of Vertebrate Paleontology 15:640–649.

Anderson, R.V.V. 1933. The diatomaceous and fish-bearing Beida Stage of Algeria. Journal of Geology 41:673–698.

Andrews, P. 1990. Owls, caves, and fossils. University of Chicago Press, Chicago.

Andrews, P., and E. M. Nesbit Evans. 1983. Small mammal bone accumulations produced by mammalian carnivores. Paleobiology 9:289–307.

Antia, D.D.J. 1979. Bone-beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering, and microbiotas. Mercian Geologist 7:93–174.

Argast, S., J.O. Farlow, R.M. Gabet, and D.L. Brinkman. 1987. Transport-induced abrasion of fossil reptilian teeth: Implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. Geology 15:927–930.

Aslan, A., and A.K. Behrensmeyer. 1996. Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: The East Fork River, Wyoming. Palaios 11:411–421.

Badgley, C. 1986. Taphonomy of mammalian remains from Siwalik rocks of Pakistan. Paleobiology 12:119–142.

Badgley, C., W.S. Bartels, M.E. Morgan, A.K. Behrensmeyer, and S.M. Raza. 1995. Taphonomy of vertebrate assemblages from the Paleogene of northwestern Wyoming and the Neogene of northern Pakistan. Palaeogeography, Palaeoclimatology, Palaeoecology 115:157–180.

Badgley, C., W. Downs, and L.J. Flynn. 1998. Taphonomy of small-mammal fossil assemblages from the Middle Miocene Chinji Formation, Siwalik Group, Pakistan. Pp. 125–166 in Advances in vertebrate paleontology and geochronology. Y. Tomida, L.J. Flynn, and L.L. Jacobs, eds. National Science Museum Monographs, Tokyo.

Baker, J., and D. Brothwell. 1980. Animal diseases in archaeology. Academic Press, London.

Bandyopadhyay, S., T.K. RoyChowdhury, and D.P. Sengupta. 2002. Taphonomy of some Gondwana vertebrate assemblages of India. Sedimentary Geology 147: 219–245.

Banish, L.D., and W.G. Gilmartin. 1992. Pathological findings in the Hawaiian monk seal. Journal of Wildlife Diseases 28:428–434.

Barnes, L.G. 1977. Outline of eastern North Pacific fossil cetacean assemblages. Systematic Zoology 25:321–343.

Barnosky, A.D. 1985. Taphonomy and herd structure of the extinct Irish elk, *Megaloceras giganteus*. Science 228:340–344.

Baroni, C., and G. Orombelli. 1994. Abandoned penguin rookeries as Holocene paleoclimatic indicators in Antarctica. Geology 22:23–26.

Bartels, W.S., T.M. Bown, C. Badgley, A.K. Behrensmeyer, M. Morgan, and S.M. Raza. 1992. Taphonomy of Paleogene and Neogene vertebrate assemblages. Fifth North American Paleontological Convention, Abstracts and Program 6:19.

Behre, C.H. Jr., and J.H. Johnson. 1933. Ordovician and Devonian fish horizons in Colorado. American Journal of Science 25:477–486.

Behrensmeyer, A.K. 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolph, Kenya. Bulletin of the Museum of Comparative Zoology 146:473–578.

Behrensmeyer, A.K. 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4:150–162.

Behrensmeyer, A.K. 1982. Time resolution in fluvial vertebrate assemblages. Paleobiology 8:211–227.

Behrensmeyer, A.K. 1987. Miocene fluvial facies and vertebrate taphonomy in northern Pakistan. Pp. 169–176 in Recent developments in fluvial sedimentology. Special publication 39. F.G. Ethridge, R.M. Flores, and M.D. Harvey, eds. Society of Economic Paleontology and Mineralogy.

Behrensmeyer, A.K. 1988. Vertebrate preservation in fluvial channels. Palaeogeography, Palaeoclimatology, Palaeoecology 63:183–199.

Behrensmeyer, A.K. 1991. Terrestrial vertebrate accumulations. Pp. 291–335 *in* Taphonomy: Releasing the data locked in the fossil record. P.A. Allison and D.E.G. Briggs, eds. Plenum Press, New York.

Behrensmeyer, A.K. This volume. Bonebeds through time. Chapter 2 *in* Bonebeds: Genesis, analysis, and paleobiological significance. R.R. Rogers, D.A. Eberth, and A.R. Fiorillo, eds. University of Chicago Press, Chicago.

Behrensmeyer, A.K., and R.E. Chapman. 1993. Models and simulations of time-averaging in terrestrial vertebrate accumulations. Pp. 125–149 *in* Taphonomic approaches to time resolution in fossil assemblages. Paleontological Society short courses in paleontology no. 6. S.M. Kidwell and A.K. Behrensmeyer, eds. University of Tennessee, Knoxville.

Behrensmeyer, A.K., and A.P. Hill. 1980. Fossils in the making: Vertebrate taphonomy and paleoecology. University of Chicago Press, Chicago.

Behrensmeyer, A.K., K.D. Gordon, and G.T. Yanagi. 1989. Non-human bone modification in Miocene fossils from Pakistan. Pp. 99–120 *in* Bone modification. Proceedings of the first international conference on bone modification. R. Bonnichsen and M. Sorg, eds. Center for the Study of the First Americans, Orono, Maine.

Behrensmeyer, A.K., R.S. Hook, C.E. Badgley, J.A. Boy, R.E. Chapman, P. Dodson, R.A. Gastaldo, R.W. Graham, L.D. Martin, P.E. Olsen, R.A. Spicer, R.E. Taggart, and M.V.H. Wilson. 1992. Paleoenvironmental contexts and taphonomic modes. Pp. 15–136 *in* Terrestrial ecosystems through time: The evolutionary paleoecology of terrestrial plants and animals. A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichelle, R. Potts, H.-D. Sues, and S.L. Wing, eds. University of Chicago Press, Chicago.

Behrensmeyer, A.K., S.M. Kidwell, and R.A. Gastaldo. 2000. Taphonomy and paleobiology. Paleobiology 26:103–144.

Bell, M.A., C.E. Wells, and J.A. Marshall. 1989. Mass mortality of layers of fossil stickleback fish: Catastrophic kills of polymorphic schools. Evolution 43:607–619.

Benton, M.J., E. Cook, D. Grigorescu, E. Popa, and E. Tallódi. 1997. Dinosaurs and other tetrapods in an Early Cretaceous bauxite-filled fissure, northwestern Romania. Palaeogeography, Palaeoclimatology, Palaeoecology 130:275–292.

Berger, J. 1983. Ecology and catastrophic mortality in wild horses: Implications for interpreting fossil assemblages. Science 220:1403–1404.

Berger, L., R. Speare, P. Daszak, D.E. Green, A.A. Cunningham, C.L. Goggin, R. Slocombe, M.A. Ragan, A.D. Hyatt, K.R. McDonald, H.B. Hines, K.R. Lips, G. Marantelli, and H. Parkes. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. Proceedings of the National Academy of Sciences 95:9031–9036.

Berger, J., S. Dulamtseren, S. Cain, D. Enkkhbileg, P. Lichtman, Z. Namshir, G. Wingard, and R. Reading. 2001. Back-casting sociality in extinct species: New perspectives using mass death assemblages and sex ratios. Proceedings of the Royal Society of London B 268:131–139.

Bergerund, A.T. 1971. The population dynamics of Newfoundland caribou. Wildlife Monographs 25. Wildlife Society, Louisville, Kentucky.

Betancourt, J. L., T. R. V. Devender, and P. S. Martin. 1990. Packrat middens: The last 40,000 years of biotic change. University of Arizona Press, Tucson.

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.

Bodkin, J.L., G.R. VanBlaricom, and R.J. Jameson. 1987. Mortalities of kelp-forest fishes associated with large oceanic waves off central California, 1982–1983. Environmental Biology of Fishes 18:73–76.

Borrero, L.A. 1990. Taphonomy of guanaco bones in Tierra del Fuego. Quaternary Research 34:361–371.

Borsuk-Bialynicka, M. 1969. Lower Pliocene rhinocerotids from Altan Teli, western Mongolia. Palaeontologia Polonica 21:73–92

Böttcher, R. 1990. Neue Erkenntnisse über die Fortpflanzungsbiologie der Ichthyosaurier (Reptilia). Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 164:1–51.

Bown, T. M., and M.J. Kraus. 1981. Vertebrate fossil-bearing paleosol units (Willwood Formation, Lower Eocene, Northwest Wyoming, U.S.A.): Implications for taphonomy, biostratigraphy, and assemblage analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 34:31–56.

Brabyn, M.W., and I.G. McLean. 1992. Oceanography and coastal topography of herd-stranding sites for whales in New Zealand. Journal of Mammalogy 73:469–476.

Brady, M., R. Rogers, and B. Sheets. 2005. An experimental and field-based approach to microvertebrate bonebed taphonomy in the Judith River Formation of north-central Montana. Geological Society of America, North-Central Section, Abstracts with Programs 37(5):24.

