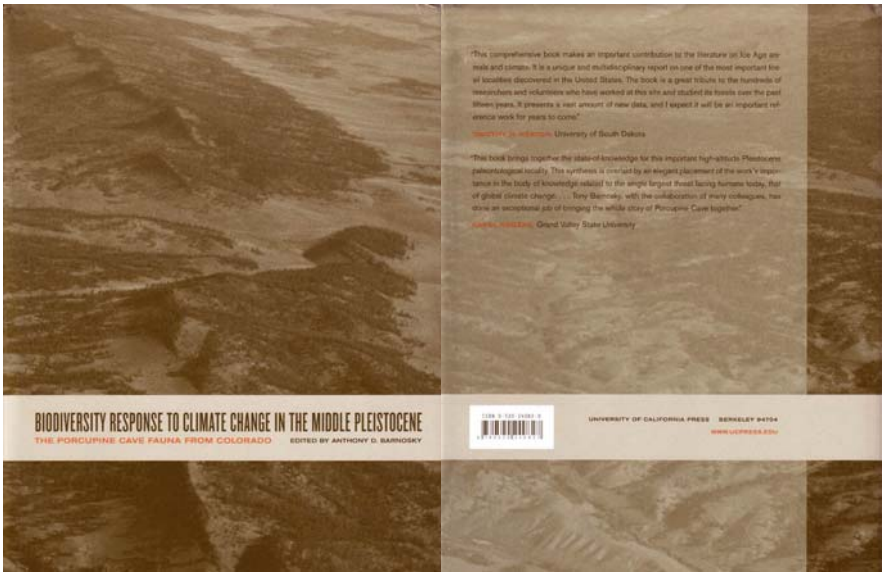
Barnosky, A.D. Ed. 2004. Biodiversity response to climate change in the Middle Pleistocene. The Porcupine Cave Fauna from Colorado. – Berkeley/Los Angeles/London, University of California Press

Book review by D.R. Williams & B.L. Beatty



A steep warming trend during the last two centuries has been linked in some degree to pollution emitted since the Industrial Revolution. Proposed effects of continued warming on the health of the world's biota range from disastrous to equivocal. Studying the response of faunas to climate change in the past increases our predictive power of climate effects on present and future biodiversity. This volume publishes research aimed at answering those questions, using the most up-to-date information from the ongoing excavations and fossil preparation at Porcupine Cave. Porcupine Cave spans a time period in Colorado during Late Blancan-Early Irvingtonian glacial-interglacial cycles. The cave has a degree of temporal resolution, a nearly uniform taphonomy, and is a vector that samples the surrounding environment thoroughly making it an ideal testing ground for climate questions.

Several different fields of study are covered and the book is broken down into three parts loosely based around a central theme. Part one 'The discovery and distribution of fossils' contains a broad range of topics. The main purpose is to introduce the reader to the geology, landforms, modern ecology, and history of the cave and South Park, the basin that contains it.

Chapter one provides an introduction of the importance of climate change to biodiversity and ecosystem health. Chapter two continues the introduction, this time with specific reference to Porcupine Cave. Topics covered here include the cave's general location, modern surroundings, fossil taphonomy, common fossil preservation state, and a detailed description of the collecting localities within the cave. The cave is mapped in several different views, providing a good idea of the general topography at any one collecting locality. Each locality is then described in detail, including collection methods and taphonomy.

Chapter three describes the modern biota against which the fossil evidence will be later compared. The brief introduction to the modern fauna and environment is expounded on here. The reader is given a more detailed description of the modern flora and fauna of the basin containing the cave, South Park. The modern biota of South Park hints at the importance the basin had in the past. The variety of underlying bedrock types has given South Park a diversity of habitat types, from wetlands to salt flats. The modern ecological mosaic surrounding the cave will be important when discussing the fossil evidence.

The next chapter, titled 'The historical context of Porcupine Cave. American Indians, Spaniards, government surveyors, prospectors, ranchers, cavers, and paleontologists in South Park, Colorado' provides an unexpected joy and rare opportunity for the reader and anyone using this book to study fossils from Porcupine Cave to get a glimpse of the long historical background behind the region and the cave itself. I (BLB) revelled in the vicarious experience of imagining the discovery of the cave, the trappers and explorers that came before its discovery, and the native American history of the region. The authors keep it concise but detailed just to the point of conveying facts and feelings of the region, without much overwhelming inclusion of too many dates or lists of events. The layout is subject-oriented; making it feasible to lookup curious details such as bear attacks (pp. 46, 47). In short, this chapter brings this magnificent location and fauna into a human context that inspires a desire for a personal visit. The figures are sparse (two maps and an illustration of a bear skull), but of fine

quality. While it would be of further interest to have old photos, it is certainly understandable due to space constraints and the primary focus of the book.

