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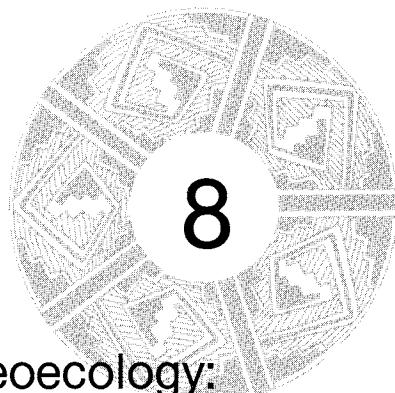
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Taphonomy and Paleoecology: A Critical Review of Archaeology's Sister Disciplines

DIANE P. GIFFORD

Earthlings are great explainers, explaining why this event is structured as it is; telling how other events may be achieved or avoided. I am a Tralfamadorian, seeing all time as you see the Rocky Mountains. All time is all time. It does not change. It does not lend itself to warnings or explanations. It simply is. Take it moment by moment, and you will find that we are all, as I've said before, bugs trapped in amber.
[Kurt Vonnegut, Jr. *Slaughterhouse Five*]

INTRODUCTION

It is always refreshing and sometimes informative to look at the same thing from a different point of view. Paleontologists and archaeologists do look at the same thing from different points of view, and a comparison of the ways in which practitioners of these two disciplines go about their work can clarify the unique features and common problems of each. Paleontologists and archaeologists both study the remnants and effects of once-living organisms and share many practical methods and theoretical concerns. The history of paleontology and of archaeology over the last 30 years displays many striking parallels. The phases of development described for archaeology by Clarke (1973) might equally well apply to paleontology, with postwar advances in technology and chronology-building leading to more

ambitious attempts to reconstruct ancient life relations. These attempts, and critiques of them, led in turn to increased attention to methods of recovery and analysis of evidence, to the nature of the prehistoric record and the processes that formed it, and to the basic goals and philosophy of the discipline as a historic science. This sequence is not unique to paleontology and archaeology, since a similar pattern of development can be discerned in the related field of biogeography (e.g. Ball 1975; Croizat *et al.* 1974), and even more distantly related disciplines have seen many of the same philosophical debates, such as those in history regarding the nature of historical explanation (e.g., Wallerstein 1974). As Ball suggests in his review of the development of biogeography, the ultimate causes of such parallel sequences of development in disciplines that share so few workers may lie in the general intellectual trends of an era.

In such similar fields as paleontology and archaeology it is not surprising that the parallels are especially striking and that the specific findings, methods, and theoretical debates of one discipline should be of interest to practitioners of the other. This chapter reviews one area within paleontology, taphonomy, that is of special interest to archaeologists concerned with the processes of "site formation," which have received increased attention in the 1970s (e.g., Binford 1978; Schiffer 1976; Gifford 1977, 1978; Sullivan 1978).

Some Definitions

Taphonomy is a word coined by the Russian paleontologist I. A. Efremov (1940) from the Greek words for tomb or burial (*taphos*) and for law or systems of laws (*nomos*), to denote that subdiscipline of paleontology devoted to the study of processes that operate on organic remains after death to form fossil deposits. Perhaps the most concise definition of the field's purview is Efremov's own: "the study of the transition (in all its details) of animal remains from the biosphere into the lithosphere, i.e. the study of a process in the upshot of which organisms pass out of the different parts of the biosphere and, being fossilized, become part of the lithosphere" (Efremov 1940:85). Following this definition, taphonomy may be seen as that area of paleontological research that defines, describes, and systematizes the nature and effects of processes that act on organic remains after death.

In common with many other branches of historical science, taphonomy involves two distinct but necessarily related lines of investigation. The first is devoted to studying observable contemporary processes involved in this transition of organic remains from biosphere to lithosphere, focusing on those which produce effects analogous to those traces observed in the fossil

evidence. The second is devoted to analysis of the prehistoric evidence in light of findings derived from the first line of investigation. This "confrontation of the record with knowledge of present processes" (Simpson 1970:84) is the basic research strategy of the modern historical sciences. It rests on the assumption that certain properties or characteristics of the universe have remained uniform in time and space, even though the configurations produced by the interactions of such properties have changed and permuted through time. Simpson (1970) called this assumption uniformitarianism with regard to "immanent" properties of the universe, in contrast to assumption of "configurational" uniformitarianism.

Observing present-day events and their effects in order to give meaning to the prehistoric record has been called *actualism*, a term which, for want of a more familiar cognate, I will use in this chapter. Actualism takes its meaning from the original significance of the Latin root, denoting those things presently or currently in existence (Simpson 1970), and has been used by European researchers to refer to the part of historical science that involves contemporary observation (e.g., the Germans' *Aktuopaläontologie*). For taphonomy, as for other branches of historical science, study of the present is the key to investigation of the past.

Many English-speaking paleontologists use the word taphonomy to denote the study of all aspects of this transition from life to fossil context. Most Europeans and some Americans, however, follow A. Müller's further division of taphonomy into two subsidiary realms. Müller (1951) called studies of the transformations of organic remains between death and final burial *biostratinomy* and those covering the span between final burial and recovery *diagenetic studies*. (Diogenesis refers to those alterations of sediments, which can include organic remains, that transform them into rock.) Since the processes that operate on organic remains in these two spans differ substantially, Müller's subdivision is a useful one, although Lawrence (1971) points out that the second label is a somewhat unfortunate choice, since diogenesis of organic remains can actually begin prior to final burial.

Taphonomy and Paleoecology: Goals and Problems

While in the strictest definition taphonomy is devoted to analysis of post-mortem processes affecting organic remains, it seldom has been pursued except as an adjunct to paleoecology, paleobiogeography, or general evolutionary studies. Few, if any, paleontologists would characterize themselves as taphonomists, but many would call what they really do a mixture of taphonomy and these other lines of investigation. Paleoecology, especially, and taphonomy have evolved together over the last 30 years, since

taphonomic analysis has been viewed as a necessary component in paleoecological research.

Taphonomy's dependent status has had critical implications for its development, since its research has been directed by the questions and perspectives current in paleoecology. While the links between these two subdisciplines are both natural and necessary, development of taphonomy as a broadly applicable body of theory and method may well have been impeded by its subordinate role in a rather poorly defined paleoecological research program. Furthermore, paleoecology has not benefited from taphonomic findings to the extent that it could in better defining its goals and methods of research. The source of these problems seems to be a poor definition of the proper role of actualistic research in informing the analysis of prehistoric materials, and a misplaced research emphasis that focuses too heavily on ancient ecosystems and not enough on paleontological accumulations.

These theoretical problems are worth discussing in a review of this sort because archaeology shares with its sister discipline an ongoing concern with defining productive strategies for "indirect observation of the past" (Fritz 1972). When I began this review, I believed that paleoecology and taphonomy, because of the wealth of available literature on analogous modern organisms and ecosystems, were probably in a more methodologically advanced state than was archaeology. As I did further reading in this literature, however, I came to conclude that archaeologists are at present more consciously and systematically applying productive approaches to the study of prehistoric remains. Specifically, there has been a trend in archaeology toward actualistic study of site and assemblage formation that very deliberately focuses on these two basic materials in the study of the prehistoric past (e.g., Binford 1977, 1978, 1980, 1981; Gifford 1977, 1978, 1980; Schiffer 1976, 1977; Sullivan 1978; Yellen 1977a). It is a research orientation that emphasizes archaeologically relevant outcomes of the processes studied, and is an optimally efficient use of actualism in historical science. As I have previously suggested (Gifford 1980), far fewer paleontological researchers have taken an assemblage- or deposit-focused approach in their actualistic research. This may be a major impediment to forward progress in taphonomy and paleoecology.

Few archaeologists would contend that the recent period of reorientation and discussion in their discipline has left it with a commonly agreed upon methodology and research program. Most, however, would probably agree that the energy spent in clarifying the nature of archaeological sites, materials, and basic research methods has had a beneficial effect on the field. It may well be time for paleontologists to engage in a similar evalua-

tion of their expectations and methods of studying the relations among living organisms.

This chapter begins by laying some historical groundwork for a critical discussion of these matters, reviewing the last three decades' developments in taphonomy and paleoecology. The English language literature will be the primary focus, since it forms a distinct unit with its own research orientations and problems. Despite the differences between vertebrate and invertebrate organisms, studies of both classes are included, because the studies share many fundamental problems of method and theory. This review is by no means bibliographically exhaustive but rather gives a selection of works that exemplifies the course of development of the two fields. The subsequent section turns to an analysis of the current state of affairs in paleoecology and taphonomy and suggests some ways of ordering extant findings and going about further research. The last major section of this chapter reviews those aspects of vertebrate taphonomy of greatest interest to archaeologists, discussing the established or hypothesized linkages between various agents of modification, attrition, and transport, and observable traces in bone assemblages.

HISTORICAL BACKGROUND

Early Research

Although I. A. Efremov coined the term taphonomy, he did not write the earliest works on postmortem transformations of animal remains. German paleontologists were the most active earlier workers in this field (e.g., Abel 1914; Weigelt 1927; Richter 1928; Hecht 1933). The term "Biostratinomy" was coined by Weigelt to delineate much of this realm of study. The German tradition of *Aktuopaläontologie*, the study of living and recently dead organisms as potential fossil entities, has continued, along slightly different lines from taphonomic research in the English-speaking world. An example of such research is Wilhelm Schäfer's (1972) massive work on the life and death processes affecting North Sea shallow-water communities, which includes a descriptive typology of various communities' life and death facies. A major synthesis and restatement of German taphonomic research was presented by A. Müller (1951). This work has influenced the analytic approaches of some English-speaking researchers (e.g., Lawrence 1971). Much of the German research of the 1970s came to be coordinated under a loose federation of scholars "*Sonderforschungsbereich 53*," (SFB) working out of a number of different institutions and including archaeol-

ogists as well as geologists and paleontologists. Much of the recent focus of the group has been on studies of "fossil diagenesis" and detailed analysis of the history of fossil-bearing deposits. A good summary of the SFB orientation and literature is to be found in an English language article by Herm (1972) and various of David Lawrence's writings (Lawrence 1971, 1979a,b,c). The German approach contrasts with that of English-speaking scholars in a number of ways, as will be discussed later in this chapter.

It is an interesting point of history that the work of Efremov, a Russian, was in the short run to be more influential in the development of taphonomy in the English-speaking world than was the German school. Efremov conducted research and did most of his primary writing in the 1930s and early 1940s. He had a strong nomothetic orientation, explicitly seeking to discover laws governing the formation of fossil accumulations of terrestrial vertebrates (Efremov 1940, 1953). Efremov's own research focused on discerning regularities in processes governing the preservation of both sediments and the organic remains they contained (Efremov 1953: 150). His observations and analytic methods, and his careful taxonomy of fossil-bearing deposits, still merit study. Partly due to the language barrier, Efremov's influence was not immediately felt in Western vertebrate paleontological circles, although a general concern with the influence of the factors Efremov discussed was not unknown. The word taphonomy, and the implications of Efremov's research, gained increasing recognition in the early 1960s through the influence of Everett Olson, who was Efremov's principal English translator and a personal friend during the last years of the Russian scholar's life. Olson's work on community evolution in the Permian and other geologic periods has long incorporated taphonomic analyses (e.g., Olson 1957, 1966, 1971; Olson and Vaughn 1970). He has recently contributed to the debate over appropriate application of uniformitarian assumptions in the paleoecologic reconstruction (Olson 1980).

The "New Paleontology"

The 1950s and 1960s saw major reorientation of research goals in paleontology. After World War II, the focus of paleontological investigations shifted from purely descriptive or chronological research to attempts at reconstructing prehistoric population dynamics and community relations, as well as detailed analyses of phyletic evolution and its possible determinants. Much as in archaeology, a point came in the late 1960s and early 1970s at which some paleontologists argued that the fossil record itself could be used to discern and study lawlike regularities in the evolution of living systems (e.g., Schopf 1972; Raup and Stanley 1971; Eldredge and Gould 1972). Prior to such manifestos, however, were a series of steps

toward a new definition of research goals and methods. This process involved the growth of taphonomy as an important part of paleontological research and increased emphasis on observations of contemporary processes as an aid in assigning meaning to patterning in the fossil record.

Just as archaeologists of the 1950s were stimulated by the accumulation of chronologic documentation and technical expertise in their fields, so too were paleontologists. Paleontologists at the same time received an added impetus to new research into prehistoric life processes with publication of new findings and generalizations in biology and ecology. The first influential publication was probably Deevy's (1947) compilation of life tables for vertebrates and invertebrates, in which relative abundances of age classes were used to construct life tables and survivorship curves and to infer the population dynamics of various taxa. Relative abundances were not long thereafter employed to analyze interspecific and community relations (e.g., MacArthur 1957, 1960). Since relative abundance data were available for both vertebrate and invertebrate fossil remains, a number of paleontologists attempted to use them to infer paleoecological relationships, which naturally led to heightened preoccupation with taphonomic effects.

Invertebrate Studies

Size frequency distributions in marine mollusks, reflecting age distributions, were discussed by Boucot (1953) as a means of studying population dynamics in fossil samples. This and other early publications emphasized the potential biasing effects of postmortem aqueous transport, through size-dependent winnowing or attrition. Several early articles cautioned against naive use of relative abundance data from fossil assemblages, citing the problems that stem from inadequate or noncomparable sampling procedures and from unrealistic descriptive terminology or paradigms of deposition, as well as those caused by transport or attrition (e.g., Craig 1953; Rigby 1958). These early essays on the potential of fossil assemblages for reconstructing population dynamics recognized the difference between what might be inferred from a catastrophically formed assemblage, in which a representative sample of all living age classes was entombed together more or less instantaneously, forming a "snapshot" of a living population structure, and those assemblages formed attritionally, by the deaths of different-aged animals over a prolonged period, indirectly reflecting the age-specific survivorship of a population. The need to identify the basic nature of sample assemblages, and to assess the possible effects of size-selective transport or destruction on them, was thus recognized at the outset.

In response to the widely perceived need for a better understanding of

the effects of postmortem processes on invertebrate remains, English-speaking paleontologists began their own brand of *Aktuopaläontologie*, undertaking observations of modern invertebrates, mainly marine, in natural and experimental settings. The rationale for such research was expressed by R. G. Johnson:

We have available at the present some of the philosophical and technical means to aid the study of organic evolution in its ecological context. Many aspects of the fossil record can be understood only in the context of community ecology. Our primary sources of data cannot be fully exploited, however, until we have detailed knowledge of the circumstances surrounding the formation of fossil assemblages (Johnson 1957:534).

In their studies of contemporary "fossils in the making," paleontologists were following the basic actualistic strategy long used by geologists in their attempts to assign processual meaning to patterns in prehistoric deposits, but little was explicitly said about the rationale for this approach.

Most such paleontological studies were intended to clarify the relation between postmortem processes and key variables observed in fossil assemblages and deposits, such as shell-size frequency distributions, relative abundances of species, degree of disarticulation and attrition of parts, and *in situ* orientation. Earlier studies concentrated on aqueous transport, sorting, destruction, and burial of biological remains. Few addressed the relation between relative species abundance in a living community and that in its immediate "fallout": the death, or surface, assemblage on which various processes of transport and attrition might work. It was not until the mid-1960s that articles discussing this relationship began to appear. These included Fagerstrom's (1964) critical review of the basic terminology and concepts involved in the search for fossil communities and Lawrence's (1968) careful recapitulation of the steps involved in analysis of a partially preserved fossil community, from which the more delicate member taxa had disappeared or were represented solely by trace fossils. Warme (1971) presented a detailed comparison of relative species abundances of a living mollusk community and the surface assemblage of shells it produced, noting strong overall equivalence between the taxonomic relative abundance constitution of the two assemblages.

Kranz (1964a,b) delineated another potential source of inconsistency between living communities and their resulting death assemblages, even in cases of catastrophic burial, by experimentally demonstrating that different mollusk species in a single community may possess substantially different capacities to escape from a catastrophic burial event. Better burrowers are often able to escape, while their less mobile neighbors suffocate and become part of the potential fossil record, giving rise to a biased species representation. Kranz supplemented his experiments with a series of com-

puter simulations modeling the outcomes of such events in a wide variety of community types and sediment load depths, and was able to characterize the situations in which the most and least "Houdini bias" could occur. Craig and Oertel (1966, 1967) have likewise employed computer simulations to model outcomes of specified growth, recruitment, and death rates on assemblage structure. Lasker (1976, 1978) used computer simulation to assess the interaction of turnover rates and time-dependent preservation rates in producing different types of benthic marine assemblages.