Brain, C.K. 1980. Some criteria for the recognition of bone-collecting agencies in African caves. Pp. 107–130 in Fossils in the making. A.K. Behrensmeyer and A. Hill, eds. University of Chicago Press, Chicago.

Brain, C.K. 1981. The Hunters or the Hunted? An introduction to African cave taphonomy. University of Chicago Press, Chicago.

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

Brand, L.R., R. Esperante, A.V. Chadwick, O.P. Porras, and M. Alomia,2004. Fossil whale preservation implies high diatom accumulation rate in the Miocene-Pliocene Pisco Formation of Peru. Geology 32:165–168.

Braun, A., and T. Pfeiffer. 2002. Cyanobacterial blooms as the cause of a Pleistocene large mammal assemblage. Paleobiology 28:139–154.

Breithaupt, B.H., and D. Duvall. 1986. The oldest record of serpent aggregation. Lethaia 19:181–185.

Brett, C.E. 1990. Obrution deposits. Pp. 239–243 in Paleobiology: A synthesis. D.E.G. Briggs and P.R. Crowther, eds. Blackwell Scientific Publications, London.

Brett, C.E. 1995. Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. Palaios 10:597–616.

Brett, C.E., and G.C. Baird. 1993. Taphonomic approaches to temporal resolution in stratigraphy: Examples from Paleozoic marine mudrocks. Pp. 250–274 in Taphonomic approaches to time resolution in fossil assemblages. Paleontological

Society short courses in paleontology no. 6. S.M. Kidwell and A.K. Behrensmeyer, eds. University of Tennessee, Knoxville.

Brinkman, D.B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada; evidence from vertebrate microfossil localities. Palaeogeography, Palaeoclimatology, Palaeoecology 7–8:37–54

Brongersma-Sanders, M. 1957. Mass mortality in the sea. Pp. 941–1010 *in* Treatise on marine ecology and paleoecology. Geological Society of America memoir 67. J.W. Hedgepath, ed. Geological Society of America, New York.

Brongersma-Sanders, M., K.M. Stephan, T.G. Kwee, and M. DeBruin. 1980. Distribution of minor elements in cores from the southwest Africa shelf with notes on plankton and fish mortality. Marine Geology 37:91–132.

Brown, B. 1935. Sinclair dinosaur expedition, 1934. Natural History 36:3–15.

Bruton, D.L. 2001. A death assemblage of priapulid worms from the Middle Cambrian Burgess Shale. Lethaia 34:163–167.

Buckland, W. 1823. Reliquiae diluvianae; or, observations on the organic remains contained in caves, fissures, and diluvial gravel, and on other geological phenomena, attesting the action of an universal deluge. John Murray, London.

Burton, R.,1985. Bird behavior. Alfred A. Knopf, New York.

Caldwell, D.K., Caldwell, M.C., and J. Walker. 1970. Mass and individual strandings of False Killer Whales, *Pseudorca crassidens*, in Florida. Journal of Mammalogy 51:634–635.

Camp, C.L. 1980. Large ichthyosaurs from the Upper Triassic of Nevada. Palaeontographica. Abteilung A: Palaeozoologie-Stratigraphie 170:139–200.

Campbell, K.S.W., and M.W. Bell. 1978. A primitive amphibian from the Late Devonian of New South Wales. Alcheringa 1:369–381.

Cantalamessa, G. C. Di Celma, and L Ragaini. 2005. Sequence stratigraphy of the Punta Ballena Member of the Jama Formation (Earlty Pleistocene, Eduador): Insights from integrated sedimentologic, taphonomic, and paleoecologic analysis of molluscan shell concentrations. Palaeogeography, Palaeoclimatology, Palaeoecology 216:1–25.

Capaldo, S.D., and C.R. Peters. 1995. Skeletal inventories from wildebeest drownings at Lakes Masek and Ndutu in the Serengeti ecosystem of Tanzania. Journal of Archaeological Science 22:385–408.

Carlson, K.J. 1968. The skull morphology and aestivation burrows of the Permian lungfish, *Gnathorhiza serrata*. Journal of Geology 76:641–643.

Case, E.C. 1935. Description of a collection of associated skeletons of *Trimerorhachis*. Contributions from the Museum of Paleontology, University of Michigan 4:227–274.

Chamberlin, L.C. 1971. The fabled moose graveyard? Alces 11:1–22.

Charig, A.J., and A.C. Milner. 1997. *Baryonix walkeri*, a fish-eating dinosaur from the Wealden of Surrey. Bulletin of the Natural History Museum 53:11–70.

Chen, P., Z. Dong, and S. Zhen. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. Nature 391:147–152.

Chiappe, L.M., R.A. Coria, L. Dingus, F. Jackson, A. Chinsamy, and M. Fox. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. Nature 396:258–261.

Chiappe, L.M., J.G. Schmitt, G.D. Jackson, A. Garrido, L. Dingus, G. Grellet-Tinner. 2004. Nest structures for sauropods: Sedimentary criteria for recognition of dinosaur nesting traces. Palaios 19:89–95.

Clark, J., J.R. Beerbower, and K.K. Kietzke. 1967. Oligocene sedimentation, stratigraphy and paleoclimatology in the Big Badlands of South Dakota. Fieldiana geology memoir 5. Field Museum of Natural History, Chicago.

Coe, M. 1978. The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya. Journal of Arid Environments 1:71–86.

Colbert, E.H. 1989. The Triassic dinosaur *Coelophysis*. Bulletin series 57. Museum of Northern Arizona Press, Flagstaff.

Cole, G.F., and D.B. Houston. 1969. An incidence of mass elk drowning. Journal of Mammalogy 50:640–641.

Cole, K.L. 1990. Reconstruction of past desert vegetation along the Colorado River using packrat middens. Palaeogeography, Palaeoclimatology, Palaeoecology 76: 349–366.

Conkin, J.E., B.M. Conkin, and Z.L. Lipchinsky. 1976. Middle Devonian (Hamiltonian) stratigraphy and bone beds on the east side of the Cincinnati Arch in Kentucky. 2. The Kidds Store section, Casey County. Studies in paleontology and stratigraphy 6. University of Louisville, Louisville, Kentucky.

Conkin, J.E., B.M. Conkin, and M.R. Dasari. 1999. Sequential disconformities in the Devonian succession of southern Indiana and northwestern Kentucky. American Association of Petroleum Geologists Bulletin 83:1367.

Conybeare, A., and G. Haynes. 1984. Observations on elephant mortality and bones in water holes. Quaternary Research 22:189–200.

Coombs, M.C., and W.P. Coombs Jr. 1997. Analysis of the geology, fauna, and taphonomy of Morava Ranch Quarry, Early Miocene of northwest Nebraska. Palaios 12:165–187.

Coope, G.R., and A.M. Lister. 1987. Late-glacial mammoth skeletons from Condover, Shropshire, England. Nature 330:472–474.

Cope, J.B., and J.C. Barber. 1978. Caching behavior of screech owls in Indiana. Wilson Bulletin 90:450.

Corfield, T.F. 1973. Elephant mortality in Tsavo National Park, Kenya. East African Wildlife Journal 11:339–368.

Cotel, A.J. 1999. A trigger mechanism for the Lake Nyos disaster. Journal of Volcanology and Geothermal Research 88:343–347

Currie, P.J., and P. Dodson. 1984. Mass death of a herd of ceratopsian dinosaurs. Pp. 61–66 *in* Third symposium on Mesozoic terrestrial ecosystems, short papers. W.E. Reif and F. Westphal, eds. Attempto, Tübingen, Germany.

Curtis, B. 1949. The life story of the fish. Harcourt, Brace and Company, New York.

Dalquest, W.W., and S.H. Mamay. 1963. A remarkable concentration of Permian amphibian remains in Haskell County, Texas. Journal of Geology 71:641–644.

Dashzeveg, D., M.J. Novacek, M.A. Norell, J.M. Clark, L.M. Chiappe, A. Davidson, M.C. McKenna, L. Dingus, C. Swisher, and P. Altangerel. 1995. Extraordinary preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. Nature 374:446–449.

Davis, S.P., and D.M. Martill. 1999. The gonorynchiform fish *Dastilbe* from the Lower Cretaceous of Brazil. Palaeontology 42:715–740.

Dechant-Boaz, D. 1982. Modern riverine taphonomy: Its relevance to the interpretation of Plio-Pleistocene hominid paleoecology in the Omo Basin, Ethiopia. Unpublished Ph.D. dissertation, University of California, Berkeley.

del Rio, C.J., S.A. Martinez, and R.A. Scasso. 2001. Nature and origin of spectacular Miocene shell beds of northeastern Patagonia (Argentina); paleoecological and bathymetric significance. Palaios 16:3–25.

Denison, R.H. 1967. Ordovician vertebrates from the western United States. Fieldiana Geology 16:131–192.

Denys, C., and M. Mahboubi. 1992. Altérations structurales et chimiques des éléments squelettiques de pelotes de régurgitation d'un rapace diurne. Bulletin Musée Nationale d'Histoire Naturelle, Paris, 4e série, 14:229–249.