Chapter five discusses the geology and speleogenesis of Porcupine Cave. Because the cave is excavated out of the Manitou Dolomite, percolating ground water has caused opening and closing of fissures throughout its depositional history. Only two localities, the Velvet Room and The Pit, appear to have been open for most of the cave's long history, from approximately 2.0 Ma -600 Ka.

Chapters six and seven address the temporal aspect of Porcupine Cave from two different approaches. The Velvet room is the only locality organised into strata by flowing water within the cave, allowing the use of magnetostratigraphy to constrain the fossil fauna temporally. Chapter seven describes the other dating resources at hand: biochronology, biostratigraphy, amino acid racemisation, and some limited sedimentary interpretations.

The last two chapters of part one are concerned with describing the means by which the fossils came to be in the cave and some of taphonomy and pathology. The dominant means of fossil accumulation was wood rats; in both the plethora of *Neotoma* fossils as well as the frequent gnaw marks on bones. Amberat, the hardened urine deposits of wood rats, is mentioned, but not as an item under study. The urine of wood rats has been recognised as excellent at preserving plant macrofossils. This was not the focus of the chapter, but study of this resource could help define the local environment of the cave further.

Chapter nine, entitled 'Paleopathology and taphonomic modification of mammalian bones from Porcupine Cave' by C. Suzanne Ware and Elaine Anderson follows. Though taphonomic studies are common in faunal descriptions, descriptions of palaeopathology are much more rare, making this chapter a welcome addition. The taphonomic portion is brief, largely due to the detailed account of it in chapter two. The authors describe the detailed palaeopathology of a number of taxa, from canids to rodents and lagomorphs (with fine SEMs, but apparently over-reduced grayscale drawings, making them too dark or washed out). Pathologies are reported as being found in 100+ specimens, though only nine specimens are described in detail. It would be informative to have presented data on the frequencies of different pathologies from different cave locations, but the authors mention plans to fully write-up the complete record (perhaps a good candidate for PalArch?!).

Part two is the section of the book for readers interested in morphology and systematics of fossil taxa. This part of the book alone makes it an essential reference. Up-to-date accounts of the major groups present in the fauna are given here. The introductory chapter includes a massive appendix of fossil taxa, broken down by locality and subsections of localities. Minimum number of individuals (MNI) as well as the number of individual specimens (NISP) is also provided for each taxon.

The limited Porcupine Cave herpetofauna is described in chapter 11. There are very few taxa represented, and very few identified to family, but the authors are able to make some environmental interpretation based on the sheer number of taxa in the Pit locality. They are able to support the interpretation of the Pit's upper level as an interglacial.

The Porcupine Cave avifauna is very small in terms of sample size, less than 200 specimens have been recovered from the entire cave. This small sample size has yielded a disproportionate diversity however. The 45 taxa represented in the cave form the most diverse avifauna from this time period in the intermountain western United States. Range extensions from modern distributions for several taxa are noted. The early diversity of wetland taxa steadily decreases in the younger deposits, supporting other evidence of drier young interglacials.

The analysis of carnivores in chapter 13 is interesting both from the standpoint of diversity and their contribution to the taphonomy. The question of carnivore contribution to the fossil assemblage is addressed and found to be significant in some parts of the cave. The total carnivore assemblage is diverse, with a total assemblage of 23 species. One of these is also an unnamed new species of *Mustela*, here simply called species A. *Miracinonyx* cf. *M. inexpectatus*, the American cheetah, is also present in Porcupine Cave. This long limbed, small headed felid has been proposed as the main reason why *Antilocapra americana* is the fastest mammal in North America.

The analysis of the lagomorphs indicates the presence of both leporids and ochotonids. The enigmatic ochotonids are sparse in North America in the Blancan and Irvingtonian. The presence of more than one species at Porcupine Cave is interesting, and further research here will be much anticipated. The leporid assemblage is diverse with at least seven and possibly ten species. Only three are still found in the vicinity, two have distributions elsewhere, and three are extinct. The stratigraphic appearances of these species in the Velvet Room support the other age data.