The effects of water transport on the constitution of invertebrate assemblages have, as noted, been intensively studied by invertebrate paleontologists in several ways. One approach entails observing the effects of transport in surface assemblages produced by natural communities, as in the work of Johnson (1960, 1962), Lawrence (1968) and others. Another approach involves controlled experimentation with different types of invertebrates, either in natural environments (e.g., Nagle 1967; Lever and Thijssen 1968) or in laboratory contexts (e.g., Chave 1960, 1964; Nagle 1967; Brenchley and Newall 1970; Abbott 1974; Weaver 1976). The effects of water transport on shell attrition have been extensively studied and described by Seilacher (1973). Driscoll (1967, 1970; Driscoll and Weltin 1973) conducted a series of informative experiments on shell attrition in natural environments with different substrates and levels of wave energy. His work bears reading by both vertebrate paleontologists and archaeologists for its consistent emphasis on the implications of such studies for understanding patterns in fossil assemblages.

By the early 1960s paleoecological reconstruction was cited as a major area of invertebrate paleontological research, and taphonomic analysis a necessary adjunct in such pursuits (e.g., Ladd 1957; Beerbower 1960; Ager 1963; Imbrie and Newell 1964; Valentine and Mallory 1965; Valentine and Peddicord 1967). In contrast to their archaeological counterparts, only a few invertebrate paleontologists involved in paleoecology have concerned themselves in print with underlying problems of method and theory in historical science. The most interesting and broadly applicable discussion of these problems by an invertebrate paleontologist are probably those of David Lawrence (1968, 1971, 1979c). Lawrence critically discussed the goals and methods of paleoecology and examined the problems involved in the use and misuse of uniformitarian assumptions in paleoecological reconstructions. He criticized (Lawrence 1971) many paleontological colleagues for what he called "transferred ecology," that is, inferring from an isomorphic physical relationship between a fossil and a modern specimen or specimen set that other aspects of structure and interactions in the fossil *community* were essentially the same as that of the modern exemplar. This is the same type of unwarranted inference as is involved in the misuse of ethnographic

analogy in archaeology (e.g., Binford 1968; Freeman 1968). Lawrence argued that projection of modern community structure into the past effectively stymies the study of community evolution, which should be one of the goals of modern paleontology. Lawrence proposed that paleoecology be defined as the study of interrelationships between living organisms and their environment in the geologic past (Lawrence 1971:594), and advocated a more conservative and painstaking approach to the use of analogic reasoning and uniformitarianism. Lawrence listed features of fossil deposits that could be used to infer relations between organisms and environments or between organisms and other organisms, using a more conservative uniformitarian approach. These include direct evidences of interactive behavior in the form of trace fossils, and aspects of functional morphology, including body structure and life orientation. Continuing problems of defining an acceptable scope and methodology in paleoecology will be discussed in more detail after a review of the history of vertebrate paleoecology and taphonomy.

Vertebrate Studies

As in invertebrate studies, the earliest attempts to go beyond simple environmental reconstruction in vertebrate paleontology were essays in reconstructing population structure and analysis of survivorship curves. In the case of vertebrates, dental eruption and wear patterns were used to assess age at death (e.g., Kurtén 1953, 1954). Another kind of reconstruction, also relying upon relative abundance data, was first attempted in the 1950s by J. A. Shotwell (1955, 1958, 1963). Shotwell tried, on the basis of adjusted relative abundance figures, to factor out the "proximal" and "distal" communities that contributed to a single fossil accumulation, that is, those elements transported from some distance and those originating near the site of deposition. The basic ideas underlying Shotwell's method have been used by other paleontologists (e.g., Estes and Berberian 1970) and even by an archaeologist (Thomas 1971). However, subsequent critiques raised serious questions about statistical and taphonomic biases for which Shotwell's approach did not account (see the following). Other similar types of early essays in vertebrate paleoecology include VanValen's (1964a,b) attempts to reconstruct population dynamics and species diversity indices from paleontological samples and Konizeski's (1957) reconstruction of a Pliocene mammalian community using fossil and sedimentological evidence and body-size distribution data from modern mammal populations.

Critical evaluations of earlier attempts at paleoecological reconstruction led vertebrate paleontologists to consider the same kinds of taphonomic ef-

fects, especially transport and attrition, as had come to concern invertebrate researchers. However, concerted experimentation with and observation of vertebrate remains in relevant contemporary situations did not begin as early nor develop as swiftly as in invertebrate studies. The earliest taphonomic analyses of vertebrate fossil assemblages, though often quite elegant, relied mainly on sedimentary rather than osteologic evidence, with some reference to the rather scanty biological literature on the fate of vertebrate remains after death (e.g., Olson 1962). In 1963, Zangerl and Richardson published a detailed reconstruction of environment and community relations of plants and animals fossilized in two Pennsylvanian shale deposits, which exemplified this approach. The report combined sedimentological analysis and close documentation of the decay and damage patterns exhibited by fossil plants and animals with modern data on the water depth and temperature requirements and behavior of descendant lineages, resulting in a detailed reconstruction of the environmental context and relations of the species studied.

When research into postmortem processes affecting vertebrate remains was undertaken, considerable emphasis was placed on disarticulation studies, since the sequence and rates of disarticulation of the vertebrate skeleton's complex of preservable parts were scarcely documented in the biological literature (but see Weigelt 1927). Many of the first taphonomic observations were reported anecdotally, either in short articles or as part of reports on fossil localities. In 1965, H. Toots (1965a,b) of the University of Wyoming published two brief articles intended to clarify aspects of vertebrate taphonomy on the significance of random orientation in fossil bone assemblages and on the sequence of disarticulation in mammals, based on observations of modern carcasses. Toot's papers, although based on observations of relatively few cases, are noteworthy for their systematic approach to the problems discussed. In 1967, Clark *et al.* published a detailed and methodologically advanced reconstruction of paleogeography and community structure in Big Badlands Oligocene deposits. In a separate chapter within the monograph, Clark and Kietzke outlined their approach to studying the effects of taphonomic processes on vertebrate remains, which included some observations on modern vertebrate bone durability and disarticulation sequences. They also discussed in detail the sources and effects of collecting bias, as monitored by their own experiments in various collecting techniques. This section of the report contains a model of the sequence and effects of taphonomic alterations of vertebrate remains (Clark and Kietzke 1967:114-120) that has served as a template for other workers in approaching taphonomic research problems.

In 1969, M. R. Voorhies published an analysis of the Pliocene vertebrate fauna from the Verdigris Quarry in Nebraska (Voorhies 1969a). His re-

search incorporated more formal experimentation than had any previously published work on vertebrate taphonomy. In addition to studies of carcass disarticulation and bone survival under natural conditions, Voorhies undertook a series of experiments on aqueous transport of bone, using a circulating hydraulic flume. On the basis of these experiments, he was able to characterize the transport potential of various types of bones. Voorhies' and others' findings will be discussed in a subsequent section of this chapter.

Voorhies (1969b) also published a brief taphonomic critique of Shotwell's community reconstruction methods. From his experimental and natural habitat observations, he argued that no simple relation could be assumed between relative abundances of elements and distance traveled from locale of life and death. Voorhies cited the variation in bone durability of various taxa in the face of both carnivore and water transport attrition and the differing transport potentials of various elements in flowing water as two important factors influencing assemblage structure with which Shotwell's numerical analysis did not reckon. More recently, the core of Shotwell's numerical method, the estimated minimum number of individuals, has been subject to critical examination (e.g., Grayson 1978a,b, 1979; Holtzman 1979). The central point of these criticisms is that minimum numbers estimates overrepresent rare taxa in relation to more numerous ones. Details of this critique and proposed alternative methods for quantifying faunal remains have recently been offered to archaeological and paleontological audiences by these authors and will not be recapitulated here.

By the end of the 1960s, many North American reports on vertebrate fossil localities devoted considerable space to paleoecological topics and incorporated taphonomic analysis as part of the research program, combining contextual analysis with what was then known about the determinants of bone transport, the action of biological agents, and other factors affecting the preservation of bone (e.g., Clark and Guensberg 1970; Estes and Berberian 1970; Dodson 1971; Wolff 1973, 1975). However, little independent taphonomic research, either natural habitat observations or experimentation, was conducted in English-speaking circles during the 1960s. During this decade, little reference was made to the methods or findings of the German school, which included research in vertebrate taphonomy. This situation began to change in the early 1970s with publication of Wilhelm Schäfer's book in English translation 10 years after it was published in Germany, and with publication of English language articles by a number of other German writers (e.g., Herm 1972). About the same time, the work of German researchers was being increasingly cited by North American in-

vertebrate paleontologists, especially with regard to method and theory (e.g., Lawrence 1971; Raup 1972).

Contemporary observations and experimental studies in vertebrate taphonomy began to increase in frequency at the very end of the 1960s, with the growth of a less traditional type of paleontological research. This could not unfairly be called the anthropocentric school of paleoecologic and taphonomic research. Much of the time and energy expended by practitioners of this kind of research have produced results relevant only to the study of hominid behavior as a category of taphonomic process, but some of the most useful of all recent research in vertebrate taphonomy and paleoecology has been carried on within the framework of hominid-oriented studies. These studies can be divided into two groups: those concerned with the restricted problem of distinguishing hominid from other agents of bone accumulation and modification, and those concerned with broader topics and procedures in taphonomic and paleoecologic research.

From the 1950s on, anthropological researchers in Africa, Australia, and North America became increasingly interested in determining whether hominids were agents of accumulation of certain "early" bone deposits that lacked other clear evidence of human activity. African deposits of this type, the australopithecine-bearing breccias of the Transvaal, are some 1-2 million years older than those of interest on the other two continents, but the basic problem faced by all researchers was the same: deciding whether bone assemblages produced by hominids bore any characteristics that distinguished them from those produced by other agents, especially bone-processing mammalian carnivores. On all three continents, experimental observations of modern human and nonhuman bone processors were undertaken as a logical course of action in elucidating this question. This review will pass very briefly over the historical development and attendant problems of such studies and will present specific findings in a later section. A forthcoming book by Lewis Binford (1981) documents and criticizes this research in great detail.

The controversy over human agency and bone accumulations heated up after World War II with Raymond Dart's vehement allegations that both the fracture patterns and the element frequencies he had documented in the bone assemblage from Makapansgat, one of the australopithecine-bearing sites in the Transvaal, could only have been produced by hominids. Dart contended that the evidence indicated that the australopithecines were predatory implement users with a homicidal bent (Dart 1956, 1957a,b, 1958; Dart and Kitching 1958). Dart's basic contentions were supported by little in the way of contemporary observations of bone fracture or attrition, although he did collect some anecdotal material on the use of bone tools by

modern peoples living in or near South Africa. Two assumptions about the dynamics of bone fracture and the formation of the breccia sites underlay Dart's arguments. First, he assumed that spiral fractures of long bones could only be produced by a "crack and twist" technique, which only hominids could execute. Second, he assumed that all the cavities in which the bone deposits formed had been inhabitable, walk-in caves or shelters of the sort inhabited by Upper Paleolithic peoples of southwestern France or later Stone Age peoples in Africa. Neither of these assumptions has stood the test of further research. Added impetus was given to researchers documenting "natural" versus hominid patterns of bone modification with discovery of animal bones and stone tools in apparent association in the lowest levels of Olduvai Gorge (e.g., Leakey 1971).

Probably the best set of experiments and observations relevant to Dart's allegations are those of C. K. Brain. In a series of methodical studies of the dynamics of bone attrition and assemblage formation, Brain established that a number of Dart's assumptions about the determinants of fracture and element frequency were incorrect (Brain 1967a,b, 1968, 1969, 1970, 1975, 1976, 1980). Brain found that patterns of damage and element frequencies very similar to those of the Makapan assemblage could be produced by nonhuman bone processors. He was among the first to point out the role that varying levels of durability of different elements of a skeleton can play in determining their survival rates. Brain also noted that a good number of the South African "caves" were, at the time the bone deposits were forming, fissures or vertical solution cavities quite uninhabitable by hominids. Other observations of carnivore effects on bone and on carcass disarticulation were made in Africa by Hughes (1954a,b, 1958, 1961), Sutcliffe (1970), Crader (1974), Hill (1975, 1976, 1979a,b, 1980), Shipman and Phillips-Conroy (1976, 1977), and myself (Gifford 1977). With the exception of Hill's more recent publications, nearly all this research was largely anecdotal or directed at "answering" Dart's allegations and has yielded little in the way of broadly transferrable generalizations.

In North America, bone specimens or deposits from time spans in which human habitation of the continent is uncertain became the subject of similar arguments over human versus nonhuman agents of accumulation and modification. Here, however, most of the debate has focused on patterns of modification rather than on element frequencies. A number of workers have undertaken experimental observations of "typical" human and carnivore bone processing with the aim of better understanding the dynamics and products of bone attrition in those situations. Bonnichsen (1973, 1975, 1979) has reported observations of human and carnivore bone processing, and similar carnivore processing observations are part of a wider range of taphonomic work with bone in North American environments conducted by Gary Haynes (personal communication 1978, 1980).

Bone attrition patterns produced by domestic dogs were reported by Binford and Bertram (1977), and a forthcoming book by Binford (1981) will present detailed descriptions of bone processing by wolves. Observations or experimental replications of bone breakage patterns of indigenous peoples have been made by Binford (1978) and Yesner and Bonnichsen (1979). Sadek-Kooros (1973, 1975) undertook controlled experiments on bone fractures caused by humans that were directed at explaining patterns of damage in prehistoric bone deposits from Jaguar Cave, Idaho. Similar experimental work has been carried on by Bonnichsen (1979) with the aim of elucidating the origin of purported bone tools from Alaska. Similarly, Australian researchers conducted observations of marsupial bone processors in an attempt to better specify the probable agents of accumulation involved in the formation of certain prehistoric bone assemblages (e.g., Douglas *et al.* 1966; Lundelius 1966), or have drawn on the general taphonomic literature to assess the nature of others of an equivocal nature (e.g., Hope 1978).

While some of the studies already cited have produced useful and broadly applicable findings, a number display serious methodological problems, either in basic research design or in confusion about basic causal relations. These will be discussed in more detail in the next section.

Perhaps it is well to remember that this entire line of investigation, which seems to border on an obsession in anthropological circles (see for example the resuscitation of the australopithecine debate—Read-Martin and Read 1975; Bonnichsen 1975; Hill 1976; Shipman and Phillips-Conroy 1977; Binford and Bertam 1977), actually deals with a very small segment of the realm of concern in vertebrate taphonomy and paleoecology.

As noted earlier, a number of persons involved in research on hominid paleoecology have devoted their energies to broader problems in the study of taphonomic processes and paleoecologic evidence. Much of this work has gone on in the Old World, primarily in Africa, and more of it has been carried on by persons who are actually earth scientists or paleontologists than is the case with the research already discussed. This research has involved substantial amounts of experimentation and observation of contemporary processes, as well as extensive sampling and comparison of vertebrate remains in a variety of depositional environments. The African bias in such research stems in part from the vastly greater amount of funding available for research on early hominids and hominoids on this continent. Moreover, parts of Africa, in addition to the North American Arctic and inland Australia, constitute some of the only places left on earth where sufficiently large numbers of terrestrial vertebrates live and die in situations of interest to paleoecologists (e.g., Shipman 1975).

As was the case in North American vertebrate taphonomy and paleoecology, earlier research heavily relied on sedimentological data to assess the operation of taphonomic processes in the formation of various fossil

deposits, and later research was specifically directed at better understanding bones as sedimentary particles. The late geologist W. W. Bishop, was among the active and influential earlier workers with a strong interest in hominoid evolution and ecology (e.g., Bishop 1971; Bishop *et al.* 1975). His thoughtful analyses of the sedimentary evidence for the contexts of vertebrate life, death, and burial (e.g., Bishop 1976, 1980) exemplify the productivity of a strongly geologic approach. Contemporary observations of bone assemblages with the specific intent of understanding more about the formation of fossil deposits were conducted by A. Hill, one of Bishop's students, who has published works on rates and sequence of disarticulation of ungulate skeletons (Hill 1976, 1979a,b, 1980).

