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WHY A BOOK ON PALEOENVIRONMENTAL RECONSTRUCTION FROM FAUNAL REMAINS?

Once *fossils* were recognized for what they are – ancient remains of organisms – early earth scientists attempted to ascertain what those remains might reveal about the past. Fossils represented ancient life, but what else might they signify? Georges Cuvier is often regarded as the first scientific paleontologist (Rudwick 1985, 1997); he initiated a now long-standing tradition of research focusing on the morphology of past animals, including their functional anatomy (Haber 1959; Rainger 1981). After the publication of Darwin's (1859) *On the Origin of Species*, the morphological tradition (Rainger 1981) included efforts to decipher the transitions between major groups of animals such that by the 1880s "paleontology was an evolutionary science" (Hall 2002:649). Paleontology's major applied value was in facilitating the exploitation of the earth's mineral resources, leading it to be typically associated with academic departments of geological sciences rather than biological sciences (Gould 1977; Rainger 1985). By the middle of the twentieth century, however, that somewhat singular focus began to broaden.

Ancient remains of animals and plants had been parts of living organisms. Those organisms must have had species-specific ecologies, just as now-living organisms do. It was a relatively easy (though perhaps a surprisingly long-time-coming) step to deciphering the paleoecological signal of fossils in order to reconstruct past environments, *habitats*, and climates. Although not without precedent in the nineteenth century (e.g., Dawkins 1871; Lartet 1875), early modern work began with Everett C. Olson in the 1940s (Rainger 1997). The focus of much paleontological research at that time was on interpreting fossil morphology and writing evolutionary history (beyond the basic geological work of biostratigraphy and mineral exploitation). Olson broadened that traditional focus to include study of the paleoecology of particular organisms and the biological and ecological interrelationships of communities of organisms, providing a framework for reconstructing terrestrial paleoenvironments through time. His relatively unique insights to past landscapes and biota were a catalyst for paleontologists, many of whom turned at least some of their attention to paleoecology.

A major landmark in the development of paleoecology was the 1957 publication of the *Treatise on Marine Ecology and Paleoecology* (Hedgpeth and Ladd 1957), followed a few years later by *Approaches to Paleoecology* (Imbrie and Newell 1964). These volumes focused on marine ecosystems, but interest in terrestrial paleoecology was blossoming at the same time. In 1961, F. Clark Howell and François Bourlière organized a symposium aiming to "integrate the results of increasingly numerous field studies bearing on the biological-behavioral evolution of the higher primates (especially hominids) with other field studies in the paleoecology and the recent mammalian ecology of sub-Saharan Africa" (Howell and Bourlière 1963:v). The proceedings were published a few years later in *African Ecology and Human Evolution* (Howell and Bourlière 1963); in the pages of that volume the contributors (paleontologists, archaeologists, geologists, and zoologists) acknowledged that paleoenvironments were the context in which humans evolved biologically and culturally. Knowing something about those ancient environments would, it was believed (and still is), facilitate understanding of humankind's deep history. This idea was echoed a year later by North American archaeologists in Hester and Schoenwetter's (1964) monograph *The Reconstruction of Past Environments*. Old World archaeologists had exploited a particular value of paleoenvironmental research based on faunal remains some years earlier, specifically thinking about what paleoenvironmental fluctuations might tell us about the possible necessity of the origins of agriculture (Reed and Braidwood 1960). Australian paleontologists held a symposium in 1978, the proceedings of which were published that same year under the title *Biology and Quaternary Environments* (Walker and Guppy 1978). The main purpose of that symposium was to review and evaluate in explicit terms the operating principles and requisite assumptions that underpin paleoenvironmental reconstruction based on faunal remains such that they did not become so implicit as to facilitate complacency among researchers. Clearly, a florescence of interest in paleoenvironmental reconstruction based on faunal remains took place during the middle of the twentieth century.

The literature concerning the paleoenvironmental implications of prehistoric faunal remains (much of it is cited in this volume) has grown considerably in the past several decades. Much of that literature is made up of case studies, that is, analyses of particular faunas that address aspects of the paleoecology and paleoenvironments in which the represented faunas participated and lived. Reading that literature can reveal the analytical techniques and requisite interpretive assumptions that attend such analyses. However, one must read numerous articles to be exposed to the myriad techniques that have been used and the various assumptions that, when stated explicitly, underscore the sometimes tenuous nature of interpretations.

