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Understanding arid environments using fossil rodent middens

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American rodent middens have made a more dramatic contribution to understanding past environments and the development of ecological theory than Australian rodent middens. This relates to differences in the natural environment, the landscape histories, the scale and scientific approaches of the researchers. The comparison demonstrates: the power of synoptic perspectives; the value of thorough macrofossil identification in midden analysis and its potential advance in Australia where pollen has dominated analyses, the value of herbaria and reference collections; the potential of environmental databases; the importance of scientific history and 'critical research mass' and; finally, the opportunistic nature of palaeoecological research.

Keywords: palaeoecology; rodent midden; radiocarbon; Quaternary; climate change

Introduction

Stick-nest rat middens found in caves and rock-shelters of arid and semi-arid Australia preserve a variety of materials many thousands of years old. Stick-nest rats (Muridae: *Leporillus apicalis* and *L. conditor*) have been extinct on the mainland for over 100 years although one species (*L. conditor*) survives on an offshore island and in captivity. This is the only species, of 23 species of extirpated mammals in arid Australia (Kerle *et al.*, 1993), to leave a conspicuous trace of its ecology in time and space. Stick-nest rat middens have been analysed by a number of researchers, yet not with the dramatic results of North American packrat (*Neotoma*) middens. This paper identifies the reasons for this and reviews and compares the approaches and achievements in Australia and the Americas. The primary aim is to improve the future efficacy of midden work in Australia.

The packrat midden record of North America provides unparalleled spatial and temporal information about late Quaternary climates and ecological change in arid and semi-arid environments (Van Devender & Spaulding, 1979; Spaulding *et al.*, 1983; Van Devender *et al.*, 1987; Thompson, 1988; Betancourt *et al.*, 1990; Thompson *et al.*, 1993). This record, based primarily on species identification of plant macrofossils and radiocarbon chronologies, has made important contributions to understanding vegetation dynamics at time-scales not always accessible using other methods. For example, the pinyon–juniper woodlands that presently cover more than 20 million ha in the western United States are, as a result of the packrat midden work, probably the best understood aridland vegetation type at the Quaternary scale anywhere (Betancourt, 1986; Van Devender, 1986; Wells, 1986; Betancourt *et al.*, 1991, 1993; Lanner & Van Devender, 1998). Arguably, packrat middens offer the richest archive of dated, identified and well-preserved plant and animal remains in the world. These archives are available for remining in geochemical (Engel *et al.*, 1978; Plummer *et al.*, 1997; Pendall *et al.*, 1999), morphological (Van de Water *et al.*, 1994; Smith *et al.*, 1995), and genetic studies (Rogers & Bendich, 1987).

Packrat middens have contributed important historical perspectives to ecological theory (Brown, 1995); some of these contributions emerge from the record's high taxonomic, spatial and temporal resolution. In arid North America, differential displacements of individual species in time and space have provided one of the more elegant rebuttals of climax theory (Clements, 1928), confirming the individualistic concept of the plant association (Gleason, 1926; Betancourt *et al.*, 1990). Middens are also contributing to management perspectives. Twentieth-century expansion of many woody species in the western U.S. is commonly attributed to fire suppression and grazing, precipitating management decisions and actions. However, in at least some of these cases, middens indicate that these expansions are embedded in ongoing, late Holocene migrations at the northern edges of species ranges (Betancourt *et al.*, 1991; Nowak *et al.*, 1994; Miller & Rose, 1995; Betancourt, 1996; Swetnam *et al.*, 1999).

Following the success of packrat midden research, methods and approaches were applied to similar deposits in Africa (Scott & Vogel, 1992; Gale *et al.*, 1993; Thinon *et al.*, 1996), Australia (Green *et al.*, 1983; Berry, 1991; Pearson & Dodson, 1993; McCarthy *et al.*, 1996; Allen *et al.*, 2000) and South America (Pearson & Christie, 1993; Markgraf *et al.*, 1997; Betancourt & Saavedra, submitted). Other areas have rodent middens that are yet to be analysed, most notably central Asia. Paradoxically, the midden record has produced no pre-Last Glacial Maximum (LGM) middens or middens that record dramatic vegetation changes in Africa or Australia despite efforts spanning almost two decades. Pre-LGM middens, which are important in the North and some of the South American records, have not been found in Africa and Australia, perhaps due to unsuitable geology, climate and physiography and/or less intense efforts. Also, in Africa and Australia, researchers have focused mostly on pollen assemblages whereas the vegetation changes were detected in the plant macrofossils in North America (Fig. 1).