A considerable amount of productive work in taphonomy and topics related to paleoecology was carried out in the 1970s by A. K. Behrensmeyer, a sedimentary geologist and paleontologist who transferred and innovated upon many of the North American approaches in East Africa and other areas. The published work of Behrensmeyer and associates is characterized by consistent attempts to link research findings to the analysis of fossil deposits. This research includes further investigations into aqueous transports of bone in the laboratory (Behrensmeyer 1975a,b; Boaz and Behrensmeyer 1976) and in the field (see Hanson 1980), description and calibration of bone weathering (Behrensmeyer 1978), description of biological agents of bone damage and deposition (Behrensmeyer *et al.* 1979; Behrensmeyer and Dechant-Boaz 1980), and tests of the effects of various sampling strategies on assemblage reconstruction (Behrensmeyer, personal communication 1975). Behrensmeyer *et al.* (1979) conducted a comparison of a living vertebrate community in a region with the surface assemblage of bones in the same area, paralleling the work of Warne (1971) with invertebrates and various German *Aktuopaläontologisten* (e.g., Schäfer 1972). Their comparison treats the effects of different species' turnover rates and size-dependent preservation potentials on the relative abundances and diversity of species in a surface assemblage. Archaeologists are now familiar with effects of the cultural equivalent of differing turnover rates on archaeological assemblages, caused by disparities in the use-lives and discard rates of various artifact types (e.g., David 1972; DeBoer 1974).

Findings from this and other research will be discussed in detail in a subsequent section of this chapter. Analyses of paleontological and archaeological assemblages that have incorporated findings of these studies are now numerous; in the Old World these include those of Hill and Walker (1972), Shipman (1977, n.d.), Gifford and Behrensmeyer (1977), Pilbeam *et al.* (1979), and Badgley and Behrensmeyer (1980).

As has been the case with invertebrate studies, extended discussions of theoretical problems have been rare in the literature of vertebrate

taphonomy and paleoecology. Some discussion of the use of uniformitarian assumptions and analogic reasoning is normally included as a rationale for contemporary observations in taphonomy (e.g., Behrensmeyer 1975b; Hill 1976; Shipman 1977, n.d.), but exactly how this strategy may apply to paleoecological research has seldom been explicitly discussed, nor has the overall goals of paleoecology. This should not be taken to reflect unanimity of opinion among vertebrate paleontologists on these issues, since substantial differences of opinion do exist concerning the goals of paleoecological research and the use of generalizations derived from modern ecological studies in such research.

These differences are often more readily discerned in informal discussions than in the published literature. In 1976, a Wenner-Gren conference on Cenozoic vertebrate taphonomy and paleoecology with a focus on Africa brought together a number of English-speaking researchers who worked in Africa with a few colleagues who dealt in North American materials. In the course of symposium discussions, participants sorted into two groups with different theoretical stances and expectations. One group contended that formulation of broadly applicable generalizations about the operation and effects of postmortem processes should be a major objective in taphonomy; others argued that the formation of fossil deposits involved sufficiently unique combinations of events that generalizations sufficient to embrace all cases would necessarily be banal. Actually, it was clear that a continuum of opinion existed among participants regarding admissible kinds of applications of generalizations in taphonomy and paleoecology (see also Behrensmeyer and Hill 1980; Olson 1980). The discussions that touched on these matters, in common with nearly all of the published works on taphonomy and paleoecology, did not explicitly come to grips with the implications of uniformitarianism or actualistic research for these fields. Classification of these theoretical stances in "nomothetic" and "idiographic" camps, which has also occurred in geology as well as archaeology, (e.g., Simpson 1963, Watson 1966), tends to obscure the underlying relation that this debate has to the use of uniformitarian assumptions in historical science. A number of basic problems in paleoecology and taphonomy today seem to stem from lack of explicit attention to just these issues.

CURRENT PROBLEMS OF METHOD AND THEORY IN TAPHONOMY AND PALEOECOLOGY

Over the last 30 years, taphonomic research has yielded numerous findings on regularities in the operation and effects of processes that form the fossil record. However, these do not yet form a coherent body of theory

and method for explicating fossil sites and assemblages. Furthermore, although these investigations were intended to facilitate paleoecological research, paleoecology itself has made little real progress toward realistically defining its objectives, or the means by which these objectives could more closely be defined. In fact, paleoecology seems to be in much the same state as was "culture process" archaeology after the first round of ethnoarchaeological research, knowing more about what assemblages are not than what they are. Likewise, debates over the proper formulation and use of generalizations in taphonomy and paleoecology are quite similar to those that have occurred in archaeology. In paleontology, however, this situation has persisted without much change for some time. One of the most striking differences between paleontology and archaeology over the last 15 years has, in fact, been the dearth of theoretical discussions in the former field and the superabundance of them in the latter. Like many "old time" archaeologists, paleontologists have been reluctant to engage in prolonged theoretical discussions when there was practical work of an apparently straightforward nature to be done.

The roots of this stasis are both methodological and theoretical. First, and more simply remedied, is the lack of focus on assemblages and deposits in most taphonomic research. With the exceptions of the few researchers noted for this orientation in the preceding historical review, most paleontologists have engaged in a rather diffuse set of inquiries that inform us considerably about the operation and effects of various processes on organic remains but much less about distinctive traces of their operation that might be discerned in fossil accumulations. This involves an undue emphasis on *ecosystems* at the expense of attention to *assemblages* and will be discussed in greater detail in the next part of this chapter.

The other source of continuing stasis in paleoecology is lack of agreement, or outright confusion, over the proper role of uniformitarianism and actualism in guiding research. In 1970, G. G. Simpson noted that paleoecological research had proceeded with curious lack of attention to its philosophical foundations, so that entire treatises on the subject had been written that never mentioned either uniformitarianism or the role of contemporary observations in assigning meaning to patterns in the fossil record. Lawrence (1971) argued that this same lack of attention to theory was responsible for serious problems in paleoecology, with misuse of uniformitarianism fostering the illusion of progress where there was in fact none. Ten years later, the situation is little altered.

Stated simply, paleoecology has been very slow to seize the initiative in defining what can be known of prehistoric ecological relations through actualistic research, which is the basic recourse of any historical science in the face of problematic materials. Taphonomy, because it involves actualistic

research, can supply paleoecology with information about the ecological meaning of patterns in assemblages of biological remains. At our present state of knowledge, it is probably the branch of contemporary studies most relevant to the pursuit of paleoecology, because it addresses the least-known aspect of the ecology of various organisms: the role of their remains as components of ecosystems.

The next parts of this chapter will examine these problems in detail and suggest some alternative approaches in taphonomic research that may prove productive. I hasten to add that these alternatives are implicit in the work of a number of vertebrate and invertebrate paleontologists and hence are nothing especially new. However, since paleontologists have seldom made explicit either the underlying methodological stance or the more practical working procedures of their research, it is worth doing so in order to stimulate further criticism and debate.

Goals in Paleoecology and Methods in Taphonomy: Some Problems

Paleoecology has repeatedly been defined as the study of the *life relations* of prehistoric organisms, including those between organisms and their environment (e.g., Imbrie and Newell 1964) and those among organisms (e.g., Ager 1963; Olson 1966; Simpson 1970; Lawrence 1971). While it shares with ecology this concern with biological interrelations, numerous writers have stressed that paleoecology must, by virtue of the nature of the fossil record, have its own purview and methods of study. Paleoecology's basic task is defining what kinds of biological relationships may actually be accessible to study in the fossil record, and by what means they can be studied.

This is no mean feat, since the methods ecologists use to study such relations cannot be used. Ecologists investigating modern organisms have sought to study energy flow and trophic structure, food webs, predation, competition, and various forms of symbiosis by measuring absolute and relative amounts of calories, biomass, and individual organisms and, to a lesser extent, by experimentally manipulating living systems. While these methods of studying ecological relations present their own problems of theory and method, they obviously require a wealth of evidence and observation not available to paleoecologists. After the initial optimistic attempts to infer intra- and interspecific biological relations from relative abundance data drawn from fossil assemblages, most paleontologists have come to acknowledge the unique problems that their samples present to any such attempts. As Clark and Kietzke (1967), Olson (1971), and most recently Holtzman (1979) have all stressed, paleontological samples, because they

can never be compared to their parent universes, can only be assumed to represent the constitution of those universes, and there are good reasons to believe that they might deviate substantially from them. Faced with these facts, paleoecologists must establish what sorts of ecologically relevant meaning may be assigned to assemblages of biological remains as they are encountered in the fossil record, and how best these can be assessed and compared. In other words, what kinds of relationships can actually be studied with fossil data, and how? The actualistic branch of taphonomy should be able to provide much valuable information on just these matters.

The lack of assemblage- or deposit-oriented research in taphonomy has detracted from its full use in redefining paleoecological goals and methods. This in turn stems from some basic problems in outlook. The taphonomic literature is still dominated by a number of concepts formulated at a more naive stage in the development of the field that, while logically correct and semantically beguiling, may not be very helpful methodologically. These could better be replaced by heuristics more in line with the basic philosophy and strategy of research in historical science. For example, numerous taphonomic writings have stressed the fact that "postmortem" processes, by destroying organic remains or transporting them away from life contexts, delete much of the information about life processes originally inherent to living communities (e.g., Olson 1957; Fagerstrom 1964; Johnson 1960; Tasch 1965; Clark and Kietzke 1967; Lawrence 1968). By skewing patterns of survival and representation of elements away from their original constitution in a living community, these processes are said to insert a kind of "bias" into assemblages of organic remains (e.g., Boucot 1953; Hill 1975; Behrensmeyer *et al.* 1979). These characterizations are appealing because they are true, arising from the obvious conclusions one can draw by comparing a living community with a fossil assemblage. Taphonomic analysis has been popularly portrayed as a means of coping with these biases, as reflected in the statement by D. Lawrence: "success in paleoecology, paleobiogeography, and evolutionary studies often depends upon the worker's ability to strip away the taphonomic overprint" (Lawrence 1979c:903). One may well ask, then, from what is the taphonomic overprint being stripped? What does one have once a sample's postmortem history has been detailed? No one would ever contend that one can "un-bias" a paleontological sample back to an original community, but this emphasis on bias, while a technically correct representation, is not very productive methodologically. Its concentration on information lost (and implicit reference back to the original community) does not lead to a definition of what can be learned from the preserved materials. Rather than suggesting a strategy for investigating meaningful linkages between

life processes and patterning in fossil assemblages, it directs our attention to the unknowable.

This perspective on "postmortem" processes also does not convey two of their essential aspects. Emphasis on these processes as agents of bias does not convey the fact that they are essentially *ecological* in nature and operation, and that traces of their operation in paleontological samples therefore constitute paleoecologically relevant evidence, a point noted by a number of paleontologists (e.g., Lawrence 1971; Hill 1980). Thus, taphonomy can investigate both the ecological and the "biasing" aspects of these processes. Taphonomists regularly derive these two lines of evidence from sedimentological analysis. Analysis of sediment texture, structure, and facies can give information on both the circumstances of deposition, which may have modified an assemblage in some way, and the context of deposition, which in a more or less gross way represents the environments in which the creatures studied lived and died (e.g., Hay 1976; Bishop 1980). This playing of the prehistoric data in two directions has a long history in historical geology; evidence for the action of processes in the biostratigraphic realm should more consciously be dealt with in the same way.

Another concept that may be more intellectually alluring than methodologically productive is that of *assemblages* undergoing postmortem processes (e.g., Olson 1971:18). In most cases, this is a convenient fiction, devised after the fact of recovery of a fossil assemblage, since elements in most such assemblages did not all leave the biosphere at the same time, nor were they all subject to the same types and intensities of processes in their postmortem histories. While assemblages are the basic units of paleoecological investigation, each element in an assemblage has its own history, and analysis must begin at the level of the individual piece.

An Approach to Taphonomic Research and Analysis

A productive approach in taphonomy, and one consonant with the basic strategy of actualism, would be to focus on the *end products* of the interaction of organic remains with postmortem processes. Thus, our attention is directed toward the two sets of phenomena that we can study: (*a*) the fossil evidence and (*b*) the observable processes in the present-day world that produce traces analogous to those perceived in the fossil evidence. Any fossil is the result of a series of events that tended to preserve rather than destroy organic remains, however selectively. A fossil assemblage is an aggregate of the outcomes of such individual histories. Any fossil has certain observable and measurable properties, including traces of the processes that affected it after the death of the organism of which it originally was a part. If there

were regularities in the ways that the properties of surviving elements interacted with such postmortem processes, these should be reflected in the aggregate patterns of their occurrence, or in traces they bear in an assemblage as a whole and in a series of assemblages. Such a product-oriented approach is in no way antithetical to studying the full range of effects of various processes on biological remains. In fact, by specifying that one is interested in the "yes" forks of various "decisions" leading to preservation, actualistic research into the full range of effects may be used to estimate the "odds" of specified elements becoming fossils (e.g., Schopf 1978).

A fruitful way to implement actualistic research and paleontological analysis has been suggested in the writings of Clark and Kietzke (1967) and Olson (1971), as well as in the writings of Efremov himself (1940). This involves ordering and studying the action of various processes on organic remains temporally, in the sequence in which they normally occur. Figure 8.1 schematically represents such a time-ordered framework; it differs, however, from those of Clark and Kietzke or Olson in that it emphasizes the events undergone by individual elements, rather than simply ordering the processes that operate on biological remains, or on some hypothetical assemblage. The scheme represents the various states through which an anatomical element that becomes a fossil would pass, beginning with its ontogeny and function as part of a living organism, through its existence as a component of a land (or underwater) surface, into its subsequent history as a sedimentary particle, in dynamic and static contexts. For the sake of simplicity, the scheme divides this history into a number of states (or in this diagram, "contexts") and a set of major events (or "transformations") that transfer an element from one state to the next. Both states/contexts and transformations are spans of time during which the element exists in a particular spatial framework and is subject to a range of specifiable processes. The only real difference between these two categories is that, at least in the earlier part of the sequence, transformations occur over a relatively shorter time span, generally involve fewer processes, and, most importantly, are events through which all fossils necessarily will have passed. The simplifications involved in this scheme necessarily do some violence to reality. For example, not every element that becomes a fossil existed as part of a surface assemblage prior to final burial. An element could conceivably move from life context to that of final burial in one transition, as did remains of animals trapped in the Le Brea tar pits. This framework does, however, help systematize a complex sequence of events. Archaeologists will note a strong resemblance between this scheme and that outlined by Sullivan (1978) for the formation of archaeological deposits. The two were

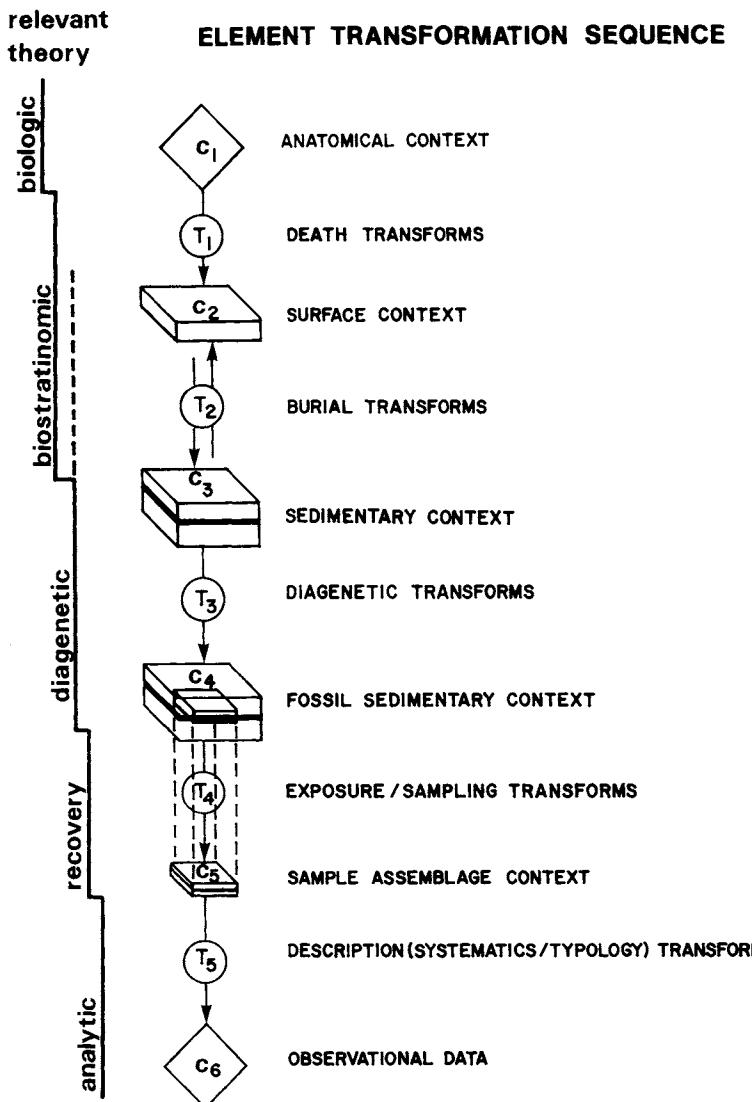


Figure 8.1. Schematic representation of the states through which a fossil element passes and the processes that transfer it from one state to another. Bodies of theory relevant to the study of elements in analogous contemporary contexts are given at the left.

originated independently and reflect an approach we each thought sensible to employ in ordering processes that form the prehistoric record. Hanson (1980) used a similar approach to the sedimentology of bone.