Not every mammal can be confidently identified to genus without the proper remains, thus a 'miscellaneous mammals' chapter seems proper to account for all the non-diagnostic elements recovered. Chapter 16 describes these fossils from the pit locality. The one insectivore genus known from the cave, *Sorex*, is described here very briefly with the promise of future publication. The application of careful screening is necessary to collect these, which chapter two revealed was not always the case. Several leporids are also placed here based on the indeterminate morphology of the specimens described. Elements of *Thomomys*, *Peromyscus*, *Erethizon* are also discussed.

The Sciuridae have an entire chapter devoted to their assessment, as is befitting this ecologically diverse group of rodents. A considerable diversity of sciurids are represented: several species of ground squirrels, a marmot of uncertain affinities, one species of chipmunk, and several species of prairie dog. The succession of prairie dog species and ground squirrels are discussed here because the species represented are reasonably ecologically specialised. The Porcupine Cave sciurid fauna is interesting from an evolutionary standpoint because of its 'modern' character. The authors comment that while several species represented are of an archaic morphology, and one is extinct (?*Cynomys andersoni)*, most are essentially representatives of the modern lineage. This is useful because the radiation that produced the modern Rocky Mountain fauna can now be said to predate the Irvingtonian. It is also remarkable because the fauna has been stable in the face of multiple glacial episodes since that point. Only one species in the fossil fauna, *C.* cf. *C. leucurus*, is out of range and only in a minor way.

Chapter 18 assigns the wood rats taxonomically and discusses their ecological implications. The wood rat species found in the cave indicate there was more contact between the Great Plain and Rocky Mountains habitat types during the Pleistocene. Three of the species are typically found in lower elevation habtitats, while one (*Neotoma cinerea)* is commonly found only above 1800 m. The woodrat fauna also supports the drying-upward glacial sequence.

Arvicoline rodents are indispensable for both biostratigraphy and ecology in fossil faunas, this chapter is mainly concerned with taxonomic assignment and discussion of new records. Chris Bell *et al.* remarked at the odd co-occurrence of *Allophaiomys* with its descendent taxa *Microtus sp., M. paroperarius* and *M. meadensis*. Finding an ancestor with a descendant, while not expected, is not at all impossible and no reason to cast doubt on that particular evolutionary relationship. A number of biogeographical scenarios, including the refugium proposal given by the authors, could result in such an occurrence. The discovery of *Allophaiomys* and *Pliolemmus* are both range expansions, neither has been found west of the Great Plains. The arvicolid assemblage of Mark's sink argues for Porcupine Cave's oldest sites dating to the Blancan. The Badger Room and Generator Dome are the next oldest, followed by Fissure Fill A. These rankings seem logical, but the authors note that none of these sites contain *Lemmiscus*. Other sites containing Badger Room and Generator Dome species also contain *Lemmiscus*, which leads Bell *et al.* to suspect a taphonomic bias or inadequate sample size in the early sites.

The next chapter, 'Pliocene and Pleistocene horses from Porcupine Cave' by Eric Scott was honest and detailed in its account of the difficulties rife in Pleistocene *Equus* taxonomy. For a chapter of manageable length to read in one sitting, Scott manages to give reference and detail concerning the locations and unique features (or lack thereof) of the numerous Pleistocene *Equus* species thus far described in North America. Particularly fascinating and equally still a mystery, is Scott's description of an unusual form of etching found on a small number of cheek teeth. Despite going through a short list of possible explanations, in the end doubt persists. This thorough and honest report is one of many sorts found in this book that accurately report findings but leave an enticing trail of future work to be done.

Chapter 21, entitled 'Pleistocene (Irvingtonian) artiodactyla from Porcupine Cave' by Jim I. Mead and Louis H. Taylor discusses the taphonomy and identification of what amounts to mostly postcranial elements of artiodactyls. Their thorough descriptions of their identifications of these postcrania exemplify what many (including BLB) have experienced with the prevalence of undetermined Pleistocene artiodactyla found in many museum collections. By explaining the morphometric and morphological characteristics of bones, such as phalanges, they have provided a service to us all. While the authors rightfully identify the need for a more taxonomically broad study of postcrania of artiodactyls, this chapter serves as a very useful first step in what could become a very useful tool in vertebrate palaeontology and zooarchaeology. The only items that remain wanting are the figures of the camelid specimens (including a *Camelops* skull) and clearer figures of some key specimens, such as the cervids. Many of the figures, especially those of occlusal surfaces of teeth, are washed out or obscured by discoloration of the fossil itself; this could have been rectified by simple line drawings. The line drawings and additional figures of camelids would have enhanced this chapter's usefulness considerably, but overall the work is still strikingly thorough and detailed.