Denys, C., K. Kowalski, and Y. Dauphin. 1992. Mechanical and chemical alterations of skeletal tissues in a recent Saharian accumulation of faeces from *Vulpes rueppelli* (Carnivora, Mammalia). Acta Zoologica Cracov 35:265–283.

Dietrich, W.E. 1983. Boundary shear stress, sediment transport and bed morphology in a sand-bedded meander during high and low flow. Pp. 632–639 *in* River meandering: Proceedings of the conference on rivers 1983. C.M. Elliott, ed. American Society of Civil Engineers, New York.

DiMichelle, W.A., R.W. Hook, R. Beerbower, J.A. Boy, R.A. Gastaldo, N. Hotton III, T.L. Phillips, S.E. Scheckler, W.A. Shear, and H.-D. Sues. 1992. Paleozoic terrestrial ecosystems, Pp. 205–325 *in* Terrestrial ecosystems through time: The evolutionary paleoecology of terrestrial plants and animals. A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichelle, R. Potts, H.-D. Sues, and S.L. Wing, eds. University of Chicago Press, Chicago.

Dodson, P. 1971. Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). Palaeogeography, Palaeoclimatology, Palaeoecology 10:21–74.

Dodson, P. 1973. The significance of small bones in paleoecological interpretation. Contributions to Geology, University of Wyoming 12:15–19.

Dodson, P. 1987. Microfaunal studies of dinosaur paleoecology, Judith River Formation of southern Alberta. Pp. 70–75 *in* Fourth symposium on Mesozoic terrestrial ecosystems, short papers. P.M. Currie and E.H. Koster, eds. Royal Tyrrell Museum of Paleontology, Drumheller, Alberta.

Dodson, P., and D. Wexlar. 1979. Taphonomic investigation of owl pellets. Paleobiology 5:275–284.

Dudley, J.P., G.C. Craig, D.S.C. Gibson, G. Haynes, and J. Klimowicz. 2001. Drought mortality of bush elephants in Hwange National Park, Zimbabwe. African Journal of Ecology 39:187–194.

Dudok van Heel, W.H. 1966. Navigation in Cetacea, Pp. 597–606 *in* Whales, dolphins and porpoises. K.S. Norris, ed. University of California Press, Berkeley.

Eastman, C.R. 1911. Jurassic saurian remains ingested within fish. Annals of the Carnegie Museum 8:182–187.

Eaton, T.H. 1964. A captorhinomorph predator and its prey (Cotylosauria). American Museum Novitates 2169:1–3.

Eberth, D.A. 1990. Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 7–8:1–36.

Eberth, D.A., and M.A. Getty. 2005. Ceratopsian bonebeds at Dinosaur Provincial Park: Stratigraphy, geology, taphonomy, origins, and significance. Pp. 501–536 in Dinosaur Provincial Park, a spectacular ancient ecosystem revealed. P.J. Currie and E. Kopplehus, eds. Indiana University Press, Bloomington.

Eberth, D.A., and M. Ryan. 1992. Stratigraphy, depositional environments and paleontology of the Judith River and Horseshoe Canyon formations (Upper Cretaceous), southern Alberta, Canada. Field trip guidebook, AAPG/SEPM annual convention, Calgary, Alberta.

Eberth, D.A., B.B. Britt, R. Scheetz, K.L. Stadtman, and D.B. Brinkman. 2006. Dalton Wells: Geology and significance of debris-flow-hosted dinosaur bonebeds in the Cedar Mountain Formation (Lower Cretaceous) of eastern Utah, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 236:217–245.

Eberth, D.A., M. Shannon, and B.G. Noland. This volume. A bonebeds database: Classification, biases, and patterns of occurrence. Chapter 3 in Bonebeds: Genesis, analysis, and paleobiological significance. R.R. Rogers, D.A. Eberth, and A.R. Fiorillo, eds. University of Chicago Press, Chicago.

Economidis, P.S., and V.P. Vogiatzis. 1992. Mass mortality of *Sardinlla aurita* Valenciennes (Pisces, Clupeidae) in Thessaloniki Bay (Macedonia, Greece). Journal of Fish Biology 41:147–149.

Elias, S.A. 1990. Observations on the taphonomy of late Quaternary insect fossil remains in packrat middens of the Chihuahuan Desert. Palaios 5:356–363.

Elles, G.L., and I.L. Slater,1906. The highest Silurian rocks of the Ludlow district. Quarterly Journal of the Geological Society of London 62:195–222.

Emslie, S.D. 1995. Age and taphonomy of abandoned penguin colonies in the Antarctic Peninsula region. Polar Record 31:409–418.

Emslie, S.D., and G.S. Morgan. 1994. A catastrophic death assemblage and paleoclimatic implications of Pliocene seabirds of Florida. Science 264:684–685.

Emslie, S.D., W.D. Allmon, F.J. Rich, J.H. Wrenn, and S.D. de France. 1996. Integrated taphonomy of an avian death assemblage in marine sediments from the late Pliocene of Florida. Palaeogeography, Palaeoclimatology, Palaeoecology 124:107–136.

Emslie, S.D., W. Fraser, R.C. Smith, and W. Walker. 1998. Abandoned penguin colonies and environmental change in the Palmer Station area, Anvers Island, Antarctic Peninsula. Antarctic Science 10:257–268.

Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. University of California Publications in Geological Science 49:1–187.

Estes, R., Z.V. Spinar, and E. Nevo. 1978. Early Cretaceous pipid tadpoles from Israel (Amphibia: Anura). Herpetologica 34:374–393.

Falcon-Lang, H.J. 1998. The impact of wildfire on an Early Carboniferous coastal environment, North Mayo, Ireland. Palaeogeography, Palaeoclimatology, Palaeoecology 139:121–138.

Falcon-Lang, H.J. 1999. Fire ecology of a Late Carboniferous floodplain, Joggins, Nova Scotia. Journal of the Geological Society of London 156:137–148.

Falcon-Lang, H.J. 2003. Growth interruptions in silicified conifer woods from the Upper Cretaceous Two Medicine Formation, Montana, USA: Implications for palaeoclimate and dinosaur palaeoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 199:299–314.

Fara, E., A.Á.F. Saraiva, D. de Almeida Campos, J.K.R. Moreira, D. de Carvalho Siebra, and A.W.A. Kellner. 2005. Controlled excavations in the Romualdo Member of the Santana Formation (Early Cretaceous, Araripe Basin, northeastern Brazil): Stratigraphic, palaeoenvironmental, and palaeoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 218:145–160.

Fay, F.H., and B.P. Kelly. 1980. Mass natural mortality of walruses (*Odobenus rosmarus*) at St. Lawrence Island, Bering Sea, autumn 1978. Arctic 33:226–245.

Ferber, C.T., and N.A. Wells. 1995. Paleolimnology and taphonomy of some fish deposits in "Fossil" and "Uinta" Lakes of the Eocene Green River Formation, Utah and Wyoming. Palaeogeography, Palaeoclimatology, Palaeoecology 117:185–210.

Fernandez-Lopez, S.R., M.H. Henriques, and L.V. Duarte. 2002. Taphonomy of ammonite condensed associations—Jurassic examples from carbonate platforms of Iberia. Abhandlungen Geologischen Bundesanstalt 57:423–430.

Finch, W.I., F.C. Whitmore Jr., and J.D. Sims. 1972. Stratigraphy, morphology, and paleoecology of a fossil peccary herd from western Kentucky. United States Geological Survey professional paper 790.

Finney, B.P., I. Gregory-Eaves, M.S.V. Douglas, and J.P. Smol. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. Nature 416:729–733.

Fiorillo, A.R. 1988. Taphonomy of Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska. Contributions to Geology, University of Wyoming 26:57–97.

Fiorillo, A.R. 1991. Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana, U.S.A. Palaeogeography, Palaeoclimatology, Palaeoecology 81:281–311.

Fiorillo, A.R., K. Padian, and C. Musikasinthorn, 2000. Taphonomy and depositional setting of the *Placerias* Quarry (Chinle Formation: Late Triassic, Arizona). Palaios 15:373–386.

Fisher, D. 1981. Crocodilian scatology, microvertebrate concentrations, and enamelless teeth. Paleobiology 7:262–275.

Forcada, J., P.S. Hammond, and A. Aguilar. 1999. Status of the Mediterranean monk seal *Monachus monachus* in the western Sahara and the implications of a mass mortality event. Marine Ecology Progress Series 188:249–261.

Fraser, N.C., and G.M. Walkden. 1983. The ecology of a Late Triassic reptile assemblage from Gloucestershire, England. Palaeogeography, Palaeoclimatology, Palaeoecology 42:341–365.

Freeman, M.M.R. 1968. Winter observations on beluga whales (*Delphinapterus leucas*) in Jones Sound, N.W.T. Canadian Field Naturalist 82:276–286.

Frison, G.C. 1974. The Casper Site. Academic Press, New York.