Each segment of this scheme has its own body of relevant research and knowledge. Some of these areas of knowledge are disciplines in their own right, such as those that apply to understanding the role and development of elements in their anatomical context, including embryology, functional morphology, and physiology. While these fields contain a wealth of information about various attributes of elements and the life processes associated with them, paleontologists occasionally may need to augment this with their own actualistic research. A good recent example of this is ongoing research in the relation between diet and the uptake of certain elements or stable isotopes (e.g., DeNiro and Epstein 1978; Parker and Toots 1980), of the modification attributes of teeth that result from different types of diet (e.g., Walker *et al.* 1978; Walker 1980). Biologists studying modern populations would have little cause to pursue these means of assessing diet, since more straightforward methods of observation are available to them.

The temporal segment between death and final burial is the almost exclusive province of taphonomic researchers and is the area most in need of contemporary experimentation and observation to establish what can be known about agents that act on organic remains from the traces that survive in the fossil record. Processes and environments of burial may be studied through sedimentary analysis. The literature of sedimentology includes a body of actualistic observations that informs the analysis of rocks and the reconstruction of earth history (e.g., Allen 1965; Pettijohn 1964; Fisher *et al.* 1969; Selley 1970; Rigby and Hamblin 1972). Sedimentary analysis provides a line of evidence on these matters that is basically independent of that provided by organic remains, thus permitting researchers to cross-check the implications drawn from each. Diagenetic studies of fossils or of fossil-bearing strata is another area in which paleontologists may have to conduct or promote their own research. Research has included experiments in replicating the conditions of diagenetic alteration of organic remains (e.g., Hare 1980) and observations of earlier phases of diagenetic changes in natural situations and comparison with paleontological samples (e.g., Chave 1960, 1964; Herm 1972; Sdzuy 1966; Wyckoff 1972; see also Rolfe and Brett 1969). In each of these realms the key to progress in research is observation of contemporary processes designed to illuminate the nature of preserved traces in the fossil record.

Actualistic research can also shed light on the variation one might expect in assemblages produced under similar conditions. Fossil assemblages are aggregates of individual elements that in many cases interact with various

agents of modification in statistical fashion, with considerable potential for variation in the traces they ultimately may bear. Analysis of the dynamics of those interactions and their effects on assemblage structure in the present can contribute to a realistic assessment of the expected range in the variation of such effects and to a recognition of the strongest and least ambiguous indicators of the operation of given processes. This points to the second productive strategy in taphonomic research, which was pioneered by Efremov: comparative study of assemblages. Comparative study of numerous assemblages produced by known agents can specify those effects that bespeak the action of given processes and agents, despite stochastic variations in the histories of individual elements of assemblages.

Problems with Uniformitarian Assumptions

Discussions about appropriate use of generalizations in taphonomy and paleoecology, although phrased in terms of the split between nomothetic and idiographic approaches, often seem to boil down to the question of when it is safe to apply uniformitarian assumptions. All analyses of prehistoric materials involve some kind of assumption of uniformitarianism. Descriptions of geologic deposits that refer to their origins (e.g., "sandstone") are based on an extensive literature that assigns a processual meaning to static patterns on the basis of contemporary observations.

Biological systems present their own special problems to the uniformitarian approach. Lawrence's (1971) criticisms of "transferred ecology" were aimed at a misapplication of this approach: the invalid assumption that the overall configuration of communities has remained the same over substantial spans of geologic time. Just as the structures or organisms have changed through time, there is every reason to believe that community structure and relations have also evolved, including those as basic as trophic relations. In such situations configurational uniformitarianism is clearly not defensible; this point was also made by Gould (1967) in his critique of "substantive uniformitarianism." However, paleoecologists and other paleontologists constantly assume temporal uniformity of a number of biological processes and their effects. Inference of function from anatomical form, considered one of the safer approaches to understanding the biological meaning of fossils (e.g., Lawrence 1971; Herm 1972), is a prime example. Moreover, paleontologists regularly extend the assumption of uniformity well beyond what can be inferred directly from the observable attributes of a preserved element, inferring associations with a specifiable complex of other elements of which no traces actually exist, and even the element's ontogenetic history. The steps in reasoning involved in such inferences are

usually not consciously noted by those practicing it, as remarked by Simpson (1970), but it might be stated as follows:

1. The observable fossil element is more or less isomorphic with specimens observable in the modern world. Therefore, it is considered to be a member of the same class of elements. For example, a fossil artiodactyl femur is only nameable on the basis of analogy with modern elements it closely resembles.
2. Since in all modern observed cases, the element's analogue functions in only one way as part of an organism, the function of the fossil element is assumed to have been the same during the life of the fossil organism. Referring again to the example of the fossil femur, inference of the past existence of a quadruped vertebrate with a specifiable number of other bones, muscles, and organs is "automatic," but based on modern analogy and uniformitarian assumptions.
3. Since in all observed modern cases, the element's analogues arise only through a series of developmental stages associated with the ontogeny of an individual organism, and through no other natural causes, the fossil element is assumed to have had the same ontogenetic history. Again using the example of the femur, a paleontologist will infer a specified ontogenetic history for the fossil bone and may go on to invoke this history to explain some of its features, such as "unfused epiphyses."

Few would contest these applications of uniformitarian assumptions, but even fewer have specified what exactly it is about these applications that makes them acceptable. A number of other applications, such as assuming that roughly similar organisms were parts of roughly similar communities, are not acceptable. Perhaps the best way to approach this is to examine what allows one to establish the analogic relationship in the first place, or the degree of similarity between the objects compared. For example, the question that was implicitly asked in points 2 and 3 was, do objects that in all ways satisfy relevant criteria of resemblance as femora ever come into being and exist in situations other than as part of a certain kind of organism? The answer is, at present, no. In other words, one asks questions about the necessary and sufficient causal conditions for the presence of a given element. Even when good modern isomorphs are lacking, the procedure is still the same, but the relevant criteria of resemblance to modern cases must be more general and the attendant inferences less specific and rich. For example, a femur for which there is no exact modern analogue may still be named a femur on the basis of very general criteria that hold true for all tetrapods, and much can still be inferred about its

history from generalizations about bone growth and function in the vertebrate body.

Turning to ecological inferences, we find a number of problems. By definition, ecology deals with the relationships between a given organism or set of organisms and other components of their environment. These relationships are more flexible and less deterministic than those of the elements of a single organism. Clearly, some anatomical features, such as dentitions of mammals, are actually indicators of a species' interactions with other organisms, again by modern analogy. But the amount of synecological inference one can draw from such features is often quite limited. To take an extreme example, the fossil jaw of a tiger may be readily grouped with modern examples of the taxon, and may furthermore be taken to have played a specific role in the morphology of the ancient animal with some degree of confidence. Again by modern analogy, the general role of the animal in the food pyramid of its community can be inferred with some confidence. However, if one wished to infer the biotic region in which the fossil animal lived, one would be faced with a much less specific set of possible inferences, since modern tigers exist in an extremely diverse set of habitats. Likewise, whether or not the paleotiger was involved in competitive interactions could not be inferred from its own existence in an assemblage. One might go about answering these questions in more definite terms by studying the associations of the element in question with other elements of other creatures and trying to isolate those statements about relations among these elements that are unequivocal in nature; in other words, isolating descriptions of causal relationships.

A good example of this approach to ecological relations is that taken by Brain (1968, 1970, 1976, 1980) in analyzing the Swartkrans australopithecine assemblage. He first managed to make some very definite statements about the depositional context of the bones, and from this, decisively eliminated the possibility of some modes of site formation. The bones apparently accumulated in a limestone solution cavity linked to the surface by a shaft or fissure. The possibility of a "walk-in" den for either human or nonhuman bone collectors was thus eliminated. Then he proceeded to ask what suite of agents could produce the patterns of damage and element representation observed in the fossil assemblage; this was accomplished through observation of modern bone processors. While he was not able to decisively eliminate some agents, he was at least able to establish that some of the damage was most probably carnivore inflicted and that the overall patterns of element representation were as likely to be produced by carnivores as by any other agents. Depressed fractures on australopithecine remains fit well with the kinds of damage inflicted by leopard teeth and

could be matched to canines in leopard jaws recovered from the deposit. Reasoning by analogy with the habits of modern leopards, Brain inferred that the ancient geomorphic setting would be a favored locale for a leopard lair and that many of the attributes noted in the fossil bone assemblage could be explained more readily by invoking carnivore action than that of hominids. Leopard toothmarks on some australopithecine fossils are interpreted as trace fossils of the interaction of one species, the leopard, preying on another, the robust australopithecines of the Swartkrans area.

The previously mentioned work of DeNiro, Walker, and others (DeNiro and Epstein 1978; Walker *et al.* 1978) is another good example of isolating attributes displayed by fossil remains that, when studied in the contemporary world, may be ascribed to restricted and closely specifiable causes that are also ecologically informative. In this case, the researchers attempted to determine whether two attributes of herbivore teeth, namely the ratio of two stable carbon isotopes and the micro-damage to enamel incurred during mastication, would provide clues to the nature of the diet of herbivores that could not, on the basis of dental morphology alone, be sorted into browsers and grazers. The entirety of these experiments were carried out with modern specimens for which dietary intake could be established, being the first step toward delineating causal linkages between attributes observable in fossils and their ecologically relevant antecedent conditions.

To summarize, the greater the degree of resemblance between a prehistoric element and a modern one with regard to relevant features (e.g., Salmon and Salmon 1979), the more assured the use of uniformitarian assumptions about the function and ontogeny of the prehistoric item. Likewise, the more uniform the relationship between a given attribute and both its cause and ecological context through a variety of modern cases, the more defensible the assumption that this relationship has been uniform through time. If an element differs substantially from any modern one, or when the only observable attributes of an element are and exist due to a multiplicity of causes or in a diversity of contexts, the inferences that may be drawn from these about function, context, and history will be less powerful or informative. This implies that prehistoric samples of rather shallow time depth have the greatest potential for richly textured reconstruction, due to the abundance of modern analogues. Deeper reaches of the fossil record, by the very fact of organic evolution, present less easily analyzed situations. They are also of greater theoretical interest to those concerned with the process of evolution at both the species and the community level. The key to working with such samples is searching out attributes of the preserved materials that result from the action of processes we have good reason to believe have remained uniform in their operation over at least the span of time in which we are interested. The fixation of

carbon isotopes by various angiosperms, and their subsequent uptake by primary and secondary consumers, is an example of such a process. Paleontologists working with Mesozoic vertebrates might find this phenomenon less relevant to their research, but other processes or relationships of a more basic kind and, by extensions, more enduring ones, may be sought out. This has been done in research into the problem of temperature regulation in dinosaurs (e.g., Bakker 1972; Case 1978), and of viviparity in mammal precursors (Kielan-Jaworowska 1979). The same approach has been employed by paleontologists seeking to learn more about the nature and ecology of the organisms that produced conodont remains, for which no modern analogues exist (e.g., Lindström 1964; Barnes 1976; Carls 1977).

Procedures in the Search for Useful Regularities

The search for regular and ecologically relevant linkages between static attributes of the fossil record and their dynamic causes and associations is the key to progress in understanding the prehistoric evidence. Research aimed at defining such linkages should proceed through two steps of actualistic research before any attempt is made to grapple with the fossil material. The first step involves studying the dynamics of interactions between organic remains and the processes that operate on them in the post-mortem span of their existence. Naturally, relevant interactions to study will be chosen by reference to attributes of fossil materials, either singly or in aggregate, and hunches about the events that produce such traces. At this stage of research the burden is on the researcher to ascertain not only the general context in which a certain trace is produced but also the dynamics of the actual events that produce them. For example, isolated oval or circular depressed fractures of a certain range of sizes are said to be produced by "carnivore gnawing." In reality, the event that produces such a trace is that which occurs when the compressive force transmitted from a carnivore's jaw through a canine tooth to a sector of bone exceeds the limits of a bone's ability to resist such stress. At this stage the researcher must also establish the nature of the causal relation between the actual event and the trace or traces it produces. For example, one must establish if any other kinds of events *not* associated with carnivore gnawing of bone could produce similar traces, as well as the expected range of variation in these effects, given bone of different levels of tensile strength and carnivores with different jaw strengths. In this step the researcher should, again on the basis of observations, advance a kind of bridging argument about the relation between the event and its immediate processual context (e.g., gnawing) and broader and ecologically relevant contexts. Following

the example given, the researcher may assert that the traces are invariably the products of carnivore processing of bone, perhaps further noting the size ranges or taxa of carnivores involved in producing specifiable types of damage.

The second step involves moving to the assemblage level, since this is the basic unit of analysis and comparison in paleoecology, and predicting the structure of assemblages produced by the action of specified processes. These predictions should be tested actualistically, that is, by evaluating the predictions in light of modern assemblages known to have been formed by the processes stipulated in the predictions. *Only* if predictions pass this test of actualistic evaluation should they be employed in analysis of fossil materials. For example, a researcher may wish to predict that bone assemblages heavily processed by carnivores will display high frequencies of depressed fractures of the kind established to result from carnivore processing in combination with other traces also causally linked to the same phenomenon. These predictions would then be tested with data from modern carnivore-processed bone assemblages, as well as assemblages known not to have been affected by carnivores. If the predictions withstood such tests, they could be employed to assign a behavioral or ecological meaning to fossil bone assemblages. If they did not, another cycle of study and formulation of predictions in light of such findings would be required. Within the context of such actualistic research, two additional aspects of methodology should naturally evolve. The first is devising appropriate means of describing and measuring the effects produced by the events documented. The second aspect is establishing the range of variation in the occurrence of key attributes in assemblages produced by the action of the same combinations of processes.

This scheme of research is so obvious as to be unremarkable, since it combines the basic actualism of historical science since Lyell with some even more basic approaches to establishing cause and effect. The only reason it has been discussed at such length is that only a few taphonomic-paleoecologic analyses of the fossil record have followed this scheme. Since some of the worst offenders in this matter have been anthropologists, and since experimental research on purely archaeological topics is also riddled with such problems, these comments should not be taken as a criticism of paleontological research alone. The gravest problem in actualistic research is assuming that a given agent is necessary and a sufficient cause of an observable attribute when no such relationship has actually been established.

For example, in an otherwise carefully documented and well-conducted experiment, Sadek-Kooros (1972) ends by contending that she has demon-

strated hominid tool manufacture in early levels of Jaguar Cave because humans could replicate the fracture patterns present in the archaeological assemblage. Her conclusion implies that hominid fracturing, and moreover, fracture intended for the production of implements rather than for any other purpose, was both a necessary and a sufficient cause of these breakage patterns. To support this conclusion, however, Sadek-Kooros would have to have demonstrated that no other agency could produce similar patterns of damage, which she did not.