We have both analyzed ancient faunas with the goal of deciphering their paleoecological and paleoenvironmental implications, having been taught some of the basics of doing so by our academic advisors and teachers, and learning more by reading much of the pertinent literature. During the course of our research, we perceived a major lacuna in the extant literature – there was no textbook that described the ecological basics, the analytical assumptions, and the numerous analytical techniques one might use to reconstruct past environments on the basis of a *collection* of ancient faunal remains. Our students' inquiries about the topic underscored this gap in the literature; there was no single title to which we could refer them. Producing a list of a dozen or fewer titles to which we could direct them might have sufficed, but that raised the question of which titles to include and which to exclude. Writing (what turned out to be) this book would fill this significant gap in the literature. And we perceived another reason to write the book, a reason we identify shortly.

In the remainder of this chapter, we continue our sketch of the history of *paleozoology* with a focus on the emergence of paleoecological research and paleoenvironmental reconstruction. Our intention is to provide some background to modern research in this area. The sketch is brief because our intentions in writing this volume are not to provide a lengthy history of this field of inquiry. We provide the history that we do because we believe that knowing something of the background of one's chosen line of research can enhance understanding of why practitioners today ask the research questions they do and seek answers to those questions in the ways they do. It is for this reason we include historical tidbits throughout the volume. Following our outline of the history of paleoenvironmental reconstruction in this chapter, we describe the structure of the remainder of the volume. Near the end of this chapter, we identify the other reason we decided to write this book, one that is of equal if not more significance than that of filling a gap in the literature.

A BIT MORE HISTORY

Old World archaeologists had long studied faunal remains recovered from archaeological deposits in order to facilitate building cultural chronologies (O'Connor 2007). It was the association of undisputed stone tools with remains of animal species believed to have gone extinct at the end of the Pleistocene ice age that persuaded the nineteenth-century scientific community that human ancestors had been present well prior to the biblically documented creation (Grayson 1983a; Van Riper 1993). Similarly, it was the association of remains of an extinct form of bison (*Bison antiquus* [at the time the specimens were attributed to *B. taylori*, a form no longer considered valid]) with stone artifacts in New Mexico (USA) that convinced local archaeologists that people had been in North America near the end of the Pleistocene (Meltzer 2006). Use of ancient faunal remains for these kinds of biostratigraphic (stratigraphic correlation and age assessment) purposes had been around for some time in geology (Rudwick 1996). For instance, Charles Lyell (1833), sometimes referred to as the father of modern geology, had used the fossil record to build a chronology of geological eras (Rudwick 1978; see also Lyman and O'Brien 2000).

In short, the remains of ancient animals have a deep history of analytical use in the earth sciences, including archaeology, but using them to decipher ancient environmental conditions did not really emerge in any consistent or formalized way until, as we noted above, the middle of the twentieth century (Grayson 1981; Lundelius 1998; Semken 1983). Nearly four decades ago Grayson (1981:28) noted that critical examinations of "the principles and processes of paleoenvironmental reconstruction using archaeological vertebrates are quite rare." North American paleontologists later provided some critical discussion (Churcher and Wilson 1990; Graham and Mead 1987; Graham and Semken 1987; Harris 1963; Semken and Graham 1987), but we note that those discussions are seldom if ever cited by archaeologists interested in paleoenvironments. The still very useful discussion produced by Australian paleontologists had appeared a few years before Grayson's analysis (Walker and Guppy 1978). Paleozoologist Peter Andrews' (1995, 1996) excellent summaries written from an Old World perspective did not appear until the end of the twentieth century. The Australian volume seems not to be well known, but the latter items do receive some attention (in the form of citations), likely as a result of Andrews' (1990) landmark book *Owls, Caves and Fossils*. That volume is a *tour de force* review of how various species of raptor accumulate and modify remains of their animal prey, how those raptors might skew the paleoenvironmental signal of an ancient fauna, and how to contend with such things when analyzing an ancient fauna.