Frison, G.C., and L.C. Todd. 1986. The Colby Mammoth Site: Taphonomy and archaeology of a Clovis kill in northern Wyoming. University of New Mexico Press, Albuquerque.

Furness, R.W., and P. Monaghan. 1987. Seabird ecology. Chapman and Hall, New York.

Fürsich F.T., and W. Oschmann. 1993. Shell beds as tools in basin analysis: The Jurassic of Kachchh, western India. Journal of the Geological Society of London 150:169–185.

Fürsich, F.T., and D.K. Pandey. 2003. Sequence stratigraphic significance of sedimentary cycles and shell concentrations in the Upper Jurasic–Lower Cretaceous of Kachchh, western India. Palaeogeography, Palaeoclimatology, Palaeoecology 193: 285–309.

Gadbury, C., L. Todd, A.H. Jahren, and R. Amundson. 2000. Spatial and temporal variations in the isotopic composition of bison tooth enamel from the Early Holocene Hudson-Meng Bone Bed, Nebraska. Palaeogeography Palaeoclimatology Palaeoecology 157:79–93

Gates, T.A. 2005. The Late Jurassic Cleveland-Lloyd dinosaur quarry as a drought-induced assemblage. Palaios 20:363–375.

Gau, K., and N. Shubin. 2000. Late Jurassic salamanders from northern China: Phylogenetic and biogeographic implications. Journal of Vertebrate Paleontology 20(supplement to 3):43A.

Geraci, J.R., and V.J. Lounsbury. 1993. Marine mammals ashore: A field guide for strandings. Texas A&M University Sea Grant College Program, Galveston.

Geraci, J.R., J. Harwood, and V.J. Lounsbury. 1999. Marine mammal die-offs. Pp. 367–395 in Conservation and management of marine mammals. J.R. Twiss Jr. and R.R. Reeves, eds. Smithsonian Institution Press, Washington, D.C.

Gillespie, J.L., C.S. Nelson, and S.D. Nodder. 1998. Post-glacial sea-level control and sequence stratigraphy of carbonate-terrigenous sediments, Wanganui Shelf, New Zealand. Sedimentary Geology 122:245–266.

Gillson, L. 2006. A "large infrequent disturbance" in an East African savanna. African Journal of Ecology 44:458–467.

Graham, R.W., V.V. Haynes, D.L. Johnson, and M. Kay. 1981. Kimmswick: A Clovis-mastodon association in eastern Missouri. Science 213:1115–1117.

Grande, L. 1980. Paleontology of the Green River Formation with a review of the fish fauna. Bulletin of the Geological Survey of Wyoming 63:1–333.

Grayson, D.K. 1984. Quantitative zooarchaeology: Topics in the analysis of archaeological faunas. Academic Press, Orlando.

Grellet-Tinner, G. 2005. Membrana testacea of titanosaurid dinosaur eggs from Auca Mahuevo (Argentina): Implications for exceptional preservation of soft tissue in lagerstätten. Journal of Vertebrate Paleontology 25:99–106.

Grindley, J.R., and F.J.R. Taylor. 1962. Red water and mass mortality of fish near Cape Town. Nature 195:1324.

Gunter, G. 1941. Death of fishes due to cold on the Texas coast, January, 1940. Ecology 22:203–208.

Gunter, G. 1947. Catastrophism in the sea and its paleontological significance, with special reference to the Gulf of Mexico. American Journal of Science 245:46–67.

Gunter, G., R.H. Williams, C.C. Davis, and F.G.W. Smith. 1948. Catastrophic mass mortality of marine animals and coincident phytoplankton bloom on the west coast of Florida, November 1946to August 1947. Ecological Monographs 18: 309–324.

Hanson, C.B. 1980. Fluvial taphonomic processes: Models and experiments. Pp. 156–181 *in* Fossils in the making. A.K. Behrensmeyer and A.P. Hill, eds. University of Chicago Press, Chicago.

Hatcher, J.B. 1901. The Jurassic dinosaur deposits near Canyon City, Colorado. Annals of the Carnegie Museum 1:327–341.

Hauff, B. 1921. Untersuching der Fossilifundstätten von Holzmaden im Posidonien-schiefer des oberen Lias Württembergs. Palaeontographica 64:1–42.

Haynes, G. 1988. Mass deaths and serial predation: Comparative taphonomic studies of modern large mammal death sites. Journal of Archaeological Science 15:219–235.

Haynes, G. 1991. Mammoths, mastodons and elephants: Biology, behavior, and the fossil record. Cambridge University Press, Cambridge.

Hayward, J.L., D.E. Miller, and C.R. Hill. 1982. Mount St. Helens ash: Its impact on breeding ring-billed and California gulls. The Auk 99:623–631.

Henrici, A.C., and A.R. Fiorillo. 1993. Catastrophic death assemblage of *Chelomophrynus bayi* (Anura: Rhinophrynidae) from the middle Eocene Wagon Bed Formation of central Wyoming. Journal of Paleontology 67:1016–1026.

Hillman, J.C., and A.K.K. Hillman. 1977. Mortality of wildlife in Nairobi National Park during the drought of 1973–1974. East African Wildlife Journal 15:1–18.

Hocket, B.S. 1989. The concept of "carrying range": A method for determining the role played by woodrats in contributing bones to archaeological site. Nevada Archaeologist 7:28–35.

Hoffman, R. 1988. The contribution of raptorial birds to patterning in small mammal assemblages. Paleobiology 14:81–90.

Hogler, J.A. 1992. Taphonomy and paleoecology of *Shonisaurus popularis* (Reptilia: Ichthyosauria). Palaios 7:108–117.

Holliday, V.T., C.V. Haynes Jr., J.L. Hoffman, and D.J. Meltzer. 1994. Geoarchaeology and geochronology of the Miami (Clovis) Site, southern High Plains of Texas. Quaternary Research 41:234–244.

Hook, R., and J.C. Ferm. 1988. Paleoenvironmental controls on vertebrate-bearing abandoned channels in the Upper Cretaceous. Palaeogeography, Palaeoclimatology, Palaeoecology 63:159–181.

Hopley, P.J. 2001. Plesiosaur spinal pathology: The first fossil occurrence of Schmorl's nodes. Journal of Vertebrate Paleontology 21:253–260.

Horner, J.R. 1982. Evidence of colonial nesting and site fidelity among orhithischian dinosaurs. Nature 297:675–676.

Horner, J.R. 1994. Comparative taphonomy of some dinosaur and extant bird colonial nesting grounds. Pp. 116–123 *in* Dinosaur eggs and babies. K. Carpenter, K.F. Hirsch, and J.R. Horner, eds. Cambridge University Press, Cambridge, U.K.

Horner, J.R., and R. Makela. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. Nature 282:296–298.

Horwitz, L.K., and P. Smith. 1988. The effects of striped hyaena activity on human remains. Journal of Archaeological Science 15:471–481.

Hu, Y., J. Meng, Y. Wang, and C. Li. 2005. Large Mesozoic mammal fed on young dinosaurs. Nature 433:149–152.

Huber, H.R., A.C. Rovetta, L.A. Fry, and S. Johnston. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. Journal of Mammalogy 72:525–534.

Hückel, U. 1970. Fossil-Lagerstaetten, Nr. 7; Die Fischschiefer von Haqel und Hjoula in der Oberkreide des Libanon. Neues Jahrbuch fuer Geologie und Palaeontologie. Abhandlungen 135:113–149.

Huene, F. von,1928. Lebensbild des Saurischier-Vorkommens im obersten Keuper von Trossingen in Württemberg. Palaeobiologica 1:103–116.

Hulbert, R.C. Jr. 1982. Population dynamics of the three-toed horse *Neohipparion* from the Late Miocene of Florida. Paleobiology 8:159–167.

Hungerbühler, A. 1998. Taphonomy of the prosauropod dinosaur *Sellosaurus*, and its implications for carnivore faunas and feeding habits in the Late Triassic. Palaeogeography, Palaeoclimatology, Palaeoecology 143:1–29.

Hunt, A.P. 1986. Taphonomy of the Cleveland-Lloyd Quarry, Morrison Formation (Late Jurassic), Emery County, Utah: A preliminary report. Fourth North American Paleontological Convention, Boulder, Colorado, A21.

Hunt, R.M. Jr. 1990. Taphonomy and sedimentology of Arikaree (lower Miocene) fluvial, eolian, and lacustrine paleoenvironments, Nebraska and Wyoming: A paleobiota entombed in fine-grained volaniclastic rocks. Pp. 69–11 *in* Volcanism and fossil biotas. Special paper 244. M.G. Lockley and A. Rice, eds. Geological Society of America, Boulder, Colorado.

Hunt, R.M. Jr., X.-X. Xu, and J. Kaufman. 1983. Miocene burrows of extinct bear dogs: Indication of early denning behavior of large mammalian carnivores. Science 221:364–366.

Jehl, J.R. Jr. 1996. Mass mortality of eared grebes in North America. Journal of Field Ornithology 67:471–476.