Another problem arises when investigators hypothesize causal linkages between some agent and an observable attribute of the fossil evidence, and then proceed, without testing the hypothesis through contemporary observations, to analyze assemblages as if the linkage were established, or at least suggesting that the postulated relationships were a good explanation of the attribute in question. This was done by Dart (1957a,b) with spiral fracture, by Shipman (1977), albeit more tentatively, in her discussion of bone damage and aqueous transport, and by Vrba (1975) in her treatment of assemblage patterns produced by different types of carnivores. (See page 413 for further discussion of Vrba's work.) Yet another variation on this problem occurs when a researcher "tests" the validity of such a linkage using data from a fossil assemblage rather than modern materials; attributes produced by unobservable causes can never be used to establish the nature of the causal agent. For example, Bonnichsen (1979:69) advanced the hypothesis that spirally fractured long bones are indicative of human processing. Rather than test this hypothesis with comparative observations of both human and nonhuman processors' effects on long bones, as well as that of other agents of bone breakage, Bonnichsen attempts to find corroboration in the fracture patterns displayed by a fossil collection which, he admits, yields equivocal results. "Testing" hypotheses regarding cause and effect with prehistoric materials, for which causation can never be observed, runs counter to the basic strategy of historical sciences for assigning processual meaning to patterning in prehistoric materials.

To date, many taphonomic studies have focused more on describing and comparing patterns of assemblage structure than on the actual dynamics that produced these patterns (e.g., Hill 1975, 1979b; Gifford 1977, n.d.). While this may be an acceptable first step in learning about the nature of assemblages in the contemporary world, it is not a final one, and any inferences from such observations about the dynamics of the processes that create assemblages is, for obvious reasons, a chancy matter. Among the better-conceived studies thus far carried out are those of Brain (1967a,b, 1968, 1969, 1970, 1975, 1976, 1980) and Binford (1981; Binford and Bertram 1977) on the determinants of ungulate bone assemblage structure, and

Behrensmeyer's and others' work on the dynamics and consequences of aqueous transport of bone (e.g., Behrensmeyer 1975b; Boaz and Behrensmeyer 1976; Hanson 1980).

Progress and the Nature of Research Support in Paleoecology and Taphonomy

Why such careful scientific procedures have not been the norm, at least on the English-speaking side of paleoecologic and taphonomic research, is an interesting matter, upon which one can only speculate. As noted earlier, one factor may be the reluctance of many paleontologists to make explicit the mental steps and methods they employ when attempting to learn more about the past. Another factor may simply be time, since research into the dynamics that produce assemblages with certain attributes, especially with vertebrate remains, are often long-term projects, which researchers may not have the time and wherewithal to pursue in a properly continuous way. Underlying this may be a more basic and mundane problem of economics, related to the way research in paleoecology and taphonomy has been funded, especially in the United States. Large amounts of paleoecological research funds are awarded on a competitive basis, and the rationale for such research usually emphasizes a pay-off in a paleoecological reconstruction of a hitherto little-known time and region. Little emphasis has been placed on the basic research in contemporary situations that underlies any reasonable reconstructions of this sort. This is not to argue that all taphonomic research is an expensive undertaking, but some does require a substantial outlay to pursue, especially studies of large vertebrates in both experimental and natural contexts. To date, much taphonomic research has been carried on within the framework of such large paleoecological research projects. While this is clearly better than not at all, taphonomy would proceed in a more concerted and productive manner were its identity as a branch of actualistic research more fully recognized, and the role of actualistic research in advancing historical science better acknowledged, by funding agencies as well as by practitioners of paleontology.

The way in which historical scientists consciously articulate their basic methodology and priorities has real consequences in terms of research funding, at least in the United States. The richest actualistic literature in any historical science is that of sedimentology, a field in which much of the basic research has been supported by the petroleum industry. One may imagine that support for actualistic research has been based less on theoretical leanings among the captains of industry than on pure pragmatism. How-

ever, the fact that such research has been so heavily subsidized testifies to the efficacy of studying modern analogues to understanding the nature of prehistoric processes and their products.

It may be of interest to compare the situation in English-speaking circles with that of German researchers who, sustained by a less competitive and more secure system of funding, have formed a loose cooperative research group, which includes archaeologists, to define long-range research goals and methods of implementation (e.g., Herm 1972). The Germans, perhaps due to a combination of choice and the circumstances of Central European geologic history, have been less concerned with problems of the biostratigraphic realm and of aqueous transport than have researchers in other countries. They have focused more on detailed aspects of functional and constructional determinants of form (e.g., Raup 1972), and on depositional and diagenetic processes of fossil-bed formation. Their approach to paleoecological reconstruction is extremely conservative and their view of the paleoecological potential of vertebrate fossil accumulations more pessimistic than that of English-speaking paleontologists (e.g., Herm 1972). Their research has generally been characterized by a systematic (and time-consuming) comparative examination of many modern or fossil cases (e.g., Schäfer 1972) and a very cautious approach to generalization. Part of this more concerted and systematic approach on the part of German workers might be ascribed to cultural factors, but their greater cooperative planning of research topics and strategies probably stems as much from the realities of academic economics as it does from any profound differences in cooperativeness and foresight on the two sides of the Atlantic.

Progress in paleoecology can only come from well-executed actualistic research aimed at clarifying the meaning of presently ambiguous attributes of fossil assemblages, and from careful comparative evaluation of suites of modern and fossil assemblages in light of the findings of such research. Research in taphonomy can provide paleoecologists with much useful information of an ecological nature as well as about how postmortem transformations of organic remains "bias" assemblages away from their community composition. Emphasis in taphonomic research should now be placed on (*a*) determining how much ecological meaning can be assigned to patterns of evidence observable in fossil assemblages and (*b*) the proper means of describing and comparing these attributes. It seems an ideal time for practitioners of paleoecology and taphonomy to return to the roots of historical science and rephrase both their research goals and methods in terms of the uniformitarian methodology and assumptions that underlie their discipline.

PRACTICAL ASPECTS OF VERTEBRATE TAPHONOMY OF USE TO ARCHAEOLOGISTS

Taphonomic methods and findings of most use to archaeologists are those pertaining to the remains of terrestrial vertebrates, especially mammals. This section reviews recent studies of bone as it interacts with various agents of modification, destruction, and transport, concentrating on the processes operating on bone in the biostratinomic realm from death to final burial. For convenience, the section is divided according to particular agents of attrition or transport and their effects on bone assemblages. It should be recalled that these agents are not themselves the actual events that cause the distinctive patterns of modification perceived, but rather the processual, and often behaviorally or ecologically relevant, contexts within which these events take place. Real understanding of the relation between these agents and the traces of their action on bone must come from examining the dynamics of the actual events that produce the traces. As the preceding discussion should indicate, many of the findings to date are tentative and should be regarded as hypotheses in need of further testing through actualistic research. This section also includes some speculations about linkages between certain kinds of transport and attrition phenomena and local ecology.

Vertebrate Remains and Assemblages: Contrasts with Archaeological Materials

It is worth establishing some of the unique features of vertebrate assemblages, as well as some of the major differences between paleontological and archaeological accumulations of vertebrate remains. Paleontological evidence, both invertebrate and vertebrate, can be divided into two major classes, fossils and trace fossils. These two kinds of preserved remains reflect the action of different types of ecological processes. Fossils reflect the interaction of genetic and environmental factors in the life-spans of individual animals and evidence which bears on diet, locomotor patterns, reproduction, and other aspects of life history. Because fossils were constituent parts of individual organisms, they can be used to estimate the numbers of organisms that are represented in a faunal assemblage. Trace fossils, either on organic or inorganic substrates (e.g., footprints and tooth-marks) reflect the interactions of an organism with elements of its environment, including other organisms. Lawrence (1971) has pointed out that from an ecological standpoint trace fossils are potentially very informative. Trace fossils may exist for organisms of which no actual anatomical elements are preserved (e.g., Seilacher 1970). While they do not normally

permit estimates of the numbers of organisms that made them, they can allow a relative scaling of the intensities of the behaviors that produced them. Archaeological materials can be seen as trace fossils of the Hominidae, reflecting the interactions of hominids with a wide variety of environmental features and offering archaeologists a vastly richer testimony to behavior than that normally available to paleontologists. This advantage is counterbalanced by the fact that archaeologists have far fewer modern analogues for the prehistoric materials they study. Unlike a vertebrate paleontologist with a fossil femur, archaeologists with their finds often lack modern isomorphs with which they can establish analogous relations, and cannot generalize from a single piece to the functional system of which it once was a part. Archaeologists therefore have frequent recourse to analyses that rely on uniformitarian assumptions about the operation of more general processes in nature, such as the physics of lithic fracture.

The nature of vertebrate assemblages differs from those of both invertebrates and archaeological remains. Because most vertebrates are mobile, and because their bodies break down into numerous preservable parts after death, dispersion of individuals in life and of their anatomical parts in death is the rule. Invertebrate paleontologists sometimes find fossil mollusks in arrangements that appear to be the result of the life habits of the organisms; these are so-called fossil communities. They may also recover the same organisms' remains in dense aggregates created by current action. Vertebrate paleontologists also may encounter bones in spatially discrete, densely concentrated aggregates, as well as in areally extensive, dispersed distributions. When bones are encountered in dense concentrations, however, it is seldom assumed that these are together because of organisms' life habits, but rather that postmortem events have brought them together. Agents of dispersal and concentration that act on vertebrate remains may be biological (such as bone-collecting carnivores) or geological (such as flowing water). Exceptions to the general rule include vertebrates caught in natural traps or preserved where they lay down and died (e.g., Clark and Guensberg 1970).

Although a few recent publications in archaeology have noted the relevance of "offsite" or "nonsite" sampling (e.g., Thomas 1975; Foley n.d.), archaeologists traditionally have drawn their assemblages from dense, spatially discrete aggregations of artifacts, features, and debris. They have assumed that the main agent responsible for creating such aggregates was human behavior. Despite the fact that much taphonomic research has been devoted to distinguishing human from nonhuman agents of bone modification or accumulation in ambiguous cases (e.g., Binford 1981), there are thousands of archaeological cases in which the association of bone and artifactual remains is unequivocal. The closest paleontological parallel to ar-

archaeological bone aggregates are carnivore den accumulations, produced by other species that also transport food to a central place. Bone in both contexts can be expected to provide some information on the general environment and ecological relations of a carnivore foraging area, as well as on the behavior of the bone-collecting species itself. However, hominid sites include a much greater diversity of evidence for behavior than would carnivore accumulations, since they yield a wide variety of "trace fossils," in the form of artifacts, facilities, debris, and other features. Analysis of bone in archaeological sites can therefore proceed with a number of assumptions about the formation of the accumulation that paleontologists normally must spend considerable effort establishing. Bone from archaeological deposits can also be integrated into a much more complex web of inferences about the behavior of the accumulating agent than is possible in paleontological analyses.

Despite these assets in dealing with bones in archaeological sites, archaeologists sometimes must ask whether distinctive patterns of damage or of element representation in an assemblage are the result of human behavior. Even unequivocally archaeological deposits are subject to reworking by other biological or geological agents. Moreover, many physical processes affect all bone regardless of its agents of accumulation and leave distinctive traces of their action on bone. These can be useful to archaeologists in understanding the processes that contributed to forming an archaeological site. The next sections of this chapter will review what is known about the interaction of bone with various agents of modification or transport. This begins with a discussion of the processes that structure bone assemblages, and of regularities of disarticulation and damage patterns in vertebrate remains.

Processes That Structure Bone Assemblages

Element frequencies of paleontological bone assemblages usually differ from those of the normally constituted vertebrate body, as the result of the action of one or both of two kinds of processes: (a) those that cause differential destruction, or attrition, of certain elements and (b) those that cause selective transport of certain elements to or away from the locale of deposition. Attrition of bone results from the interaction of bone as a material with some kind of destructive force, either biological or nonbiological; it is determined in part by the relative durability of the bone itself and in part by the relative intensity of action of the destructive process. Selective transport of certain elements to or from a given locale results from the interaction of the vertebrate body, which tends to dissociate into

segments after death, with biological agents, such as meat- or bone-collecting animals or nonbiological ones, such as flowing water. Properties of the vertebrate body, such as the strength of particular joint articulations, the food value of a given body segment, or the hydrodynamic properties of a given bone will determine an element's liability to transport. The same agent may disperse bone from one locale and concentrate it in another, and many of the same agents as transport bone can also act to destroy them, as in the case of a carnivore that carries a bone back to its lair and then gnaws it. Evidence of the action of such agents can therefore be found both in patterns of damage and in element frequencies in an assemblage. Since element frequencies can reflect either differential destruction of bone or its transport, identification of the dominant process that affected an assemblage presents some problems. The approaches to distinguishing these are better understood with some knowledge of the basic materials on which these various agents act.

Bone as a Constituent of a Body: Postmortem Disarticulation and Transport

The breakdown of a vertebrate body after death results in the dissociation of bones that originated as and formed part of a functional unit. Since individual bones perform different mechanical and physiological functions in the vertebrate body, they differ in both form and content. These differences affect their transport potentials in relation to both biological and nonbiological agents. The amount of muscle and fat associated with, or blood and marrow contained in, a mammal bone will determine its appeal to carnivorous animals, which in turn will govern the frequency with which it will be subject to both damage and transport by such animals. The shape, size, and density of a bone determines its behavior as a sedimentary particle in flowing water, making some elements more liable than others to be winnowed away from the site of death if disarticulated and subject to a flood event.

Disarticulation of carcasses can be more or less passive, resulting from the action of microorganisms and larger invertebrates (e.g., Payne 1965; Payne and King 1968) or it can be more active, as in the intervention of vertebrate carnivores in detaching limbs or head from the trunk. In a typical mammalian body the strengths of articulations between various bones and body segments vary considerably. Because of this, carcasses break down in predictable sequences, with the least tightly articulated joints dissociating first and the most tightly last. The exact sequence of disarticulation will vary according to the joint structure of a specific taxon.

Hill (1979a,b) has recently described the sequence of disarticulation for ruminant artiodactyls, based on his studies of bovid carcasses in East Africa. The regularities displayed by this disarticulation sequence are considerable and have also been noted for caribou by Binford (1981).

While various agents may accelerate the sequence of disarticulation, intervention by other organisms normally does not alter the actual sequence. Exceptions to this rule are hominids, who can breach tightly articulated joints "before their time" with implements, a topic recently discussed in detail by Binford (1978, 1981). Because of the regularity with which the natural disarticulation of a carcass proceeds, this sequence can be used as a kind of baseline against which hominid intervention can be measured. Due to the strength of some articulations, certain body segments containing sets of bones are highly likely to be transported as a unit. Other elements are highly unlikely to be transported together, if any decomposition of a carcass has occurred, due to the weakness of the linkages connecting them. The actual dynamics of transport of disarticulated body segments or of isolated bones depends on the agents involved and will be detailed in subsequent sections.

Bone as a Material Subject to Damage

A substantial literature exists on the structure of physiology of mammal bone (e.g., Bourne 1971; Lacroix 1951; McLean and Urist 1968) and on the response of bone to various types of stress (Watson-Jones 1941; Bonfield and Li 1966; Evans 1966, 1973) which has been helpful to those researching taphonomic aspects of bone breakage (e.g., Bonnichsen 1973, 1979). While the basic organic and inorganic makeup of mammalian bone is not highly variable, different elements display great diversity in the arrangement of bone tissue, reflecting the wide range of functions they serve in the body. This structural variability among bones results in a considerable range of resistance to destructive forces. Compact bone, with its high ratio of bone tissue per unit volume, may resist localized stress better than cancellous, or spongy bone, with its low ratio of bone tissue to volume; thicker compact bone resists damage better than thin. However, compact bone readily transmits stress that causes fractures and may propagate more extensive fractures than cancellous bone.

In his study of surface assemblages of goat bones from Hottentot villages in the Namib Desert, C. K. Brain established that, in the absence of any selective transport, destructive agents (human and canine bone consumers and trampling goats) acting on the bones derived from whole goat carcasses produced assemblages that were markedly skewed from the relative element frequencies in a living animal (Brain 1967b, 1969, 1976). He

further established that a positive correlation existed between bones' specific gravities and their survival potential. Different bones, or even different segments of one bone, were thus shown to have different survival potentials, related to the amount of bone tissue per unit volume of which they were composed. More recent work by Binford and Bertram (1977) on durability of bone in face of carnivore processing supports Brain's correlation. Binford and Bertram further allege, on the basis of a few reference samples, that age-dependent changes in bone "densities" (and hence durability) are sufficiently regular within a given taxon to allow deduction of age structure from the element and bone segment representation in an assemblage. Their tests of this prediction with modern, age-documented assemblages appear to support their contention, although the predictive model could be strengthened, or at least made more acceptable to skeptics, by inclusion of a larger sample of individuals from one species.