As indicated above, part of the reason for the expansion of interest in paleoenvironments is that it is those environments that served as the context of evolution of today's biotas. Therefore, knowledge of paleoenvironments as the evolutionary context, especially that of human biological and cultural evolution, has come to be seen as mandatory to writing and understanding evolutionary history (e.g., Behrensmeyer 2006; Kingston 2007). Archaeological and anthropological concerns over paleoenvironments grew as interest in the driving forces of hominin evolution expanded coincident with the discovery of more and more fossils of human ancestors (e.g., compare select chapters in Coppens et al. [1976] with the entire volume of Bobe et al. [2007]). Determination of what those ancient environments were like has become commonplace, particularly in the Old World where the majority of human biological and cultural evolution took place. Several excellent texts are available that cover many of the kinds of data and analytical techniques that can be used to reveal aspects of paleoenvironments (e.g., Bradley 1985, 2015; Dodd and Stanton 1990; Lowe and Walker 1997, 2015). Barring Dodd and Stanton (1990), who deal primarily with marine invertebrates, there is, from our admittedly biased viewpoint, surprisingly little discussion in those volumes on how ancient (terrestrial) faunal remains might be studied and analyzed, despite the fact that most researchers realize that paleozoological specimens are sometimes all that is available and that paleozoological data can be used to supplement those other data.

VOLUME STRUCTURE

A major purpose of this volume is to summarize many of the varied analytical techniques that have been applied to paleozoological remains for the purpose of reconstructing past environmental conditions, including climatic parameters, habitat characteristics, etc. Our discussion and analytical examples focus on mammals, as remains of other kinds of animals – birds, fish, shellfish, reptiles – tend to be less abundant in the terrestrial paleozoological record. This does not mean non-mammalian remains are not valuable when it comes to their paleoenvironmental implications. The study of shellfish is, in fact, where much modern paleoecology began (e.g., Hedgpeth and Ladd 1957). Nevertheless, our expertise tends to be with mammalian remains, so that is where the bulk of our attention is directed. Even so, much of what we say throughout the volume pertains to all taxa of organisms, plant or animal. We do reference some of the pertinent literature with respect to insects, shellfish, herpetofauna, and birds, though perhaps not surprisingly, the literature on mammals outweighs that on those other kinds of animals, ignoring for the moment the truly ancient paleontological record wherein invertebrate faunas dominate ecosystems.

Given our intention (and hope) that this volume serve as a text, it is necessary that we outline some basic ecological and biogeographic principles that underpin paleoenvironmental reconstruction based on zoological remains. We describe these principles in Chapter 2, where we also emphasize that taking courses in *ecology* and *biogeography*, reading widely on the subjects, or both are highly recommended.

Analytical methods in virtually any field of inquiry rest on one or more assumptions. Many of these are implicit and few are typically discussed in textbooks. We have, for example, been somewhat baffled by how few of the requisite assumptions to paleoenvironmental reconstruction have been identified in the paleoecological literature, and even more baffled by how seldom the mentioned assumptions are critically evaluated (e.g., Dodd and Stanton 1981; Lowe and Walker 1997; Wing et al. 1992). Even though the assumptions underpinning paleoenvironmental reconstructions based on zooarchaeological remains (e.g., Findley 1964; Harris 1963; Lundelius 1964; Redding 1978; Yalden 2001) and on paleontological remains (e.g., Walker and Guppy 1978) have been previously outlined, none of these earlier discussions have discussed all key assumptions, nor have those assumptions been critically evaluated from a modern ecological or taphonomic perspective. We think it exceptionally important to do just that within the context of this volume. Therefore, in Chapter 3 we identify and critically discuss ten assumptions underpinning the analysis and limitations to the interpretation of taxa represented by a set of faunal remains in terms of their paleoenvironmental implications. We focus on the assumptions and limitations that result from analytical dependence on taxonomic identifications of faunal remains; such analyses typically concern biogeography, taxonomic presences and abundances, and skeletal morphometry. Assumptions necessary to paleoenvironmental reconstruction based on analytical methods not directly resting on taxonomic identifications are covered as necessary in other chapters.

In Chapter 4 we describe several previously published mammalian faunas that are used in exemplary analyses in later chapters. Although we do not always use these same faunas and often refer to others to illustrate certain things, subjecting the same faunas as often as possible to the different analytical techniques discussed in later chapters accomplishes two things. First, it ensures that detected differences in analytical results must be a function of the analytical techniques that are used. Second, use of the same faunas throughout means the reader can focus on variability in analytical techniques rather than on variability in faunas and their paleoenvironmental implications.