For the LGM in Australia, there are few palaeoecologic data (Kershaw, 1995) but, based largely on geomorphic evidence, arid Australia was apparently drier than today. Little is known about how this aridity might have shaped biotic distributions. In North America, an analogous situation existed ca. 1950 AD, before the discovery and application of the midden record. Classic interpretations of western U.S. lakes provided evidence of greater effective moisture (Russsell, 1889; Gilbert, 1890; Meinzer, 1922) though the biotic record during the LGM was tangential (e.g. Deevey, 1949) until the discovery of the packrat midden record. In the Australian arid zone, similar data were used to infer possible changes in distributions of plants and animals species (e.g. Barker & Greenslade, 1982). Most biogeographers infer that biota survived in the periphery of the arid core of Australia or in local refugia during the Last Glacial. However, these biogeographic theories remain untested by palaeoecological evidence comparable to packrat middens in North America.

The North American midden record, at least in the beginning, developed haphazardly and circumstantially. Accumulation of midden evidence was both

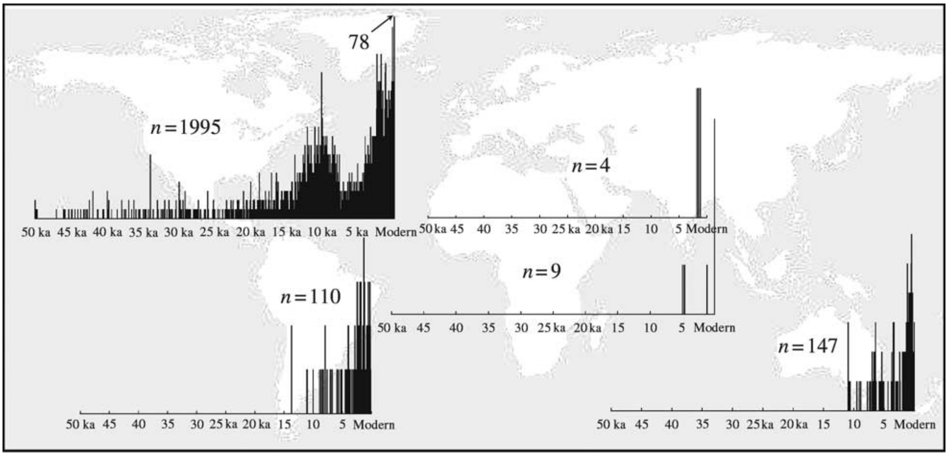

Figure 1. Distribution of radiocarbon analyses on rodent middens in four areas of the world.

Table 1. *Features of some arid zone biological records*

Feature of record	Macrofossils from middens	Pollen from middens	Pollen from swamps
Ease of search	Hard	Hard	Easy
Spatial resolution	Excellent	Poor	Good–poor
Representation of all landscapes	Poor	Poor	Poor
Spatial continuity of deposits	Good	Good	Poor
Availability of sites in the arid zone	Good	Good	Poor
Temporal resolution	Good	Good	Excellent–poor
Stratigraphic continuity	Poor	Poor	Good
Taxonomic resolution	Excellent	Poor	Poor
Vegetation reconstruction	Semi-quantitative	Quantitative	Quantitative

opportunistic and followed research paths of a handful of individual researchers who carved out particular territories and funding opportunities. Global change research in areas with rich fossil records now demands a more systematic and synoptic approach to test specific palaeoclimatic and biogeographic hypotheses at subcontinental scales (Bartlein *et al.*, 1998). Efficiency of effort may also be a necessity in Australia, where resources are in shorter supply, middens less ubiquitous or ancient and the interpretive framework (elevational and latitudinal displacements through time) perhaps less obvious than in North America.