In any case, element durability in interactions with destructive agents has been shown to be strongly influenced by intrinsic qualities of individual bones, specifically, the amount of bony tissue per unit volume, an attribute relatively easy to assess. Since major groups of mammals vary in their biomechanics and bone structure, it is advisable to establish relative durability rankings for elements in every major order or anatomically significant group treated. Brain (1976, 1980) documented striking differences in the patterns of element survival between baboon and like-sized gazelle carcasses fed to the same group of cheetahs. Shipman (personal communication 1977) noted similar contrasts between bones of the giant *Theropithecus* monkey from the Olorgesailie prehistoric site and of fossil bovids from other Pleistocene fossil localities. Bones more prone to damage in most land mammals include the vertebrae, ribs, and blades of scapulae and pelvis. The heads and proximal regions of both humerus and femur are doubly at risk of destruction by carnivores, since they are composed largely of spongy bone filled with appetizing blood and also form the path of least resistance for entry into the marrow cavity of the bone. Other bones and bone segments vary so considerably according to the particular morphology of major taxa that few sweeping generalizations can be made. Although the bones of very small animals are more prone to be totally destroyed than are those of larger animals subject to the same destructive agents, the same pattern of anatomical variation in durability is found, as demonstrated by recent work by Dodson and Wexlar (1979).

As a living tissue that stores and supplies nutrients to the body, bone can vary considerably in its levels of fat, protein, and calcium, depending on an organism's nutritional state. These factors can influence an element's potential durability in two ways: (a) by enhancing or reducing its capacity to resist destruction and, (b) in the case of damage inflicted by carnivores,

by enhancing or reducing the intensity of destructive action directed at an element (see the following). However, variations in such properties do not alter the basic pattern of durability displayed by bones of a given taxon.

Bone breaks when stress applied to it exceeds its plastic and elastic capacities (e.g., Watson-Jones 1941; Bonfield and Li 1966; Evans 1973). Fracture may divide a bone into several segments; it may involve less extensive damage in the form of depressed fractures, chipping, or flaking; or both kinds of damage may result from a single event. The way in which bone actually fractures under stress is partially determined by its shape and internal structure. The so-called "spiral fracture" pattern in long bones illustrates this point. Dart's allegation that only hominids striking and then twisting long bones could produce spiral fracture patterns was one of the major components of his argument for an osteodontokeratic culture. A review of the literature on mechanical stress to long bones indicates that such fractures can be produced by a variety of stresses and depend more on the cross-sectional structure of the bone than on the agent of fracture. Bonnichsen's brief discussions of experiments with fracture of glass tubes and long bones (Bonnichsen 1973:13-14, 1979:8-15, see also 42-43) are succinct summaries of the dynamics of fracture in tubular bones. He noted that, in hollow tubular structures, whether glass or bone, waves of fracturing force tend to move out from their point of origin in a spiral around the cylinder, causing full breaks through the element when they intersect. Long bones subject to the same stresses as glass cylinders tended to produce somewhat longer spiral fragments, which Bonnichsen attributed to the fact that the waves of forces moving through bone would be transmitted along the lines of the longitudinal bone growth structures within the compact bone walls. Cancellous bone at the ends of long bones does not respond to these waves of stress in the same manner as the compact bone of the shaft, and most breaks terminate at the beginning of the spongy bone areas. Although cancellous bone can easily be damaged by locally applied stress, its structure strongly resists stresses applied to it along the natural anatomical alignment of the bone.

The key to gross fracture patterns is thus the shape of the bone and the type of bone structure, in combination with the amount and incidence of stress exerted on the bone. Bonnichsen (1968) recorded spiral fractures in carnivore-processed bone, as has Hill (1976), Shipman and Phillips-Conroy (1977), and Binford (1981). Miller (1975) observed that spiral fractures did not occur in a natural assemblage of cow and horse bone from the southern California desert, which had been scavenged by coyotes and concluded that this kind of breakage was not typical of carnivore damage to bone. In view of other findings to the contrary, I would suggest that coyotes may lack the jaw strength to exert compression sufficient to produce spiral fractures on

long bones of cow-horse size, whereas wolves, hyenas, and very large cats studied by other workers possess the capacity to inflict such damage with their jaws.

Description of Bone Damage

Nearly all the literature on bone fracture patterns has employed very general descriptive categories, often simply classifying gross fracture patterns according to the segment represented (e.g., proximal, distal, or shaft) or by general and often poorly defined descriptions of the shape of the break (e.g., spiral or transverse). Considering the strong influence that the structure of a bone has on the ways it breaks, such gross categories may mask attributes that are better indicators of agents of modification. Sadek-Kooros (1972, 1975) presented a more detailed set of long bone fracture descriptors, combining break shape with descriptions of minor damage. Her descriptive system is weakened by labeling that ascribed intentional human manipulation to specific break types, because no invariable linkages between this causal agent and the break types has been established. Bonnichsen (1979:221–239) presents his own system for describing and classifying long bone breakage, which includes a number of attributes of the break surface, its relation to epiphyseal ends, and the presence of secondary damage attributes. The utility of the specific damage attributes given in either of these descriptive systems in diagnosing agents of damage has not been established, because neither author evaluated a range of modern fracture patterns produced by *all* major kinds of bone processors. Both Sadek-Kooros (1972) and Bonnichsen (1979) have concentrated their experimental examination of fracture patterns on human bone-smashing, and have not subjected a suite of carnivore-processed long bones to similar analyses. Shipman (1977, n.d.) applied a detailed system of break description in her analysis of the Fort Ternan Miocene fossil locality, including descriptions of both fracture shape and the quality of the fracture surface. However, she had little in the way of contemporary observations with which to evaluate whether attributes selected in this descriptive system strongly correlate with the effects of different agents of fracture.

Fracture attributes that are relevant keys to identifying agent or method of fracture include the quality of the break surface, that is, whether it is smooth, stepped, etc. Bonnichsen (1973) noted some differences in the surfaces of long bone breaks produced by the anvil and hammerstone (bipolar) technique as opposed to those produced by simple use of hammerstone (unipolar) technique. Because humans break long bones of larger mammals by striking them with a tool, the break surface may be different from that caused by animals exerting compressive force. These different

types of stress merit further experiment and observation. Other keys to agent of damage include the location of the break with regard to epiphyses and various distinctive forms of secondary damage. These will be discussed in the following section.

Patterns of Damage Caused by Humans and Carnivores

Both nonhuman carnivores and bone-processing humans leave distinctive traces on fractured bones. While it is now clear that the agency of one or the other cannot be defined simply by the presence or absence of spiral fracture, the *placement* of fracture damage, when viewed in an assemblage aggregate, may provide a clue to the processing agent. Larger carnivores tend to obtain marrow and other nutrients from long bones of medium to larger animals by attacking the articular ends. Some of these provide both a "nest" of nutritious, blood-rich cancellous bone and a more easily breached entry into the marrow cavity. If an animal's jaw is sufficiently strong, it can buckle the bone under the exerted force, breaching the marrow cavity and often in the process creating spiral fractures that originate at the articular ends (Bonnichsen 1973; Haynes 1980), or elongated fragments of the split and collapsed shaft (Bonnichsen 1973, 1979; Binford 1981). Failing a clean entry into the marrow cavity, carnivores will gnaw at the articular end, gradually wearing away enough bone to extract marrow with their tongues (Sutcliffe 1970; Bonnichsen 1973; Binford 1981). This leaves a distinctive tubular shaft, with articular ends partially or completely gone, often bearing irregular scratches inflicted by the gnawing processes (Bonnichsen 1973; Binford 1981; Haynes 1980). Binford (1981) noted distinctive triangular-sectioned long bone splinters in wolf-processed assemblages, consisting of a section of shaft with some eminence (such as the crest of the tibia). This resulted from the animals' seizing the area around these prominences and snapping them off the shaft in an attempt to breach the bone.

Stone-wielding hominids tend to obtain the marrow in long bones by striking the shaft, thereby creating spiral fractures and occasional transverse fractures that originate away from the epiphyseal ends (Bonnichsen 1973; Brain 1975, 1976; Binford 1978, 1981; Gifford, personal observation). Humans using heavy metal implements may attack the marrow cavity from articular ends, either parallel with or transverse to the main axis of the bone (e.g., Yellen 1977b; Binford 1978). While both the gnawing process and hominid bone-smashing produce chips and small splinters, Binford (1981) has noted a consistent underrepresentation of such fragments in bone assemblages produced by wolves, since these are apparently swallowed during gnawing, to either be totally digested or redeposited in other areas with defecation. Damage that completely destroys elements, thus

removing them from an assemblage, will be discussed in the next section of this review.

In addition to gross patterns of breakage and fragment morphology, secondary damage features are often excellent indices (and less equivocal) of the action of carnivore or human bone-processors. Carnivores processing bones leave depressed fractures from canine teeth and longitudinal gouges from working bone over carnassial teeth during the gnawing process (Bonnichsen 1973, 1979; Miller 1979, 1975; Binford 1981). They can also, in the process of exerting compressive force on bone, remove bona fide flakes from the edges of break surfaces; Binford (1981) describes both "microdenticulate" and larger flake scars on wolf-processed bone. Another apparently distinctive form of damage created by canids is "channelling" of longbone shaft pieces by progressive carnassial punctures as an animal advances further into the shaft in an effort to buckle it (Binford 1981).

Impacts of stone tools or other implements on bone leave crescentic, notchlike depressions at the point of impact (Bonnichsen 1973, 1979; Binford 1981). Cut marks are normally clustered around either the articular surfaces of bones or at points of major muscle attachment, since cutting implements are used both to facilitate disarticulation and to remove major muscle groups. Since certain joints of even large mammals are readily disarticulated by hand, cut marks can be expected to cluster around tighter articulations, such as that of the humerus and radioulna in artiodactyls (e.g., Binford 1981). Because the relative strength of different joints varies from taxon to taxon, the frequency of occurrence of such marks at different joints should also vary, a phenomenon I recently documented in a comparison of cut marks on bones of bovids and equids from an archaeological site in Kenya (Gifford *et al.* 1981). Recent experimental work by Walker and Long (1977) suggests that the type of cutting implement can be inferred from study of the cross-sectional proportions of the cut marks. A similar approach might be employed to distinguish true cut marks from linear marks inflicted by carnassial teeth.

Although tooth marks and impact notches are normally strong and unambiguous indicators of the bone-processing agent, the problem is that they may only appear on a few of the bone fragments generated in a fracture event. This is especially true of impact marks, which on long bones might be borne by only a couple of shaft fragments. Bonnichsen (1973) noted that many of the pieces likely to bear such damage are scraps that archaeologists normally consign to a minimally identifiable category without any close examination. These modern observations suggest that archaeologists interested in butchery and processing attributes that reflect patterned human behavior should devote attention to minimally identifiable scraps of bone, and to refitting bone fragments. Good illustration of secondary damage features may be found in Bonnichsen (1979) and Binford (1981).

Another secondary damage feature typical of bone processed by larger carnivores is etching by stomach acids. Bone fragments that are swallowed by carnivores are often retained in the stomach long enough for this to occur before being either regurgitated or passed in feces. The surface of such bone fragments exhibits a high polish and, often, rounded edges. Etched bone of this sort has been noted with some frequency in bone assemblages produced by hyenas (Sutcliffe 1970; Behrensmeyer 1978; Andrew Hill, personal communication 1978) and for North American canids (Bonnichsen 1979; Binford 1981). Shipman (1977, n.d.) and Behrensmeyer (personal communication 1978) have both encountered similar types of damage on fossil specimens.

The discussion thus far has focused on the effects of larger carnivores on the elements of larger animals. Predators that take smaller prey than themselves often consume their victims, bones and all. Mammalian predators of this type, like foxes, bobcats, and, in many situations, coyotes, masticate their victims, breaking down body segments and bones. The fragmentary remains of such prey are concentrated in feces, which often are deposited at regular marking stations by territorial carnivores (Mellet 1974; Behrensmeyer *et al.* 1979). These territorial marking behaviors may be responsible for the spatially dispersed but locally concentrated pockets of microfaunal remains sometimes recovered in the Cenozoic fossil record. Avian predators, especially owls, concentrate microfaunal remains at home bases, by repeatedly regurgitating pellets of bone and fur of their victims (e.g., Dodson 1974; Dodson and Wexlar 1979). Because they do not masticate their prey, owls usually produce better preserved suites of microfaunal remains than do either hawks or mammalian carnivores; these remains normally include parts of all zones of the body. Dodson and Wexler (1979) have documented distinctive patterns of bone damage and destruction produced by different species of owl fed the same kind of small mammal; these differences are related to fixed patterns of prey preparation prior to consumption. Bones contained in owl pellets are provided with temporary protection from weathering and other kinds of damage. Dodson (1974) has shown that the buoyant pellets can "raft" microfaunal remains considerable distances in flowing water. A cave or rock-shelter may be the home base of both avian raptors and mammalian carnivores, and even, in the past, of humans. Therefore, such a shelter may produce mixed assemblages of better-preserved microfauna and more fragmentary larger animals. (e.g. Brain 1975, 1980). Understanding the agents involved in such accumulations requires both a good knowledge of the habits and effects of modern bone-concentrating carnivores and the analysis of the faunal remains in question for traces distinctive of specific agents.

The Behavioral and Ecological Contexts of Bone Damage

The foregoing discussion has dealt with the dynamics of bone damage inflicted by a variety of agents and has been, for the sake of concision, overly simplistic. Among humans, the actual constitution of a bone assemblage, and the types and intensities of damage such bones may show is extremely variable. Binford (1978, 1980) has argued that bone assemblages produced by one foraging group can vary markedly, according to the perceived and projected nutritional needs of the group; he further contends that groups in environments that demand greater amount of food storage and "logistical" planning will produce the greatest diversity in such assemblages. Hence, beyond the distinctive damage patterns produced by the use of tools, there is no such thing as a "typical" human pattern of bone modification. Noe-Nygaard (1977) has discussed what she interprets as functional variation in bone fracture patterns among archaeological occurrences in northwestern Europe. Likewise, there is no such thing as a "typical carnivore" pattern of bone damage, although one can probably specify more distinctive patterns of damage that are typical of specific carnivore families or guilds. For example, large cats do not habitually break into prey's long bones to extract marrow (e.g., Miller 1975). Bone damage by large felids is normally incidental to the consumption of flesh. An exception to this generalization may be the leopard, which normally feeds on prey substantially smaller than its own size and has sufficient jaw strength to demolish and consume most of the bones of its victims. Because leopards are known to resort to lairs or trees with their prey, they may create accumulations of heavily damaged bone (Brain 1975, 1976, 1980). Canids, on the other hand, consume soft bone and breach marrow bones (e.g., Bonnichsen 1973, 1979; Miller 1975; Binford and Bertram 1977; Binford 1981). Hyenas will do the same, and can consume even very large bones completely (e.g., Kruuk 1972, 1976). Knowledge of this group-specific variation in intensity of bone damage, and in damage patterns, can be applied in the analysis of fossil or archaeological assemblages in two ways: it can indicate what bone-processing agents probably did affect an assemblage, and it can indicate those which probably did not.

In addition to variations in the bone-processing behaviors of major carnivore groups, situational or local ecological factors may influence the degree of bone processing practiced by members of one species. Binford and Bertram (1977) noted that hungry dogs will inflict more damage on the first in a series of bones they are fed than on the last. So, too, in a broader sense local availability of food resources may influence the intensity of action of populations of potential bone-consumers. Factors involved may include

local scarcity of vital nutrients (such as various salts and minerals), locally low densities of prey species, or high densities of competing carnivores. These relationships have not been explored in a systematic way, and any discussion of them is highly speculative, but a possible example of this intraspecific variation in bone damage can be proposed. Spotted hyenas (*Crocuta crocuta*) can be very efficient bone consumers. They exist in very high densities in the Ngorongoro Crater and southern Serengeti Plains of Tanzania. Intraspecific competition is quite high, as well as the rate of hostile interactions between hyenas and other carnivores (Kruuk 1972). In this region, the hyenas actively hunt in packs and are very efficient bone consumers, defending their hunting and scavenging territories from other hyena packs. Bones of prey and scavenged animals are consumed as they are encountered, and elements up to those the size of a rhinoceros last only a few days on the ground.