One of the most challenging aspects of this volume, and a major reason for wanting to put it together, was to produce a summary of the diverse analytical methods that have been developed over the years to decipher the paleoenvironmental meaning of ancient animal remains. Several excellent introductory overviews of analytical methods applicable to paleozoological remains are available (e.g., Andrews 1996; Graham and Semken 1987; Reed 2013; Reed et al. 2013). There are also texts that discuss how to analyze and interpret paleobiological remains in terms of their paleoenvironmental implications (e.g., Bradley 1985, 2015; Dodd and Stanton 1990; Lowe and Walker 1997, 2015), but these tend to focus most closely on geological data, marine invertebrates, and botanical remains such as pollen while terrestrial faunal remains receive minimal discussion. And while there are several excellent volumes that are made up of case studies of individual faunas (e.g., Bobe et al. 2007; Graham et al. 1987), a text that focuses on zoologically pertinent ecology and analytical assumptions and techniques does not exist.

We organize the myriad techniques for analyzing faunal remains in terms of their paleoenvironmental implications into what we believe is a sensible framework, even if the boundaries between them are not hard and fast. In Chapter 5 we describe some of the most basic techniques, ones that depend on the identity of the taxa that are found and their ecological and biogeographic predilections; these techniques rely on what are often called presence/absence data. Analytical techniques that focus on taxonomic abundances are the subject of Chapter 6. Techniques discussed in Chapter 7 extend into the realm of taxon-free methods, in which taxa and communities are characterized according to ecological or morphological variables. The topics we cover in that chapter include such things as community structure analysis, *ecomorphology* and *ecometrics*, and paleodietary reconstruction. Taxonomic *diversity* (*richness*, *evenness*, and *heterogeneity*) is sometimes considered a taxon-free metric, but because it poses a distinct set of analytical challenges we address it separately in Chapter 8. In Chapter 9 we address the suite of techniques – relying on taxonomic presences, abundances, and taxon-free characterizations – that are designed to provide numerical estimates of paleoenvironmental variables (e.g., temperature, precipitation). And lastly, Chapter 10 discusses the use of size *clines* and ecogeographic rules, including the well-known *Bergmann's rule*, in paleoenvironmental reconstruction.

It has become increasingly clear over the past three or four decades that the taphonomic histories of assemblages of faunal remains can variously mute or skew the paleoecological implications of those assemblages (e.g., Behrensmeyer et al. 2000, 2007a; Fernández-Jalvo et al. 2011; Lyman 1994; Soligo 2002; Soligo and Andrews 2005; Turvey and Cooper 2009). An appreciation of taphonomic processes enhances our confidence that faunal signals of potential paleoenvironmental significance are meaningful, or at least reminds us to be sufficiently cautious with our interpretations. In this volume we do not, however, spend much time trying to disentangle taphonomic processes, especially for case studies where our main goal is to demonstrate how a particular analytical technique works; to do so would result in tremendous lengthening of the discussion. But we do call attention to taphonomic issues relevant to the exemplary case studies and that are also likely to cause problems with future applications of the techniques. A topic raised several times in Chapter 3 also merits attention here: any paleoenvironment reconstructed on the basis of faunal remains (or any other data source) should be evaluated against independent data, such as palynological or geomorphic data. Means to understand and overcome the limitations of paleoecological analyses of ancient faunas have grown markedly in the past several decades, and these are mentioned throughout the volume as occasions arise.