Johanson, Z. 1998. The Upper Devonian fish *Bothriolepis* (Placodermi, Antiarchi) from near Canowindra, New South Wales, Australia. Records of the Australian Museum 50:315–348.

Johnson, R.G. 1960. Models and methods for analysis of the mode of formation of fossil assemblages. Bulletin of the Geological Society of America 71:1075–1085.

Johnson, B.W., and P.A. Johnson. 1981. The Hawaiian monk seal on Laysan Island: 1978. Report no. MMC-78/15, Marine Mammal Commission, U.S. Department of Commerce.

Jones, T.P. 1997. Fusain in Late Jurassic sediments from the Witch Grond Graben, North Sea, U.K. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 58:93–103.

Jordan, D.S. 1920. A Miocene catastrophe. Natural History 20:18–22.

Kahlke, R.-D., and S. Gaudzinski. 2005. The blessing of a great flood: Differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. Journal of Archaeological Science 32:1202–1222.

Kellogg, R., and F.C. Whitmore Jr. 1957. Marine mammals; annotated bibliography. Pp. 1021–1024 *in* Ecology, vol. 1 of Treatise on marine ecology and paleoecology.

Geological Society of America memoir 67. J.W. Hedgpeth, ed. Memoir, Geological Society of America, New York.

Kerbis-Peterhans, J.C., and L.K. Horwitz. 1992. A bone assemblage from a striped hyaena (*Hyaena hyaena*) den in the Negev Desert, Israel. Israel Journal of Zoology 37:225–245.

Khajuria, C.K., and G.V.R. Prasad. 1998. Taphonomy of a Late Cretaceous mammal bearing microvertebrate assemblage from the Deccan inter-trappean beds of Naskal, peninsular India. Palaeogeography, Palaeoclimatology, Palaeoecology 137:153–172.

Kidwell, S.M. 1986. Models for fossil concentrations: Paleobiologic implications. Paleobiology 12:6–24.

Kidwell, S.M. 1989. Stratigraphic condensation of marine transgressive records: Origin of major shell deposits in the Miocene of Maryland. Journal of Geology 97:1–24.

Kidwell, S.M. 1991a. The stratigraphy of shell concentrations. Pp. 211–290 *in* Taphonomy: Releasing the data locked in the fossil record. Topics in Geobiology 9. P.A. Allison and D.E.G. Briggs, eds. Plenum Publishing, New York.

Kidwell, S.M. 1991b. Condensed deposits in siliciclastic sequences: Expected and observed features. Pp. 682–695 *in* Cycles and events in stratigraphy. G. Einsele, W. Ricken, and A. Seilacher, eds. Springer Verlag, Berlin.

Kidwell, S.M. 1993. Taphonomic expressions of sedimentary hiatuses: Field observations on bioclastic concentrations and sequence anatomy in low, moderate and high subsidence settings. Geologische Rundschau 82:189–202.

Kidwell, S.M., F.T. Fürsich, and T. Aigner. 1986. Conceptual framework for the analysis and classification of fossil concentrations. Palaios 1:228–238.

Kirschvink, J.L., A.E. Dizon, and J.A. Westphal. 1986. Evidence from strandings for geomagnetic sensitivity in cetaceans. Journal of Experimental Biology 120:1–24.

Kling, G.W., M. Clark, H.R. Compton, J.D. Devine, W.C. Evans, A.M. Humphrey, J.P. Lockwood, and M.L. Tuttle. 1987. The 1986 Lake Nyos gas disaster, Cameroon, West Africa. Science 236:169–175.

Klinowska, M. 1985. Cetacean live stranding sites relate to geomagnetic topography. Aquatic Mammals 1:27–32.

Klinowska, M. 1986. Cetacean live stranding dates relate to geomagnetic disturbances. Aquatic Mammals 11:109–119.

Kondo Y., S.T. Abbott, A. Kitamura, P.J.J. Kamp, T.R. Naish, T. Kamataki, and G.S. Saul. 1998. The relationship between shellbed type and sequence architecture: Examples from Japan and New Zealand. Sedimentary Geology 122:109–128.

Kormos, T. 1911. Der Pliozäne Knochenfund bei Polgardi. Földtani Közlöni 41:48–64

Korth, W.W. 1979. Taphonomy of microvertebrate fossil assemblages. Annals of the Carnegie Museum 48:235–285.

Koster, E.H. 1987. Vertebrate taphonomy applied to the analysis of ancient fluvial systems. Pp. 159–168 *in* Recent developments in fluvial sedimentology. Special publication 39. F.G. Ethridge, R.M. Flores, and M.D. Harvey, eds. Society of Economic Paleontologists and Mineralogists.

Kruuk, H. 1972. The spotted hyena: A study of predation and social behavior. University of Chicago Press, Chicago.

Kuhk, R. 1956. Hagelunwetter als Verlustursache bei Störchen und anderen Vögeln. Vogelwarte 18:180–182.

Kurtén, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. Acta Zoologica Fennica 76:5–122.

Kusmer, K.D. 1990. Taphonomy of owl pellet deposition. Journal of Paleontology 64:629–637.

Lam, Y.M. 1992. Variability in the behavior of spotted hyaenas as taphonomic agents. Journal of Archaeological Science 19:389–406.

Laudet, F., and N. Selva. 2005. Ravens as small mammal bone accumulators: First taphonomic study on mammal remains in raven pellets. Palaeogeography, Palaeoclimatology, Palaeoecology 226:272–286.

Lawrence, G.E. 1966. Ecology of vertebrate animals in relation to chaparral fire on the Sierra Nevada foothills. Ecology 47:278–291

Lawton, R. 1977. Taphonomy of the dinosaur quarry, Dinosaur National Monument. Contributions to Geology, University of Wyoming 15:119–126.

Le Boeuf, B.J., and K.T. Briggs. 1977. The cost of living in a seal harem. Mammalia 41:167–195.

Le Boeuf, B.J., and R.S. Condit. 1983. The high cost of living on the beach. Pacific Discovery 36:12–14.

Le Boeuf, B.J., and R.M. Laws. 1994. Elephant seals: Population ecology, behavior, and physiology. University of California Press, Berkeley.

Leckie, D.A., C. Singh, J. Bloch, M. Wilson, and J. Wall. 1992. An anoxic event at the Albian-Cenomonian boundary: The Fish Scale Marker Bed, northern Alberta, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 92:139–166.

Le Rock, J.W. 2000. Sedimentology and taphonomy of a dinosaur bonebed from the Upper Cretaceous (Campanian) Judith River Formation of north central Montana. Unpublished masters thesis, Montana State University, Bozeman, Montana.

Leggitt, V.L., and H.P. Buchheim. 1997. Bird bone taphonomic data from Recent lake margin strandlines compared with an Eocene *Presbyornis* (Aves: Anseriformes) bone strandline. Geological Society of America, Abstracts with Programs 29:105.

Leonardos, I., and A. Sinis. 1997. Fish mass mortality in the Etolikon Lagoon, Greece: The role of local geology. Cybium 21:201–206.

Lisle, T.E. 1976. Components of flow resistance in a natural channel. Unpublished Ph.D. thesis, University of California, Berkeley.

Loope, D.B., L. Dingus, C.C. Swisher III, and C. Minjin. 1998. Life and death in a Late Cretaceous dune field, Nemegt basin, Mongolia. Geology 26:27–30.

Loope, D.B., J.A. Mason, and L. Dingus. 1999. Lethal sandslides from eolian dunes. Journal of Geology 107:707–713.

Lubinski, P.M., and C.J. O'Brien. 2001. Observations on seasonality and mortality from a Recent catastrophic death assemblage. Journal of Archaeological Science 28:833–842.

Lyman, R.L. 1994. Vertebrate taphonomy. Cambridge University Press, Cambridge.

Maas, M.C. 1985. Taphonomy of a Late Eocene microvertebrate locality, Wind River Basin, Wyoming (U.S.A.). Palaeogeography, Palaeoclimatology, Palaeoecology 52:123–142.

Macquaker, J.H.S. 1994. Palaeoenvironmental significance of "bone-beds" in organic-rich mudstone successions: An example from the Upper Triassic of south-west Britain. Zoological Journal of the Linnean Society 112:285–308.

Maguire, J.M., D. Pemberton, and M.H. Collett. 1980. The Makapansgat Limeworks Grey Breccia: Hominids, hyaenas, hystricids or hillwash? Paleontologia Africana 23:75–98.

Mandel, R.D., and J.L. Hofman. 2003.Geoarchaeological investigations at the Winger site: A late Paleoindian bison bonebed in southwestern Kansas, USA. Geoarchaeology, an International Journal 18:129–144

Mandic, O., and W.E. Piller. 2001. Pectinid coquinas and their palaeoenvironmental implications; Examples from the early Miocene of northeastern Egypt. Palaeogeography, Palaeoclimatology, Palaeoecology 172:171–191.