In the northern Serengeti and other parts of eastern Africa, spotted hyenas exist in much lower densities and, while their actual feeding behavior is not well documented, they clearly do not engage in such intensive bone consumption nor do they necessarily avail themselves of carrion (Kruuk 1972; Shipman and Phillips-Conroy 1976, 1977; Behrensmeyer *et al.* 1979; Gifford 1977, 1980). The intensity of bone consumption by hyenas, which does extract certain costs in terms of tooth wear and risk of more serious damage to teeth, may be a function of scarcity of food resources, which may be conditioned by intra- and interspecific competition. Galdikas' (1978) description of the rapid consumption of bone by Bornean bearded pigs may be another example of destruction of bone conditioned by local scarcity of food for a particular species.

The foregoing are speculations that require critical evaluation through contemporary observation. They should, however, indicate that the dynamics of carnivore damage to bone is highly variable, not only from species to species but perhaps also from one population of a species to another, according to local ecology. They imply that analysts of prehistoric bone assemblages cannot expect to apply some global constant of "carnivore effect." On the other hand, they also imply that a considerable amount of information about local ecology may be derived from close examination of patterns of damage within and among assemblages.

Humans, Nonhuman Carnivores, and Patterns of Element Representation

Element frequencies in bone assemblages processed by humans or non-human carnivores can result from selective destruction, from selective transport of elements to or from a locale of deposition, or from both pro-

cesses. Various agents can destroy more fragile bones or segments of bones, either by totally consuming them or by reducing them to unidentifiable fragments. The foregoing discussion of carnivore bone processing indicated that wholesale destruction of certain elements or element segments, and hence their disappearance from a potential fossil assemblage, is a more common occurrence in the normal course of such animals' feeding behavior than it is in human bone-processing. Leaving aside the question of transport, it is safe to say that the loss of certain elements or element segments from bone assemblages processed by carnivores is due more to actual consumption of the elements, whereas loss in assemblages processed by humans is due more to reduction of those parts to totally unidentifiable fragments in the process of extracting nutrients, or through subsequent unintentional damage from trampling (see the following).

Binford (1981) has compared patterns of survival of elements and element segments of caribou bone processed by wolves and by Nanamiat Eskimos. While I will not recapitulate his detailed discussion of damage to individual elements, a number of generalizations drawn from this comparison merit review. It should be emphasized again that these findings bear on aspects of assemblage structure resulting from attrition, as opposed to those which result from transport of elements. Binford and Bertram (1977) noted three common forms of surviving long bone segments in Eskimo and Navaho dog yards: (a) articular ends alone, (b) articular ends with a segment of the bone shaft or "shank," and (c) cylindrical segments of shaft with no articular ends. Binford (1981) argued that these reflect three different intensities of gnawing addressed to individual bones. Comparing the relative frequencies of these three types of element segments in wolf-processed assemblages to those in Eskimo-processed ones, he consistently noted a much higher frequency of articular ends alone in the Eskimo assemblages, with articular ends plus shank and cylinders nearly absent. In contrast, wolf-processed assemblages were much higher in articular ends plus shank, and in the frequency of cylinders, with moderate frequencies of articular ends.

These differences result from the ways that canids and humans go about getting marrow from bones. Canids gnaw off the articular ends of long bones as a standard strategy for reaching the marrow they contain. Other less resistant elements, such as vertebrae, may be gnawed and consumed by carnivores for the nutrients they contain. Phalanges of prey may be consumed completely by carnivores, as may be carpals and tarsals. Readers are referred to Brain's documentation of gazelle and baboon element survival after consumption by captive cheetahs (Brain 1976, 1980), for another example of the influence carnivore destruction has on element survival, as well as an illustration of the variation in durable element segments in two different taxa.

Although a considerable amount has been written on the effects of transport by carnivores on the constitution of bone assemblages, there has been little actual observation of such behaviors. However, a number of analyses of carnivore lair assemblages have been made or will soon be available (Behrensmeyer and Dechant-Boaz 1980; Binford 1981; Gifford n.d.; H. Bunn and A. Hill, personal communication 1980). Based on these analyses and anecdotal information, it is possible to outline the process. Larger carnivores often prey on animals close to or even greater than their own body weight; this means that a single predator cannot consume the entire carcass at one sitting. While large cats such as tigers and lions normally do not transport prey very far, larger canids and hyenids often remove body segments from the kill site and transport them some distance to a spot where they are consumed. The meat-rich limbs are preferentially carried off, leaving the bulkier and less meaty axial skeleton at the kill site. This behavior may or may not contribute to the formation of a bone accumulation. The critical ingredient in the creation of a carnivore bone accumulation is repeated transport of body segments or bones to a fixed location. Arctic wolves hunting cooperatively may break down a caribou carcass into limb segments but only disperse it over a relatively small area around the kill site, with each adult taking its share off to eat in a comfortable and undisturbed place (L. R. Binford personal communication 1979). Spotted hyenas observed by Kruuk (1972) in the southern Serengeti areas more often cached limbs in out-of-the-way spots in the landscape, to which they returned later to transport the elements to their lairs. These caching spots are often adventitiously chosen and not reused. Striped and brown hyenas, however, engage in both caching and transport of limb segments to dens (Kruuk 1976; Mills 1973; Owens and Owens 1978).

Denning and lairing behavior often includes the transport of food back to a home base, and it is in the context that such assemblages of bone could develop. In view of the preferential transport of limbs by carnivores, one would predict that carnivore-accumulated assemblages would be dominated by limb bones and elements that, due to tight articulations, travel with them. One might also expect that residual land surface assemblages, derived from carcasses on which carnivores acted, might have a relatively higher proportion of axial elements. I have evaluated these predictions with data from a number of carnivore lairs, kill sites, and land surface assemblages on which bone-collecting carnivores are known to have acted. Expectations regarding element representation in carnivore accumulations were met by the samples. The kill site and land surface assemblages also tended to bear out predictions, although land surface assemblages, as expected, showed less skewing than did kill site assemblages (Gifford n.d.).

The results of bone transport by carnivores are similar to some of the so-

called "schlepp" effects hypothesized by archaeologists for bone assemblages accumulated by humans who hunted large game out of a home base. The parallel is scarcely surprising and points to the inadvisability of using element frequencies alone as a sole criterion for distinguishing human from nonhuman agents of accumulation. Assemblages produced by human hunters killing large game at a remove from a home base may, however, be more highly variable in their composition than those produced by carnivores. In part, this results from the variety of options tools give humans in breaking down a carcass and in part from the fact that human hunters may make decisions to retain body segments of relatively low immediate food value and high transport costs in order to fulfill long-term goals (cf. Binford 1978, 1980, 1981).

The Behavioral and Ecological Context of Carnivore Bone Transport

Once again in a speculative vein, both Binford (1981) and I have hypothesized that the intensity with which carnivores accumulate bone as part of their denning or lairing behavior may be related to levels of interspecific competition in a given region. Aggressive competition between carnivore species can manifest itself in mutual interference with feeding at kill sites as well as predation on subadults and unwary or unhealthy adults of one species by members of another (e.g., Rosenzweig 1966; Kruuk 1972, 1976; Schaller 1967, 1972; Mills, cited in Brain 1980). Denning and related behaviors probably constitute a carnivore coping strategy for protection from both feeding competition and predation by other carnivores. Canids, hyenids, and some mustelids transport whole carcasses, segments of carcasses, or bones back to a den, either to consume themselves or to sustain their offspring. If adults of such species resort to this behavior to stay out of the way of competitors while eating, local accumulation rates should be substantially higher than when adults are simply transporting food to a den while rearing offspring. Thus, the intensity of accumulation of body segments (and bones) by carnivores may be related to the degree of "packing" of competitive species in a region. If any such relationship could actually be established through comparison of modern carnivore behavior in a variety of ecological settings, it would be of use to paleontologists in evaluating the amount of carnivore transport they could expect in given paleoenvironments. Establishing the number of carnivore species, and the degree to which size and/or hunting habits might bring them into competition through comparative anatomy would be a relatively straightforward procedure, at least for Quaternary mammals.

In her analysis of bovids from the Transvaal australopithecine assem-

blages, E. Vrba (1975, 1980) contended that it may be possible to distinguish assemblages accumulated by primary predators from those accumulated by scavengers, on the basis of the range of prey body weights represented. She contended that scavengers would accumulate remains from a wider range of sizes than would primary predators. While Vrba's argument is appealing on a commonsense level, and her analysis of the various Transvaal bovid assemblages demonstrated differences in the occurrence of size and age classes, her hypothesis has not been tested with data from modern carnivore accumulations of known origin. Only actualistic research can ascertain whether the actual dynamics of carnivore predation and accumulation of bone produces the patterning suggested by Vrba.

Other Biological Agents and Patterns of Damage and Element Representation

Numerous reports indicate that herbivorous animals can modify or totally destroy bone by gnawing. Rodents are the best-known gnawers of bone, ranging from the numerous small burrowing species that can attack buried bone (see Miller 1969, for a description of rodent gnawing marks) to very large forms like the beaver (Miller 1969) and the African porcupine (Brain 1976, 1980). Rodents favor bone that is somewhat weathered and free from fat and sinew. Other mammals also chew or completely consume bone. Bone gnawing has been reported for red deer by Sutcliffe (1973), who noted that the resulting pieces resembled alleged tools from European Paleolithic sites; for caribou by Gordon (1976), with similar observations; and for sheep by Brothwell (1976). Total consumption of bone by gemsbok and other ungulates has been reported by Yellen (1976). The areas in which these observations were made are noted as lacking sufficient salts and minerals essential to mammals, and therefore ungulate bone gnawing is explained as a strategy for obtaining these nutrients.

Ungulates can also damage bones lying on a land surface by trampling them. Behrensmeyer and others (1979) have noted that ungulate trampling is a relatively common cause of bone damage in the Amboseli Basin in Kenya. I have noted similar trampling damage to bones of ungulates observed through the first 5 years of postmortem history (Gifford 1977, n.d.). Bones most liable to such damage are the same structurally weaker elements less able to withstand carnivore damage. Even more durable elements, when exposed to weathering for a few years (see the following), become so structurally weakened that they may be fractured by trampling. Trampling damage naturally depends on the frequency with which an area is traversed by animals capable of inflicting damage on them. Bones lying in habitual trackways or near watering places may be subject to much

higher rates of trampling than those lying elsewhere (Myers *et al.* 1980; Gifford n.d.).

The damage patterns produced on bone by trampling may differ somewhat from those produced by carnivore gnawing or human manipulation, but this has not been closely documented. Myers and others (1980) have found that spiral fractures can be produced on slightly dry bone through trampling. Among the distinctive kinds of fracture observed by Behrensmeyer, myself, and others are "wishbone" breaks of fused mandibular symphyses and "snaps" (much like those of broken lithics) of scapular and pelvic blades. Weathering develops deep longitudinal cracks into the medullary cavity of ungulate long bones; when such weathered elements are trodden upon, they collapse into a series of long, rectangular-sectioned fragments, and articular ends that display the negatives of such fragmentation (Gifford 1977). Brain (1967) has noted that heavy treadage of long bone fragments on a sandy substrate can produce polished, awl-like pseudo-tools. At the same time, trampling may act to selectively preserve certain elements, by pushing them down into a yielding substrate, such as loose or moist sediments. Smaller, dense bones appear to be preferentially pushed into the substrate by the same events that damage larger elements (Gifford 1977, n.d.; Gifford and Behrensmeyer 1977).

The best-documented noncarnivorous collectors of bone are probably the African porcupines (*Hystrix*), which regularly transport bone to their lairs for gnawing. Brain (1976, 1980) has analyzed bone accumulations from a few such porcupine lairs and found that distinctive gnaw marks could be found on only some of the bones in these assemblages, indicating the rodents were collecting more bones than they actually processed. Brain's reports indicate that porcupines seldom reduce bone to unidentifiable scraps, at least not in the area of southern Africa in which he made his collections. Porcupines select bone according to a different set of criteria than do carnivores, reflecting their different use of it. In contrast to those in carnivore accumulations, the bones collected by Brain from porcupine lairs were free of flesh, sinew, or bone grease. He also found element frequencies to be somewhat different from those in carnivore accumulations, with relatively more axial elements, especially vertebrae. Brain opined that rodents were attracted to bone and other objects (which in one of his samples included bits of a bicycle) of the basis of bulk. Creation of bone accumulations of this sort will depend on a number of factors, including whether or not bone-gnawers habitually den, whether they engage in gnawing in their dens, and how much bone is available to them as a raw material.

Shipman (1979) reported collection of rodent, bird, and lizard bones by African harvester ants, which apparently consume scraps of flesh left on

the bones and then discard them in heaps of chaff and other refuse around the entrances to their colonies.

Other animals that may damage bone include termites and teneaid moth larvae, which consume bone in some environments (Behrensmeyer 1978). Behrensmeyer (1978) has noted that rootlets growing over and through recent bones on or close to the surface in Amboseli National Park produce small acid-etched grooves (see also Bonnichsen 1979:26). As far as I know, little close documentation of the effects of plants on bone has been carried out.

Chemical/Mechanical Processes and Damage Patterns

Among the most useful of recent studies in taphonomy have been those of Behrensmeyer on subaerial weathering rates of mammal bone in various environments. As used here, "weathering" refers only to processes affecting unfossilized bone, and not to postexposure alterations of diagenetically altered elements, which is sometimes also called "weathering" (e.g., Rolfe and Brett 1969). Behrensmeyer (1978:153) defines weathering as "the processes by which original microscopic organic and inorganic components of a bone are separated from each other and destroyed by physical and chemical agents operating *in situ*, either on the surface or within the soil zone." Behrensmeyer (1978) devised a scale of 0 to 5 for qualitatively defining "weathering stages" that describe fresh through totally disintegrated bone. While these stages describe what is obviously a continuum of change, the categories as defined actually appear to characterize states in which bones remain for some time, before changing relatively quickly to the next state. Behrensmeyer (1978:54) reported that organic geochemist P. E. Hare's preliminary study of amino acids in her weathering reference collection indicated a correlation between the weathering stages and progressive stages of amino acid racemization. A number of local factors can influence the rates at which this breakdown occurs. Amino acid racemization is enhanced by fluctuations in humidity and temperature, as well as by absolute levels of temperature, humidity, and pH in the immediate environment of a bone (Behrensmeyer 1978; Hare 1980). This means that one end of a single bone could conceivably weather at a much faster rate than the other, a phenomenon observed in the field by Behrensmeyer, Brain (personal communication 1976), and myself (Gifford 1977, 1980). Bone exposed to direct sunlight weathers more swiftly than those in shaded areas, including those shaded by vegetation (carnivores and other bone-collecting animals thus protect bones from weathering damage by depositing them in their lairs). I have observed long bones of one hippopotamus weathering at radically different rates over a 3-year period, ap-

parently due to the fact that one element lay in a shallow periodically flooded pan while another lay on better-drained ground only a few meters away (Gifford 1977, 1980).

Weathering proceeds along lines of structural weakness in the bone, developing a fine network of "split lines" over time (e.g., Tappen and Peske 1970; Tappen 1969, 1976). Miller (1975) found that these split lines could be quickly developed in experimental situations, by repeated cycles of freezing and thawing or wetting and drying. Behrensmeyer reports that the "upside" of bones usually weathers faster than the "downside," except in moist environments, in which salts forming in split lines on the downside may hasten disintegration by forcing these cracks further open.

Despite all these potential sources of variability in weathering rates within a given locale, Behrensmeyer (1978) and I (1977, 1980) have found considerable regularity in the rates at which medium-large mammal bones weather on land surfaces in semiarid parts of East Africa. It is likely that bone-weathering rates can be calibrated for other types of environment. Whereas bone may endure for 15 or more years in East Africa, albeit in steadily degenerating condition, there are indications that bones weather more swiftly in other areas, such as the Great Plains of North America (Voorhies 1969a). Assessment of bone-weathering rates in an environment thought to be analogous to a prehistoric one is therefore an absolutely necessary first step in attempting to calibrate weathering of prehistoric bone.