There are increasing efforts to forecast future environments in the face of what seems to be increasingly anthropogenically (humanly) driven climate change (e.g., Blois et al. 2013; Williams et al. 2013). The record of ancient environmental and climatic changes revealed by paleozoological data can be used to test models of the future and also provide insight to, for instance, how individual species of animals as well as communities thereof may respond to those changes. As testimony to this, we note the emergence since about 1990 of what is today known as conservation paleobiology (Dietl et al. 2015), the paleontological equivalent to what archaeologists sometimes refer to as applied *zooarchaeology* (Lyman 1996). The paleozoological record, whether paleontological or zooarchaeological, comprises an archive of experimental results concerning how biota respond to environmental change (Barnosky et al. 2017; Dietl et al. 2015; Sandweiss and Kelley 2012, respectively). As such, that record is being consulted more and more often as conservation biologists and others seek to predict the future biological health of planet earth. As custodians of a large portion of the paleozoological record, archaeologists, paleoecologists, and paleobiologists have, we believe, along with a growing number of other scientists, a moral and ethical responsibility to not only protect but utilize that record for humankind's benefit (e.g., Dietl and Flessa 2009; Dietl et al. 2012; Faith 2012b; Lyman and Cannon 2004; Wolverton and Lyman 2012; Wolverton et al. 2016). By "utilization" we emphatically do not mean collection of ancient animal remains only to learn about the past. Rather we mean one should use those remains for just such purposes, but also and equally importantly, use those remains to help conservation biologists learn about what might happen in the future as humankind's influences on ecological processes and biotic and abiotic resources take on ever greater onerous implications. If, for example, anthropogenically driven global warming continues (e.g., Barnosky 2009), what might be the effects on plants and animals? Numerous instances of climatic warming occurred in the past; the end of the Pleistocene ice age about 11,700 years ago is an obvious recent example, but there are also important examples much deeper in time (e.g., Gingerich 2006). Knowing how biota responded to those shifts in climatic regimes would suggest what we could expect, and also how we might work to avoid (or adapt to) such changes if they would seem to adversely impact the ecological goods and services humans depend on for survival. We return to this issue in the final chapter (Chapter 11) of this volume where we describe some real-world examples.

The applied aspects of paleoenvironmental reconstruction are, to us as parents, extremely important. There are now numerous efforts to forecast changes in biota that may occur as a result of future (anthropogenically driven) climatic change (e.g., Hijmans and Graham 2006; Parmesan 2006; Williams and Jackson 2007; Yackulic et al. 2011). That large and growing body of literature contains several nuanced discussions of the limitations of using biological data as proxies for environmental variables that are directly pertinent to using paleozoological remains to reconstruct or "hindcast," the modelers say, paleoenvironments (e.g., Belyea 2007; Birks et al. 2010; Huntley 2012; Varela et al. 2011). That literature also includes rather nifty studies of what early urbanization can do to local faunas (e.g., Weissbrod et al. 2014); urbanization has long been perceived as a threat to *biodiversity*, and the paleozoological (particularly the zooarchaeological) record demonstrates the threat has a deep history (see also Boivin et al. 2016). Finally, we note the argument has recently been put forth that the basic subject of paleoecology should be used to facilitate teaching students and the public, too, about modern ecological topics such as global warming, the loss of biodiversity, ecological sustainability and resilience, and disruption of ecosystem services (e.g., Raper and Zander 2009). In our admittedly biased opinion, we think this is a swell idea!

WHAT WE DO NOT DO

In this volume we do not spend significant time discussing the quantification of faunal remains; that topic has been covered in detail elsewhere (e.g., Grayson 1984b; Lyman 2008b). Instead, we acknowledge that the topic is in fact contentious, but for sake of simplicity throughout the volume we presume the favored unit of quantification for measuring taxonomic abundances is not a significant issue, although in the minds of some it is (e.g., Domínguez-Rodrigo 2012; Giovas 2009; Lyman 2008b; Morin et al. 2017a, 2017b; Nikita 2014; Thomas and Mannino 2017; Turvey and Blackburn 2011). For analyses that require quantification of taxonomic abundances, we rely exclusively on the number of identified specimens (NISP) of a taxon, where a specimen is a bone, shell, or tooth or fragment thereof, or the minimum number of individuals (MNI), though others have used alternative measures such as biomass (e.g., Pokines 1998; Staff et al. 1985).

We discuss the geochemical approaches (e.g., stable isotopes) used to reconstruct paleoenvironments from faunal remains in Chapter 7, but we do not spend any time discussing the biogeochemical foundations of these techniques or the appropriate laboratory methods. To do so would require one or more additional chapters, which we feel is unnecessary given the numerous books that deal with these issues (e.g., Allègre 2008; Faure and Mensing 2004; Hoefs 2015; Sharp 2007), as well as volumes and reviews written for archaeological and paleontological audiences (e.g., Ambrose and Katzenberg 2000; Lee-Thorp 2008; Lee-Thorp and Sponheimer 2006, 2013; Pate 1994; Sandford 1993; Schoeninger 1995). Just as one should learn the basics of faunal analysis

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J. Tyler Faith , R. Lee Lyman
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(e.g., identification and quantification – topics we do not cover here) from experienced paleozoologists, those interested in geochemistry should seek training and laboratory experience from experienced geochemists.