Mandic, O., M. Harzhauser, and R. Roetzel. 2004. Taphomomy and sequence stratigraphy of spectacular shell accumulations form the type stratum of the Central Paratethys stage Eggenburgian (Lower Miocene, NE Austria). Courier Forschungs-Institut Senckenberg (Frankfurt) 246:69–88.

Manning, E. 1990. The late early Miocene Sabine River. Transactions Gulf Coast Association of Geological Societies 40:531–549.

Marsh, R., B. Petrie, C.R. Weidman, R.R. Dickson, J.W. Loder, C.G. Hannah, K. Frank, and K. Drinkwater. 1999. The 1882 tilefish kill: A cold event in shelf waters off the north-eastern United States? Fisheries Oceanography 8:39–49.

Martill, D.M. 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. Palaeontology 31:1–18.

Martill, D.M. 1991. Bones as stones: The contribution of vertebrate remains to the lithologic record. Pp. 270–292 *in* The processes of fossilization. S.K. Donovan, ed. Columbia University Press, New York.

Matthew, W.D. 1923. Fossil bones in the rock. Natural History 23:358–369.

Matthew, W.D. 1924. Third contribution to the Snake Creek fauna. Bulletin of the American Museum of Natural History 50:61–210.

Maxwell, J. 1995. Swimming with the salmon. Natural History (September):26–39.

Mayhew, D.F. 1977. Avian predators as accumulators of fossil material. Boreas 6:25–31.

McDaniel, J.D., and S.D. Emslie. 2002. Fluctuations in Adélie penguin prey size in the mid to late Holocene, northern Marguerite Bay, Antarctic Peninsula. Polar Biology 25:618–623.

McEachron, L.W., G.C. Matlock, C.E. Bryan, P. Unger, T.J. Cody, and J.H. Martin. 1994. Winter mass mortality of animals in Texas bays. Northeast Gulf Science 13:121–138.

McGrew, P.O. 1975. Taphonomy of Eocene fish from Fossil Basin, Wyoming. Fieldiana Geology 33:257–270.

McHugh, T. 1972. The time of the buffalo. University of Nebraska Press, Lincoln.

McKenna, M.C. 1962. Collecting small fossils by washing and screening. Curator 5:221–235.

Mead, J.I., T.R. Van Devender, and K.L. Cole. 1983. Late Quaternary small mammals from Sonoran Desert packrat middens, Arizona and California. Journal of Mammalogy 64:173–180.

Mellet, J.S. 1974. Scatological origins of microvertebrate fossils. Science 185:349–350.

Mellink, E., and P.S. Martin. 2001. Mortality of cattle on a desert range: Paleobiological implications. Journal of Arid Environments 49:671–675.

Meltzer, D.J., L.C. Todd, and V.T. Holliday. 2002. The Folsom (Paleoindian) type site: Past investigations, current studies. American Antiquity 67:5–36.

Meng, Q., J. Liu, D.J. Varricchio, T. Huang, and C. Gao. 2004. Paleontology: Parental care in an ornithischian dinosaur. Nature 431:145–146.

Morlan, R.E. 1984. Toward the definition of criteria for the recognition of artificial bone alterations. Quaternary Research 22:160–171.

Müller-Schwarze, D. 1984. The behavior of penguins. State University of New York Press, Albany.

Murphey, P.C. 1996. Depositional setting and fauna on the *Omomys* Quarry, a possible owl site in the Bridger Formation (Middle Eocene) of Southwestern Wyoming. Journal of Vertebrate Paleontology 16(supplement to 3):55A.

Myrick, A.C. 1979. Variation, taphonomy, and adaptation of the Rhabdosteidae (Eurinodelphidae) (Odontoceti, Mammalia) from the Calvert Formation of Maryland and Virginia. Unpublished Ph.D. dissertation, University of California, Los Angeles.

Naish, T., and P.J.J. Kamp. 1997. Sequence stratigraphy of sixth-order (41 k.y.) Pliocene-Pleistocene cyclothems, Wanganui Basin, New Zealand; a case for the regressive systems tract. Geological Society of America Bulletin 109:978–999.

Nelson, J.G. 1973. The last refuge. Harvest House, Montreal.

Neraudeau D., R. Allain, V. Perrichot, B. Videt, F.L. de Broin, F. Guillochaeu, M. Philippe, J.-C. Rage, and R. Vullo. 2003. A new Early-Cenomanian paralic deposit with fossil wood, amber with insects and Iguanodontidae (Dinosauria, Ornithopoda) at Fouras (Charente-Maritime, southwestern France). Comptes Rendus Palevol 2(3): 221–230.

Nesbitt, S.J., A.H. Turner, G.M. Erickson, and M.A. Norell. 2006. Prey choice and cannibalistic behaviour in the theropod *Coelophysis*. Biology Letters 2(4):611–614.

Nevo, E. 1968. Pipid frogs from the Early Cretaceous of Israel and pipid evolution. Bulletin of the Museum of Comparative Zoology 136:255–318.

Norris, R.D. 1986. Taphonomic gradients in shelf fossil assemblages. Pliocene Purisma Formation, California. Palaios 1:252–266.

Northwood, C. 2005. Early Triassic coprolites from Australia and their palaeobiological significance. Palaeontology 48:49–68.

Nriagu, J.O. 1983. Rapid decomposition of fish bones in Lake Erie sediments. Hydrobiologica 106:217–222.

NWHC. 1998. USGS National Wildlife Health Center quarterly mortality reports: Fourth quarter.

NWHC. 2001. USGS National Wildlife Health Center quarterly mortality reports: Fourth quarter.

Nyman, S. 1986. Mass mortality of larval *Rana sylvatica* attributable to the bacterium, *Aeromonas hydrophila*. Journal of Herpetology 20:196–201.

Odell, D.K., E.D. Asper, J. Baucom, and L.H. Cornell. 1980. A recurrent mass stranding of the False Killer Whale, *Pseudorca crassidens*, in Florida. Fishery Bulletin 78:171–177.

Oliver, J.S., and R.W. Graham. 1994. A catastrophic kill of ice-trapped coots: Time averaged versus scavenger-specific disarticulation patterns. Paleobiology 20:229–244.

Olson, E.C. 1939. The fauna of the *Lysorophus* pockets in the Clear Fork Permian, Baylor County, Texas. Journal of Geology 46:389–397.

Olson, E.C., and K. Bolles. 1975. Permo-Carboniferous freshwater burrows. Fieldiana Geology 33:271–290.

Ostrom, J.H. 1978. The osteology of *Compsognathus longipes*. Wagner Zitteliana 4:73–118.

Ovsyanikov, N.G., L.L. Bove, and A.A. Kochnev. 1994. Walrus mortality causes on hauling-out grounds. Zoologicheskij Zhurnal 73:80–87.

Palmqvist, P., and A. Arribas, A. 2001. Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. Paleobiology 27:512–530.

Parras, A., and S. Casadio. 2005. Taphonomy and sequence stratigraphic significance of oyster-dominated concentrations from the San Julian formation, Oligocene of Patagonia, Argentina. Palaeogeography, Palaeoclimatology, Palaeoecology 217:47–66.

Parrish, W.C. 1978. Palaeoenvironmental analysis of a Lower Permian bonebed and adjacent sediments, Wichita County, Texas. Palaeogeography, Palaeoclimatology, Palaeoecology 24:209–237.

Pedley, H.M. 1978. A new fish horizon from the Maltese Miocene and its palaeoecological significance. Palaeogeography, Palaeoclimatology, Palaeoecology 24:73–83.

Peng, J., A.P. Russell, and D.B. Brinkman. 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman Formations of the Judith River Group (Campanian) of southeastern Alberta: An illustrated guide. Natural history occasional paper no. 25. Provincial Museum of Alberta, Edmonton.

Perea, D., M. Ubilla, A. Rojas, and C.A. Goso. 2001. The West Gondwanan occurrence of the hybodontid shark Priohybodus, and the Late Jurassic-Early Cretaceous age of the Tacuarembo Formation, Uruguay. Palaeontology 44:1227–1235.

Peterson, O.A. 1906. The Agate Spring fossil quarry. Annals of the Carnegie Museum 3:487–494.

Pitelka, F.A., P.Q. Tomich, and G.W. Treichel. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecological Monographs 25:85–117.

Popova, L.V. 2004. The micromammal fauna of the Dnieper modern channel alluvium: Taphonomic and biostratigraphic implications. Quaternaire 15:233–242.

Potts, R. 1986. Temporal span of bone accumulation at Olduvai Gorge and implications for early hominid foraging behavior. Paleobiology 12:25–31.

Potts, R. 1989. Olorgesailie: New excavations and findings in Early and Middle Pleistocene contexts, southern Kenya rift valley. Journal of Human Evolution 18:477–484.

Potts, R., A.K. Behrensmeyer, and P. Ditchfield. 1999. Paleolandscape variation and early Pleistocene hominid activities: Members 1 and 7, Olorgesailie Formation. Journal of Human Evolution 37:747–788.