A few general remarks that probably hold true in any situation, regardless of the actual rate of weathering, can be made. Smaller mammals' bones weather at faster rates than do those of larger mammals (Behrensmeyer 1978). Not all bones of the same mammal weather at the same rate; those with high ratios of surface area to volume naturally break down faster than those with lower ratios (Gifford n.d.). Bones of roughly like-sized mammals of different taxa may weather at somewhat different rates, due to constructional differences. In bovid and equid bones I monitored for 5 years after death, the more heavily constructed equid bones weathered at a somewhat slower rate than homologous bovid bones (Gifford n.d.). Due to basic structural differences, the results of weathering on bone of fish, reptiles, and birds can be expected to differ from those of mammal bone. Based on casual observations of fish, reptile, and mammal bone at human campsites in Kenya for which I have dates of death of the animal, it appears that fish and reptile bones do not hold up as well as mammal bone over equal amounts of time, even in the case of large reptile bones of sizes equivalent to those of mammals (Gifford 1977). Again, these observations are only suggestive; detailed work on weathering of nonmammalian bone is required.

Weathering-stage information can provide valuable keys to the circumstances that formed a fossil assemblage. Behrensmeyer (1978) argues that uniform weathering stages in an assemblage may denote a catastrophic mortality pattern, in which all the animals contributing bone to a sample died and were buried within a relatively brief span of time. She contends that assemblages with wider ranges of weathering stages are likely to be the results of attritional mortality. In her discussion, Behrensmeyer was referring mainly to assemblages derived by aqueous processes from open land surfaces. Clearly, in a carnivore den fresh bones may be brought for scores of years or more, and the bones are substantially protected from weathering. These bones may display "catastrophic" weathering patterns but nonetheless contain an attritional sample. Weathering stages have been discerned by Shipman (1977, n.d.) in the Fort Ternan assemblage and used to infer the time span involved in formation of the sample. Weathering-state evidence is being used by Behrensmeyer and others in the Siwalik Miocene fossil localities (e.g., Badgley and Behrensmeyer 1980) for the same purposes.

The temporal information that weathering-stage analysis can provide is of obvious use to archaeologists concerned with establishing duration and repetition of occupation, even if absolute time values cannot be assigned to different stages. It may, for example, be possible to infer that a site created by meat-eating hominids was formed over a brief span or a longer one prior to burial. Conspicuous "gaps" in the suite of weathering stages may indicate gaps in the input of bone, due either to interrupted episodes of occupation or to cycles in meat acquisition. I have recently used weathering-stage criteria to argue that a Pastoral Neolithic bone midden in Kenya was created and buried within a very short span of time (Gifford *et al.* 1981).

Sedimentary Processes and Patterns of Damage

While a substantial amount of work has been done in the damaging effects of aqueous transport in invertebrate remains, (e.g., Driscoll 1967, 1970; Seilacher 1973), very little parallel experimental work has been done in vertebrate taphonomy. Most research on the effects of sedimentary processes on bone has dealt with evaluating the hydrodynamic properties of bone elements and the effects of water transport on element frequencies. Therefore little of a specific nature can be reported.

Abrasion of bone has been assumed to result from the action of sedimentary processes on bone. As noted by Shipman (1977, n.d.) abrasion has not been rigorously defined, but it normally has been diagnosed by rounding of natural features or break surfaces of bone. Most of the taphonomic articles that have employed abrasion of bone as a line of evidence have

linked it with aqueous transport arguing that degree of abrasion to pieces roughly reflected the distance transported (e.g., Voorhies 1969a; Shipman 1977, n.d.b). In these cases the sedimentary contexts of the bone assemblages analyzed indicated water transport and deposition as the means of final burial. However, abrasion could theoretically result as well from sandblasting of bone on a land surface (eolian processes) or, as noted by Brain (1967a), from trampling against an abrasive substrate by animals (bioturbation). It falls to any researcher using abrasion as an indicator of the operation of preburial processes to narrow these possibilities.

As far as I know, no one has conducted experiments on rates of abrasion damage to bone in any of these contexts. One would logically expect that, just as various bones weather or react to other stresses at the different rates, vertebrate elements would be differentially liable to damage by abrasive processes. Shipman (1977) noted a high positive correlation between advanced stages of weathering and degree of abrasion in fossil bone from Fort Ternan, suggesting that weathered bone resists such damage less well than fresh bone. She suggested that elements with greater proportion of spongy to compact bone would be more easily damaged by abrasion.

Driscoll's (1967, 1970; Driscoll and Weltin 1973) approach to abrasion damage in invertebrates may be useful in experimental assessment of abrasion rates in bone. He found a strong positive correlation between abrasion rates in a water-transported shell and the ratio of surface area to weight. This ratio is of course akin to the ratio of surface area to volume previously discussed, and can be seen as expressing the relative amount of an element's tissue exposed to abrasive agents at a given point in time. However, ratios of surface area to volume and surface area to weight do not express exactly the same thing, because each has reference to a different critical variable in the dynamics of transport in a fluid medium, and should not be used interchangeably. It remains to be seen which of these two measures provides the better predictor of abrasion damage.

Sedimentary Processes and Patterns of Element Representation

Since Shotwell's first discussion of the effects of water transport on the structure of fossil assemblages, a considerable amount of experimental work has been done on vertebrate remains as sedimentary particles. Bones can be studied as sedimentary particles using the same methods applied to the study of the transport of any element in a fluid medium. Hydraulic transport results from the interaction of an element with the fluid medium; at a critical level of shear stress between an element and a moving fluid the element will begin to move. The velocity of flow at which this occurs is

determined by properties of both the element and the fluid. Hydrodynamically relevant properties of the element are its size, density, and shape. Viscosity of the fluid will affect transport, with more viscous fluids entraining an element at lower flow velocities than less viscous fluids. Measurements used in the study of particle transport are: (a) the rate of flow at which the critical shear stress level of a piece is exceeded and it begins to move as part of the bedload, (b) the rate of flow at which the piece begins to be transported as a suspended particle in the flow, and (c) the rate at which the piece settles in still water. In studies of perfectly rounded particles, these velocities correlate positively with the sizes and densities of the element. Elements that depart from the basic spherical shape, which offers the least surface area and resistance to flow, will be expected to behave differently from spheres with equal size and density characteristics. Most of the experiments on bone transport have investigated the relation of element shape to its hydrodynamic behavior.

Voorhies (1969a,b) conducted a series of transport experiments with sheep and coyote bones in a circulating hydraulic flume. He was able to group skeletal elements into three major "transport groups," based on their degree and mode of movement when subject to a variety of flow velocities. Voorhies noted that certain elements did not behave in a consistent pattern, sometimes falling with bones of one transport category, and sometimes with another (Table 8.1), but his experiments did not further specify the underlying determinants of these observed patterns. Voorhies

TABLE 8.1

Voorhies' Transport Groups^a

Group 1 Transported by low-velocity current	Group 2 Transported by moderate velocity current	Group 3 Transported only by high-velocity current (lag deposit)
Ribs	Femur	Cranium
Vertebrae	Tibia	Mandible
Sacrum	Humerus	
Sternum	Radius	
	Metapodia	
	Pelvis	
Scapula	Scapula	
Phalanges	Phalanges	
Ulna	Ulna	
	Mandibular ramus	Mandibular ramus

^a Groups of medium-sized bones were found by Voorhies to have similar transport potentials in flume experiments. Elements in lower case were found to sometimes behave as members of one transport group and at other times as members of another.

went on to predict the element frequencies to be expected in assemblages subject to low, moderate, and high stream flow velocities. Assemblages subject to little winnowing action would of course include representatives of all transport categories, those formed by higher rates of flow would be expected to be comprised predominantly of either transported species (Groups 1 or 2 or a combination) or residual assemblages (Group 3). These experimentally based predictions of assemblage structure differ from what one would expect in a natural situation in that they assume that the winnowing processes operate on the isolated elements of whole skeletons. Preceding sections have outlined the ways in which differential durability and selective transport can skew element frequencies in a land surface assemblage prior to sedimentary transport. Aqueous processes may therefore act on a limited suite of elements, and "ideal" assemblages composed of all elements enumerated in Voorhies' transport categories may not result. Likewise, elements may not be transported as single pieces but rather as parts of body segments or still articulated bone units, which will have different hydrodynamic properties than isolated elements.

Behrensmeyer (1975b) undertook experiments to more closely examine the role of element shape, size, and density, as well as the form and texture of the bed, in determining bone transport. She created a baseline against which to assess the effects of shape by calculating the "nominal quartz grain diameter equivalent" for various bones. This figure refers to the size of a round grain of quartz that settles at the same velocity in still water as the element under study. There are actually two ways of obtaining this figure, one derived from a piece's volume (as a measure of size) and the other derived from the actual settling velocity. Because some fossils don't have modern analogues, and because the settling velocities of fossilized specimens will differ from that in their unfossilized states, whereas their volumes will not, the former method is more readily applicable to fossil bones than is the latter. To assess the comparability of predictions based on these two methods, Behrensmeyer checked calculation of nominal quartz equivalents derived from volumes of modern bones against those calculated from their settling velocities. She found that quartz equivalents based on volume predicted faster settling rates (were larger) than those calculated from actual observation of the pieces' settling velocities. She contended this difference was created by variation in the elements' shapes, since elements with higher ratios of surface area to volume settled at slower rates. Bones in each of Voorhies' transport categories displayed roughly similar quartz-equivalent sizes.

In later, as yet unpublished flume experiments, Behrensmeyer checked predicted entrainment and transport velocities for different elements (based

on the more accurate method of quartz equivalent calculation) against the actual performance of the bones in flowing water. She found that quartz equivalents predicted the behavior of most elements well, but that there were some exceptions. The elements were bones which, she contended, had specific shape features that either enhanced their transport potential (e.g., an ungulate scapula with a high surface area to volume ratio and a dorsal spine that in certain positions contributes to lift) or diminished it (e.g., an ungulate half mandible that, when lying flat, presents little resistance to flow). Based on these experiments, she concluded that bone density was a better predictor of the transport potential of an element than was volume, but that shape played an important role in determining an element's performance in flowing water.

Other factors affecting absolute rates of flow at which movement of elements occurs include the texture (particle size) of the bed, although this should not affect the overall pattern of sorting already outlined. Variation in the morphology of the bottom can create different types of current flow patterns, which would also affect the rates at which transport and sorting occur. Finally, greater amounts of suspended sediment in flowing water increase its viscosity and alter critical transport velocities for various classes downward. Highly viscous fluids, such as mud flows, will move all classes of bone together, transporting them without sorting. A depositional situation of this sort was inferred by Shipman (1977, n.d.) for the main fossil deposits at Fort Ternan, Kenya.

Behrensmeyer and Hanson (see Hanson 1980) have undertaken long-term experimental observations of bone transport in a natural river situation, which to date have produced much the same patterns of differential element transport as observed in flume experiments. Most of these experimental observations have focused on ungulate remains, and it is clear that results from these must be modified for taxa with any radically different skeletal constitution. Flume experiments by Boaz and Behrensmeyer (1976) on human skeletal materials indicated that undamaged hominid crania may be transported readily if air is trapped inside the cranial vault.

Behrensmeyer and others (e.g., Badgley and Behrensmeyer 1980) have employed an abbreviated analytic key in assessing and comparing the degree of water transport-dependent sorting in assemblages. The ratio of teeth to vertebrae for assemblages dominated by ungulate, carnivore, and primate species should be roughly one if the assemblage was subject to little winnowing action, greater than one in the case of a residual (lag) assemblage, and less than one in the case of a transported (winnowed) assemblage. The tooth to vertebra ratio is especially useful because both of these elements are among the least likely to be transported by carnivores.

They therefore may be assumed to be subject to roughly comparable intensities of deletion from a land surface due to the action of these biological agents.

In summary, water transport can strongly structure element frequencies in an assemblage by "winnowing" it prior to final burial. This process can produce two general types of assemblages, transported (winnowed) and residual (lag). While a variety of features of the bed may influence the absolute velocities at which specific elements will move, the relations of transport potential among different bones remains constant (except in extremely viscous fluids). Of the three major determinants of bone's hydrodynamic properties, density and shape seem to be those most important. An element's particular shape can either enhance or diminish its transport potential. The transport potentials of bones and other elements of interest are best assessed through experimental observations of both settling velocity and their movements in flowing water.

The sedimentary context of fossil bone, in both texture and structure, provides an independent line of evidence regarding the conditions that affected a bone assemblage during deposition. In the case of aqueous deposition, considerable information on the structure and texture of beds, current direction, and velocities of flowing water can be gained from analysis of sediments.

Sedimentary Processes and Patterns of Spatial Orientation

Through experiment it is possible to predict the probable behavior of individual bones of different shapes in flowing water. However, studies of the spatial relations (long-axis orientation and dip) of bones in assemblages have thus far not yielded any fruitful generalizations. Shipman (1977, n.d.) noted that a number of supposedly significant clusterings in long axis orientation published by other researchs could just as likely be random distributions. Very little experimental work has been attempted on the behavior of groups of bones in flowing water. Since so many variables, each with varying potential values, influence the aqueous transport and burial of a bone, and since bones traveling as part of the bedload or in suspension in a current can be expected to interact, creating even more complex situations, the search for powerful and consistent indicators of the operation of aqueous transport in bone orientation may be less than realistic.

By modern analogy, Behrensmeyer (personal communication 1979) has noted that bones or footprints and other depressions caused by animals can act to capture smaller elements that would normally be continuously trans-

ported in flowing water, forming small sediment traps in which clusters of fossil may be recovered.

For a review of geologic and biologic processes that can operate on deposits after deposition, see Wood and Johnson (1978).

Analysis of Real Assemblages

Since any assemblage can be the result of the action of a variety of the processes discussed in this section, one can expect that taphonomic analysis will be a rather complex exercise. The depositional context of an assemblage is the logical place to begin analysis, because it provides an independent and often more easily read line of evidence on the last phases of elements' histories in the biostratinomic realm. The earlier biostratinomic history of an assemblage is best unravelled by fastening on the most unambiguous traces of the operation of a given agent that cannot be obliterated by the operation of subsequent ones. In the face of ambiguous evidence, the logical recourse is actualistic research.

CONCLUSIONS

We still do not know how much taphonomic analysis will help us in understanding the ecology of ancient organisms. This situation is partly due to the fact that taphonomy has not been used to its fullest potential in exploring the ecological meaning of patterning in the assemblages with which paleoecologists must deal. However, it is also due to the fact that taphonomic research deals with a complex set of interactions that demand the investment of time and energy if they are to be understood. The only way to find out what can be known is by proceeding to reduce the ambiguities in the materials through properly devised actualistic research that focuses on the dynamics of the interactions that produce the preserved evidence and the ecological contexts of those interactions. Equally important is comparative analysis of suites of assemblages, in order to isolate those indicators of the greatest reliability in the widest variety of cases.

Properly pursued, taphonomy can provide paleoecologists with information about the spatial, temporal, and biological factors involved in the formation of fossil assemblages. Elucidation of those three aspects of assemblage formation will bring us closer to answering the two fundamental questions: First, are the inferences drawn from a given assemblage war-

ranted, in light of what we know about the formation of similar assemblages in the observable world? Second, are two assemblages comparable in terms of the features we wish to examine, again in terms of what we know about the histories of assemblages with similar features in the present-day world?

Implicit in much of the foregoing discussion is the idea that the same approach to learning more about the past should be applied in archaeological research, that the use of analogic reasoning and uniformitarian assumptions be equally conscious and cautious, and that the search for meaning in the archaeological record begin with well-conceived and well-executed observations of the contemporary world.

Neither paleoecologists nor archaeologists should be naively optimistic about what might actually be known about the ecology or behavior of creatures that lived in the remote and undocumented past. Nor should they be overly confident that their research will quickly yield answers to their questions. What they can have some confidence in is the fact that they have in their possession a strategy for learning more about these questions. Historical inquiry based on properly applied actualism and uniformitarianism can produce, not the past in all its detail, but scientifically acceptable progress.

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