This paper is an attempt to compare and contrast the American and Australian midden experiences as a blueprint for future research. Any comparison of inputs or outputs of the stick-nest rat and packrat midden work underscores the differences of scale in the research resources available (Table 1).

History and nature of packrat midden research

The history of packrat middens is summarized in Betancourt *et al.* (1990). Saliently, the packrat work developed alongside radiocarbon dating, it quickly recorded dramatic altitudinal responses of species that are still visible elsewhere on steep topographic gradients, it attracted a strong postgraduate research 'mass' from the late 1960s to the early 1980s, it was well-funded by nuclear, national park and global climate change interests. The record reflects the immediate needs and hypotheses of the researchers and their funding sources with only informal collaboration (e.g. Van de Water *et al.*, 1994) and limited public archiving (Bob Thompson http://climchange.-cr.usgs.gov/data/midden/). The midden research involved detailed macrofossil analysis with only a few middens being analysed for pollen (Thompson, 1985; Davis & Anderson, 1987). Unlike Africa and Australia, there are no instances in North America where midden pollen was analysed without recourse to the macrofossil record. Without the plant macrofossil record from packrat middens, both lake and midden pollen would have yielded a flawed picture of late Quaternary vegetation dynamics in the North American deserts (Wells, 1976; Van Devender & Spaulding, 1979; Betancourt & Van Devender, 1981; Betancourt & Davis, 1984; Spaulding, 1990). There have been arguments about the palaeoecological value of pollen and macrofossils from middens (Davis & Anderson, 1987, 1988 with Van Devender, 1988; Hall, 1982, 1986, 1988, 1997 with Betancourt & Van Devender, 1981). Pollen continues to be analysed by a minority of researchers and only in conjunction with macrofossils and other pollen sources (e.g. Mehringer & Wigand, 1990).

African hyrax and dassie rat middens

Hyrax (*Procavia*) middens are widespread and have been studied in the Middle East (Fall *et al.,* 1990), north Africa (Pons & Quezel, 1958; Thinon *et al.,* 1996), Namibia (Scott, 1996) and South Africa (Scott & Vogel, 1992; Carrión *et al.,* 1999). Dassie rat (*Petromus*) middens have more macrofossils than hyrax but are restricted to the Namib region. The changes reported by Fall *et al.* (1990) are a dramatic record of human impact on vegetation near Petra. African taphonomic studies have deduced that little correction is needed to interpret the pollen in hyrax middens because the rats do not gather material and the midden is a simple urino-fecal deposit (Scott & Cooremans, 1992; Scott & Vogel, 1992). Resolving major changes in vegetation appears difficult due to the amount of between-sample variation, for example Scott & Cooremans (1992, Figs 3 and 4) report modern sample ranges of 1–10% for AP and 10–45% for the 'other non arboreal pollen' at the same site. The resolution of change becomes even more problematic when the data are presented at the taxa level because same site samples vary greatly (Scott & Cooremans, 1992, Figs 8–11). The African work has been very strongly pollen-based.

History and nature of stick-nest rat midden research

Stick-nest rat midden research in Australia was started by Watts & Eves (1976) using macrofossils to identify the diet of the extinct *Leporillus* species. Green *et al.* (1983), Pearson (1989), Nelson *et al.* (1990) and Berry (1993) analysed late Holocene middens that all recorded the vegetation as being similar to the present. Copley (1988) described middens throughout the range; however, they are isolated from the few University-based palaeobotanical researchers who are engaged in projects in south-eastern Australia, north-eastern Queensland, Papua New Guinea and Indonesia. In fact, like the Great Basin of North America in the 1950s, more is known about central Australia's Tertiary flora than the last 20,000 years of vegetation change. The analysis of salt lake pollen records has provided the only botanical information about central Australia (e.g. Singh, 1981; Singh & Luly, 1991) and the fascination with the Last Glacial was satiated with geomorphic evidence of mobile dunesheets and source-bordering dunes that were interpreted as indicating little or no vegetation cover (e.g. Bowler, 1976).