Pough, F.H., C.M. Janis, and J.B. Heiser. 2005. Vertebrate life, seventh edition. Prentice-Hall, Upper Saddle River, New Jersey.

Pratt, A.E. 1989. Taphonomy of the microvertebrate fauna from the early Miocene Thomas Farm locality, Florida (U.S.A.). Palaeogeography, Palaeoclimatology, Palaeoecology 76:125–151.

Pybus, M.J., D.P. Hobson, and D.K. Onderka. 1986. Mass mortality of bats due to probable blue-green algal toxicity. Journal of Wildlife Diseases 22:449–450.

Ralrick, P.E. 2004. Subfossil vertebrate mass kill event at Little Fish Lake (Alberta, Canada): Preliminary observations. Pp. 45–50 *in* Alberta Palaeontological Society, eighth annual symposium. Alberta Paleontological Society, Calgary.

Reif, W.-E. 1982. Muschelkalk/Keuper bone-beds (Middle Triassic, SW-Germany): Storm condensation in a regressive cycle. Pp. 299–325 *in* Cyclic and event stratification. G. Einsele and A. Seilacher, eds. Springer-Verlag, Berlin.

Reiter, J., N.L. Stinson, and B.J. Le Boeuf. 1978. Northern elephant seal development: The transition from weaning to nutritional independence. Behavioral Ecology and Sociobiology 3:337–367.

Rogers, R.R. 1990. Taphonomy of three bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: Evidence for drought-related mortality. Palaios 5:394–413.

Rogers, R.R. 1995. Sequence stratigraphy and vertebrate taphonomy of the Upper Cretaceous Two Medicine and Judith River formations, Montana. Unpublished Ph.D. dissertation, University of Chicago.

Rogers, R.R. 2005. Fine-grained debris flows and extraordinary vertebrate burials in the Late Cretaceous of Madagascar. Geology 33:297–300.

Rogers, R.R., and S.M. Kidwell. 2000. Associations of vertebrate skeletal concentrations and discontinuity surfaces in terrestrial and shallow marine records: A test in the Cretaceous of Montana. Journal of Geology 108:131–154.

Rogers, R.R., A.B. Arcucci, F. Abdala, P.C. Sereno, C.A. Forster, and C.L. May. 2001. Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), northwestern Argentina: Spectacular preservation in volcanogenic concretions. Palaios 16:461–481.

Rolf, W.D.I., G.P. Durant, A.E. Fallick, A.J. Hall, D.J. Large, A.C. Scott, T.R. Smithson, and G.M. Walkden. 1990. An early terrestrial biota preserved by Visean vulcanicity in Scotland. Pp. 13–24 *in* Volcanism and fossil biotas. Special paper 244. M.G. Lockley and A. Rice, eds. Geological Society of America, Boulder, Colorado.

Romer, A.S., and L.W. Price. 1940. Review of the Pelycosauria. Geological Society of America Special Papers 28:1–538.

Rothschild, B.M., and L.D. Martin. 1993. Paleopathology: Disease in the fossil record. CRC Press, London.

Ryan, M.J., A.P. Russell, D.A. Eberth, and P.J. Currie. 2001. The taphonomy of a *Centrosaurus* (Ornithischia: Ceratopsidae) bone beds from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny. Palaios 16:482–506.

Sahni, A. 1972. The vertebrate fauna of the Judith River Formation of Montana. American Museum of Natural History Museum Bulletin 147:321–412.

Sander, P.M. 1987. Taphonomy of the Lower Permian Geraldine Bonebed in Archer County, Texas. Palaeogeography, Palaeoclimatology, Palaeoecology 61:221–236.

Sander, P.M. 1992. The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. Palaeogeography, Palaeoclimatology, Palaeoecology 93:255–299.

Saunders, J.J. 1977. Late Pleistocene vertebrates of the Western Ozark highland, Missouri. Reports of investigations, no. 33. Illinois State Museum, Springfield.

Schäfer, W. 1962. Aktuo-paläontologie nach studien in der Nordsee. W. Kramer, Frankfurt.

Schäfer, W. 1972. Ecology and paleoecology of marine environments. University of Chicago Press, Chicago.

Schaller, G.B. 1972. The Serengeti lion. University of Chicago Press, Chicago.

Schaller, G.B. 1973. Golden shadows, flying hooves. Alfred A. Knopf, New York.

Schmitt, D.N., and K.E. Juell. 1994. Toward the identification of coyote scatological faunal accumulations in archaeological contexts. Journal of Archaeological Science 21:249–262.

Schröder-Adams, C.J., S.L. Cumbaa, J. Bloch, D.A. Leckie, J. Craig, S.A. Seif El-Dein, D.-J.H.A.E. Simons, and F. Kenig. 2001. Late Cretaceous (Cenomanian to Campanian) paleoenvironmental history of the Eastern Canadian margin of the Western Interior Seaway: Bonebeds and anoxic events. Palaeogeography, Palaeoclimatology, Palaeoecology 170:261–289.

Schwartz, H.L., and D.D. Gillette. 1994. Geology and taphonomy of the *Coelophysis* quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico. Journal of Paleontology 68:1118–1140.

Seilacher, A., W.E. Reif, and F. Westphal. 1985. Sedimentological, ecological, and temporal patterns of fossil Lagerstätten. Philosophical Transactions of the Royal Society of London B 311:5–23.

Sergeant, D.E., and G.A. Williams. 1983. Two recent entrapments of narwhals, *Monodon monoceros*, in arctic Canada. Canadian Field Naturalist 97:459–460.

Shipman, P. 1975. Implications of drought for vertebrate fossil assemblages. Nature 257:667–668.

Shipman, P.G. 1981. Life history of a fossil: An introduction to taphonomy and paleoecology. Harvard University Press, Cambridge.

Shipman, P., and A. Walker. 1980. Bone-collecting by harvesting ants. Paleobiology 6:496–502.

Shipman, P., G. Foster, and M. Schoeninger. 1984. Burnt bones and teeth: An experimental study of color, morphology, crystal structure and shrinkage. Journal of Archaeological Science 11:307–325.

Siegstad, H., and M.P. Heide-Jørgensen. 1994. Ice entrapments of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in Greenland. Meddelelser om Grønland, Bioscience 39:151–160.

Sinclair, A.R.E. 1979. The eruption of the ruminants. Pp. 82–103 *in* Serengeti: Dynamics of an ecosystem. A.R.E. Sinclair and M. Norton-Griffiths, eds. University of Chicago Press, Chicago.

Singer, F.J., W. Schreier, J. Oppenheim, and E.O. Garton. 1989. Drought, fire, and large mammals. BioScience 39:716–722.

Skinner, J.D., and R.J. van Aarde. 1991. Bone collecting by brown hyaenas *Hyaena brunnea* in the Central Namib Desert, Namibia. Journal of Archaeological Science 18:513–523.

Skinner, J.D., J.R. Henschel, and A.S. van Jaarsveld. 1986. Bone-collecting habits of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. South African Tydskrif Dierk 21:303–308.

Smith, G.R., R.F. Stearley, and C.E. Badgley. 1988. Taphonomic bias in fish diversity from Cenozoic floodplain environments. Palaeogeography, Palaeoclimatology, Palaeoecology 63:263–273.

Smith, R.M.H. 1993. Vertebrate taphonomy of Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa. Palaios 8:45–67.

Smith, R.M.H. 2000. Sedimentology and taphonomy of Late Permian vertebrate fossil localities in southwestern Madagascar. Palaeontologia Africana 36:25–41.

Smith, R., and P. Haarhoff. 2004. Taphonomy of an Early Pliocene Sivathere bonebed at Lange-Baanweg, Cape Province, South Africa. Journal of Vertebrate Paleontology 24(supplement to 3):115A.

Smith, R., and J. Kitching. 1997. Sedimentology and vertebrate taphonomy of the *Tritylodon* Acme Zone: A reworked paleosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 131:29–50.

Smithers, R.H.N. 1938. Notes on the stranding of a school of *Pseudorca crassidens* at the Berg River mouth. Transactions of the Royal Society of South Africa 25:403–411.

Spencer, L.M., B. Van Valkenburgh, and J.M. Harris. 2003. Taphonomic analysis of large mammals recovered from the Pleistocene Rancho La Brea tar seeps. Paleobiology 29:561–575

Sternberg, C.M. 1970. Comments on dinosaurian preservation in the Cretaceous of Alberta and Wyoming. Publications in Palaeontology 4. National Museums of Canada, Ottawa.

Stock, C. 1972. Rancho La Brea: A record of Pleistocene life in California. Science series no. 20, paleontology no. 11, Los Angeles County Museum of Natural History, Los Angeles.

Storey, M., and E.W. Gudger. 1936. Mortality of fishes due to cold at Sanibel Island, Florida, 1886–1936. Ecology 17:640–648.

Straight, W.H., and D.A. Eberth. 2002. Testing the utility of vertebrate remains in recognizing patterns in fluvial deposits: An example from the lower Horseshoe Canyon Formation, Alberta. Palaios 17:472–490.