We also do not cover aspects of paleoecology beyond those topics relevant to the reconstruction of past environments – considered here to include things like ancient climate, floras, habitats, biomes, and the like. As a discipline, paleoecology is concerned with the study of interactions of ancient organisms with each other and with their environment. Although a major focus of paleoecological research deals with paleoenvironments, many paleoecologists are also interested in a broader range of topics, including, for example, the assembly and disassembly of biotic communities, food webs and trophic linkages, and evolutionary processes. We deal only with paleoenvironmental reconstruction here, and this is why we have entitled this book *Paleozoology and Paleoenvironments* rather than *Paleozoology and Paleoecology.*

FINAL COMMENTS

Although we have already used them above, there are several terms appearing throughout the volume that we need to define at the outset. We use the term *fossil* to denote any ancient remain of an animal, regardless of the specimen's age or fossilization (mineralization) condition. We use the term *assemblage* to denote a collection of faunal remains whose aggregation is the result of an analytical decision. That decision might be to aggregate (analytically) all fossils recovered from a depositional unit such as a geological stratum, or to aggregate all the remains of a particular taxon recovered from a particular multi-stratum site. We emphasize that the aggregation, or choosing the spatio-temporal-taxonomic boundaries of an assemblage is an analytical decision, sometimes facilitated by stratigraphic boundaries.

The remains of ancient animals – bones, teeth, shells, dermal structures – have been and are regularly recovered from two general kinds of deposits. Archaeological deposits are those that include human artifacts such as arrowheads and fragments of pottery. Faunal remains from these deposits are often referred to as zooarchaeological remains. The oldest reported zooarchaeological remains are about 3.4 million years old and are from Africa; in the Americas the oldest generally accepted (there is ongoing debate over the validity of proposed more ancient remains) zooarchaeological remains are about 14,000 years old. Paleontological deposits are those that do not include human artifacts and can be of virtually any age. The included fossils are typically referred to as faunal remains or paleontological remains. It is not always possible to determine whether a particular assemblage of faunal remains is archaeological or paleontological, in part because some faunal remains thought to have been accumulated and deposited by hominins have no associated artifacts. And in many cases, substantial portions of the faunal remains from archaeological deposits are accumulated by geological processes (e.g., fluvial action) or other taphonomic agents (e.g., raptors, carnivores). Because for our purposes the distinction is not always pertinent, we refer to any set of ancient faunal remains, zooarchaeological or paleontological, as paleozoological. Other terms will be defined when first encountered in the text. For convenience, we have compiled the specialized terminology in this book into a Glossary of key terms, each of which is italicized at first appearance.

We attempt to be objective in presenting the numerous analytical techniques that have been proposed, and not be too judgmental. We do, however, point out what we believe to be particular weaknesses of some techniques, and strengths of others. Finally, although we reference much of the pertinent literature, particularly examples of paleoenvironmental analyses of ancient faunas, the list of references we cite is in no sense complete, but we have tried to include literature from all major continents. Our combined linguistic expertise is English, so that puts a limit on what we have read while writing this volume. Faith has focused his research attention on southern and eastern Africa, and Lyman on western North America. That likely puts another constraint on the literature with which we are familiar. Something that became increasingly apparent while writing this book is that many of the analytical techniques commonly used by paleozoologists working in the Old World differ from those used by paleozoologists working in the New World, even though our goals (paleoenvironmental reconstruction) are the same. There is no good reason why these geographic traditions should remain distinct, and the divergence likely reflects the simple fact that paleozoologists working in any particular part of the world are most familiar with the literature from that part of the world. Our effort to include literature from all continents reflects our hope to facilitate cross-over between these traditions and to include literature that might be familiar to anyone who reads the volume. We look forward to hearing from colleagues who wish to identify our weaknesses, both in literature cited and in our reasoning.