Stick-nest rat middens from the broad vegetation ecotones in Australia have not detected Holocene vegetation changes. In 1991, Jay Quade from the University of Arizona Desert Laboratory where much of the packrat work has been done, collected midden material from the Flinders Ranges (South Australia). Archaeological palynologist Lesley Head and Lynne McCarthy researched the macrofossils and pollen (McCarthy, 1994) from these middens including one that was much older than the other middens dated (11,950 $\pm$ 320 B.P. OZA318) (Fig. 1).

Stick-nest rat middens have not attracted funding or research mass comparable to the packrat middens. Innovations such as alkanes (Hugh Dove, CSIRO, pers. comm.), epidermal analysis (Corlis, 1993), mammal hair cross-sections (Pearson *et al.*, in press) and Accelerator Mass Spectrometry Radiocarbon Dating (Pearson *et al.*, 1999) have been applied in Australia. Taphonomic questions of sample variability, temporal resolution and contamination have been partly addressed by Head (1993), Pearson (1999) and Head *et al.* (1998). This may represent a disproportionate effort on taphonomic study, when compared to the proportion of American taphonomic work relative to applications (Spaulding *et al.*, 1990). In hindsight perhaps the resources, particularly radiocarbon analyses concentrated on resolving stratigraphic and possible contamination problems, may have been put to better use dating more deposits and increasing the chance of extending the chronology into the Last Glacial. Although both research groups in Australia examined macrofossils, only Lesley Head's group included macrofossil analysis in their publications (McCarthy *et al.*, 1996; Allen *et al.*, 2000), and most of the effort has gone into palynology. It is significant that only palynologists have persisted in the field and no macrobotanical palaeoecologists have engaged the records.

In Australia, analysts worked on middens that were readily available possibly without a synoptic plan or before asking fundamental research questions or considerating the kind of changes that could be expected, the type of data that was needed and the type of record available in the middens. Research was directed to find a midden sequence that showed gross changes in the pollen or macrofossil record. There is a distinct possibility that macrofossil methods pioneered in the U.S. were not as rigorously applied in Australia and changes may have been missed through reliance on pollen. Perhaps greater attention to macrofossil analysis at all sites and careful reflection on the evolving record would have suggested a different approach.

Australia's geomorphology provides caves suitable for preserving middens only in heavily weathered ranges and more extensive low breakaway (mesa-form hills) caves under cap rock of silcrete, laterite or silicified sediments. Nevertheless, the excellent preservation of organic materials in caves in arid Australia is similar to that seen in North America. However, unlike the south-west of North America, Australia has broad and highly variable climatic gradients with diffuse ecotones occupied by a flora that has tolerance across wide ecological gradients (Nix, 1982) of temperature, substrate, fire and rainfall regimes.

The rainfall regime in the Australian arid zone is dominated by the winter–summer oscillation of the subtropical high that allows westerlies with imbedded frontal rains to penetrate the southern section in winter and tropical lows and a local monsoon to penetrate the north in summer (Harrison, 1993). Rainfall also results from local thunderstorms in summer and unpredictable, but biologically important, rain occurs as cyclonic lows track inland and decay into south-penetrating low-pressure troughs. These relatively simple mechanisms are highly variable in time and space and are not well constrained. Severe drought and extreme rainfall regimes are characteristic of the Australian zone and are linked to global circulation systems, such as El Níño-Southern Oscillation (ENSO). The floristic signatures of these different events are not well understood and the local vegetation apparently reflects unstructured climatic variability (Friedel *et al.*, 1994). There may be a continental-scale, rainfall-controlled (Hattersley, 1983) and sensitive, palaeoecological gradient between plants with C3 or C4 carbon pathways (Johnson *et al.*, 1999).