The five chapters of part three describe the long-term climate changes shown in Porcupine Cave and how the local fauna reacted to each. The most startling conclusion of each chapter is that the glacial-interglacial cycles represented in the sediments of Porcupine Cave result in the faunal changes that one would expect. A steady turnover rate is shown, but niches remain filled.

The first chapter reconstructs the ecology particular to the time period represented in the Badger Room. The Badger Room, based on comparison of the arvicoline assemblage with that of the stratified Pit, is thought to represent a time period of at most 10,000 years between 800 and 950 Ka. The primary taphonomic agents are carnivores and wood rats, as evidenced by frequent fractures, pitting, and rodent gnawing. Based on the presence of *Spermophilus* cf. *elegans*, *Mictomys kansasensis*, and the lack of *Lemmiscus curtatus* the authors reconstruct the Badger Room winters as longer, cooler, and moister than the modern South Park winter. The

absence of *L. curtatus*, while possibly sample bias as noted in Bell *et al.,* may indicate even cooler winters. Due to the mixed nature of the Badger Room fauna, two local landscape hypotheses are considered: a mosaic of habitats like South Park today, or the presence of extinct ecosystem types in the montane valleys surrounding the cave. The existence of a similar habitat at that time is possible, despite high species turnover, the relative level of biodiversity in the Badger Room remains constant when compared with the modern fauna.

Due to its stratified nature, the Pit locality is utilised in every chapter in this volume. The Pit proves its usefulness once again, in chapter 23, where the climate connections to small mammal diversity are discussed more fully than in earlier chapters. Once again the faunal assemblage of Porcupine Cave is noted for its long-term stability. The same small mammal genera present today, subfamilies for the arvicolines, are also found in Porcupine Cave. However, the population proportions represented in the exhaustively sampled Pit area have changed. The numbers of *Lemmiscus* and *Microtus* peak, both indicative of drier environments, during the dry upper interglacials indicated by sedimentary evidence. Moreover, faunal composition at the level of species was not stable as is the case for the Badger Room fauna. The authors estimate that 4-10 species immigrated into the area gradually, while extinctions were clustered at glacial-interglacial transitions. Two became extinct at the lower glacial-interglacial interval, and three more at the upper one.

Chapter 25 attempts to address the morphological change with time noted in the *Marmota* population within the Pit locality. The taxonomic associations as noted in the sciurid chapter are uncertain, the decision is split between assignment to *Marmota monax* and *M. flaviventris*. Morphometric evidence places the fossils in *M. monax*, but enough morphological differences exist to make this uncertain. This has some bearing on determining the effects of changing climate on marmot populations as each species exhibits different timing and method of hibernation. The morphological data based on teeth in the Pit sequence suggests that climate had an effect on average body size in the marmot population through the glacial-interglacial shifts. The data definitely displays a trend, the histograms for log area of P4 become bimodal in the upper, drier sequences of The Pit. Unfortunately no two levels are significantly different. Further sampling of the upper levels would be interesting to see if the trend noted might strengthen into something statistically significant.

Barnosky dedicates the last chapter to putting all of the preceding works into an overarching framework of climate change. He comments on the different taxonomic levels of inquiry when studying diversity and enters into a tantalizing prediction of future changes. I must emphasise to the potential reader of this volume to read this chapter thoroughly, in addition to the chapters dealing with your specific taxonomic interest. The framework of study offered here is invaluable to the graduate student, or to anyone interested in the field.

This volume is thorough enough with details to serve as THE source for info on Porcupine Cave, possibly the most thorough account of a locality ever put into one unified text (with room to grow as newer methods of analysis and research develop). The thorough taxonomic appendixes attached to each chapter are an especially invaluable resource to researchers studying North American Pleistocene vertebrates. One persistent feature that remains poor is the quality of figures and the persistent use of photographs instead of line drawings where specimens are obscured by differences in coloration or lighting. In several cases, this makes diagnosis of specimens from figures useless, questioning the reason for the figure at all. And where grayscale drawings are done, they come across as washed out and visibly patchy in their texture/shading, as if they were done at the size they were printed at, not drawn larger and then scaled down. Thus, plan to make time to visit the holding institution or converse with the corresponding author for the organism you are interested in for more detailed images. Still, as a detailed study of a Pleistocene fauna, this book stands tall and will remain a very useful resource for the study of not only Porcupine Cave but Pleistocene faunas in general.

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D.R. Williams & B.L. Beatty
Division of Vertebrate Paleontology
University of Kansas Natural History Museum & Biodiversity Research Center
1345 Jayhawk Blvd.
Lawrence, KS 66045