Sundell, K.A. 1999. Taphonomy of a multiple *Peobrotherium* kill site: An archaeotherium meat cache. Journal of Vertebrate Paleontology 19(supplement to 3):79A.

Swift, P.K., J.D. Wehausen, H.B. Ernset, R.S. Singer, A.M. Pauli, H. Kinde, T.E. Rocke, and V.C. Bleich. 2001. Desert bighorn sheep mortality due to presumptive type C botulism. Journal of Wildlife Diseases 36:184–189.

Sykes, J.H. 1977. British Rhaetian bone-beds. Mercian Geologist 5:39–48.

Taber, R.D., K.J. Radeke, and D.K. Paige. 1982. Wildlife-forest interactions in the Mt. St. Helens blast zone. Final Report US National Forest, contribution no. 0m-40-055K3-1-2572. United States Forest Service, Vancouver, Washington.

Talbot, L.M., and M.H. Talbot. 1963. The wildebeest in western Masailand, East Africa. Wildlife monographs, no. 12. National Academy of Sciences and National Research Council, Washington, D.C.

Terry, R.C. 2004. Owl pellet taphonomy: A preliminary study of the post-regurgitation taphonomic history of pellets in a temperate forest. Palaios 19:497–506.

Terry, R.C. 2005. Raptors, rodents, and paleoecology: Testing paleoecological assumptions using taphonomic damage patterns at Homestead Cave, Utah. Geological Society of America, Abstracts with Programs 37(7):528.

Thompson, P.M., and A.J. Hall. 1993. Seals and epizootics: What factors might affect the severity of mass mortalities? Mammal Reviews 23:149–154.

Tramer, E.J. 1977. Catastrophic mortality of stream fishes trapped in shrinking pools. The American Midland Naturalist 97:469–478.

Trapani, J. 1998. Hydrodynamic sorting of avian skeletal remains. Journal of Archaeological Science 25:477–487.

Trueman, C. This volume. Trace element geochemistry of bonebeds. Chapter 7 *in* Bonebeds: Genesis, analysis, and paleobiological significance. R.R. Rogers, D.A. Eberth, and A.R. Fiorillo, eds. University of Chicago Press, Chicago.

Trueman, C.N., and M.J. Benton. 1997. A geochemical method to trace the taphonomic history of reworked bones in sedimentary settings. Geology 25:263–266.

Tulloch, D.G. 1970. Seasonal movements and distribution of the sexes in the water buffalo, *Bubalus bubalis*, in the Northern Territory. Australian Journal of Zoology 18:399–414.

Turnbull, W.D., and D.M. Martill. 1988. Taphonomy and preservation of a monospecific titanothere assemblage from the Washakie Formation (Late Eocene), southern Wyoming: An ecological accident in the fossil record. Palaeogeography, Palaeoclimatology, Palaeoecology 63:91–108.

Turner, A.H., C.E. Brett, P.I. McLaughlin, D.J. Over, and G.W. Storrs. 2001. Middle-Upper Devonian (Givetian-Famennian) bone/conodont beds from central Kentucky; reworking and event condensation in the distal Acadian foreland basin. Geological Society of America, North-Central Section, Abstracts with Programs 33(4):8.

Ulrichs, M., R. Wild, and B. Ziegler. 1979. Fossilien aus Holzmaden. Stuttgarter Beiträge zur Naturkunde, Serie C 11:1–34.

Vander Wall, S.B. 1990. Food hoarding in animals. University of Chicago Press, Chicago.

Van Devender, T.R., and J.I. Mead. 1978. Early Holocene and Late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. Copeia 1978(3):464–475.

Varricchio, D.J. 1995. Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana. Palaeogeography, Palaeoclimatology, Palaeoecology 114:297–323.

Varricchio, D.J. 2001. Gut contents from a Cretaceous tyrannosaurid; implications for theropod dinosaur digestive tracts. Journal of Paleontology 75:401–406.

Varricchio, D., F. Jackson, B. Scherzeer, and J. Shelton. 2005. Don't have a cow, man! It's only actualistic taphonomy on the Yellowstone River of Montana. Journal of Vertebrate Paleontology 25(supplement to 3):126A

Voorhies, M.R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Contributions to geology, special paper 1. University of Wyoming, Laramie.

Voorhies, M.R. 1975. Vertebrate burrows. Pp. 325–350 *in* The study of trace fossils. R.W. Frey, ed. Springer-Verlag, New York.

Voorhies, M.R. 1981. Ancient skyfall creates Pompeii of prehistoric animals. National Geographic 159:66–75.

Voorhies, M.R. 1985. A Miocene rhinoceros herd buried in volcanic ash. National Geographic Research Reports 19:671–688.

Voorhies, M.R. 1992. Ashfall: Life and death at a Nebraska waterhole ten million years ago. Museum Notes no. 81. University of Nebraska State Museum, Lincoln.

Voorhies, M.R., J.A. Holman, and X. Xiang-Xu. 1987. The Hottell Ranch rhino quarries (basal Ogallala: medial Barstovian), Banner County, Nebraska. 1. Geologic setting, faunal lists, lower vertebrates. Contributions to Geology, University of Wyoming 25:55–69.

Waldman, M. 1971. Fish from the freshwater Lower Cretaceous of Victoria, Australia with comments on the palaeoenvironment. Special papers in palaeontology 9. The Palaeontological Association, London.

Walsh, S.A., and D. Martill. 2006. A possible earthquake-triggered mega-boulder slide in a Chilean Mio-Pliocene marine sequence: Evidence for rapid uplift and bonebed genesis. Journal of the Geological Society, London 163:697–705.

Walsh, S., and D. Naish. 2002. Fossil seals from Late Neogene deposits in South America: A new pinniped (Carnivora, Mammalia) assemblage from Chile. Palaeontology 45:821–842

Weigelt, J. 1927. Rezente wirbeltierleichen und ihre paläobiologische bedeutung. Verlag von Max Weg, Leipzig.

Weigelt, J. 1989. Recent vertebrate carcasses and their paleobiological implications, J. Schaefer, trans. University of Chicago Press, Chicago.

Wells, J.W. 1944. Middle Devonian bone beds of Ohio. Bulletin of the Geological Society of America 55:273–302.

Whitfield, A.K., and A.W. Paterson. 1995. Flood-associated mass mortality of fishes in the Sundays Estuary. Water SA 21:385–389.

Wilkinson, D., and G.A.J. Worthy. 1999. Marine mammal stranding networks. Pp. 396–411 *in* Conservation and management of marine mammals. J. R. Twiss Jr. and R. R. Reeves, eds. Smithsonian Institution Press, Washington, D.C.

Wilson, M.V.H. 1987. Predation as a source of fish fossils in Eocene lake sediments. Palaios 2:497–504.

Wilson, M.V.H. 1996. Taphonomy of a mass-death layer of fishes in the Paleocene Paskapoo Formation at Joffre Bridge, Alberta, Canada. Canadian Journal of Earth Sciences 33:1487–1498.

Wolff, R.G. 1973. Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California (U.S.A.). Palaeogeography, Palaeoclimatology, Palaeoecology 13:91–101.

Wood, J., R. Thomas, and J. Visser. 1988. Fluvial processes and vertebrate taphonomy: The Upper Cretaceous Judith River Formation, south-central Dinosaur Provincial Park, Alberta, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 66:127–143.

Wood, R.C. 1988. A monospecific death assemblage of fossil side-necked turtles from the Cretaceous of Brazil. International Symposium on Vertebrate Behavior as Derived from the Fossil Record, occasional paper 22. Museum of the Rockies, Bozeman, Montana.

Worthylake, K.M., and P. Hovingh. 1989. Mass mortality of salamanders (*Ambystoma tigrinum*) by bacteria (*Acinetobacter*) in an oligotrophic seepage mountain lake. Great Basin Naturalist 49:364–372.

Wurtsbaugh, W.A., and R.A. Tapia. 1988. Mass mortality of fishes in Lake Titicaca (Peru-Bolivia) associated with the protozoan parasite *Ichthyophthirius multifiliis*. Transactions of the American Fisheries Society 117:213–217.

Yeager, L.E. 1943. The storing of muskrat and other food by minks. Journal of Mammalogy 24:100–110.

Zeigler, K.E. 2002. A taphonomic analysis of a fire-related Upper Triassic fossil assemblage. Unpublished masters thesis, University of New Mexico, Albuquerque.

Zeigler, K.E., L.H. Tanner, and S.G. Lucas. 2005. Mass mortality and post-paleowildfire erosion: Evidence from a Late Triassic death assemblage, Chama Basin, north-central New Mexico. Geological Society of America, Rocky Mountain Section, Abstracts with Programs 37(6):7.

Zonneveld, J.P., W.S. Bartels, S.D. Wolfe, G.F. Gunnell, and J.I. Bloch. 2001. The occurrence of fossil vertebrates along strandlines of paleo-Lake Gosiute, Wasatch Formation, South Pass, Wyoming. Journal of Vertebrate Paleontology 21(supplement to 3):117A.