The observations of vegetation in study sites and inadequate reference material make it difficult to detect climate change. There is no recently published flora for the arid zone (Jessop, 1981) and site collections are likely to be incomplete. Palynologists are able to recover records at a similar level of taxonomic resolution to the current understanding of the arid zone vegetation and within the possible responses of the local vegetation. Perhaps as a consequence of this, midden analysis in Australia has provided information about slight changes (Allen *et al.*, 2000) or stability within the limits of contemporary natural variability in the late Holocene (Berry, 1991; Pearson & Dodson, 1993; McCarthy *et al.*, 1996). Researchers may have hoped that applying a selection of packrat midden analysis methods would produce results as dramatic as those found in the packrat middens. It is ironic that they emphasized pollen for this investigation when it had been tried and, in the main, rejected in North America. Nevertheless, the findings so far, that the vegetation is stable in the Holocene, are important and should not be understated, nor over-interpreted. It may suggest that reassembly of vegetation was either complete relatively quickly, or was entirely unnecessary, after the LGM. However, we do not believe that the sites and analysis yet provide a definitive view of the Holocene in the arid zone. It is entirely possible that other floristic and structural changes may be occurring beyond or beneath the current midden interpretations based on imperfect macrofossil analysis and pollen analysis.

Unlike the south-west of North America, the LGM was a hyper-dry period in Australia, characterized by deflated lake surfaces (Magee & Miller, 1998), dust plumes in ocean cores (McTainsh, 1989), mobile continental and source bordering dunes (Bowler, 1976; Wasson, 1984) and rises in arid taxa in the pollen spectra on the periphery (Kershaw, 1995). It is unclear if key species survived *in situ*, in refugia or migrated enormous distances during the Last Glacial Maximum (Burbidge, 1960; Beard, 1981). The only evidence of LGM vegetation in arid Australia comes from charcoal macrofossils of several woody species in an archaeological site (Smith *et al.*, 1995). From the evidence available, it is likely that the LGM was a period of low vegetation productivity in central Australia and, hypothetically, fewer middens were constructed. Certainly, most of the middens dated in Australia are late Holocene in age (Fig. 1 and Pearson *et al.*, 1999). However, there are early Holocene stick-nest rat middens; perhaps if more of these older middens were found they would record species turnovers or dramatic changes in the importance of taxa and, from a spatial pattern of middens, they might record species migration, refugia survival and local extinction. These processes, if they occurred around the LGM, are not currently evident in the mid and late Holocene middens. In addition to the probable shortage of these early Holocene middens, there is currently no compositional change that can be used to identify them, as there is in American middens, making sampling middens less efficient (and more expensive) in Australia. Furthermore, the spatial continuity of mid or early Holocene midden records is likely to be lower in Australia due to a scarcity of caves. It then becomes less likely that species turnover or migration could be detected due to low midden densities and the recent age of Australian middens.

The future—systematic approaches to midden research

Recently, one of us (J.L.B) has been involved in a systematic effort to export midden methodologies to arid regions of South America (Argentina, Bolivia, Chile and Peru), with support from the Inter-American Institute for Global Change Research (IAI) (Betancourt & Saavedra, submitted). IAI, founded in 1992, is a multinational institution for the study of global change issues that affect the Americas; its intent is to also foster collaboration between scientists from different countries and overcome physical, geopolitical and philosophical barriers. The IAI midden effort pivots on demonstration field projects in each country; training of Latin American scientists and students; joint publications on the nature and timing of vegetation change in arid South America based on middens collected during the demonstration field projects; and execution of several spinoff projects that exploit the rich archive of plant and animal remains identified from these deposits. In addition, there has been a modest effort to launch independent laboratories in Latin America, principally in Santiago, Chile and Mendoza, Argentina. The effort thus far has been concentrated in Argentina and Chile, where there are strong traditions in both natural history and paleoecology. Middens similar to packrat and stick-nest rats are made by a surprising variety of rodents in South America, principally by the genera *Abrocoma*, *Lagidium*, *Octodontomys* and *Phyllotis* (Betancourt & Saavedra, submitted). Presently, there are 109 radiocarbon dates from the western foothills of the Andes in Bolivia and Argentina, roughly comparable to the numbers for Australia ($n = 146$). Age distributions follow an exponential decay curve similar to Australia (Fig. 1). The scarcity of middens less than a thousand years old probably reflects Betancourt's bias in collecting only well-indurated, older-looking middens. Thus far, regions west of the Andes have produced only one midden of glacial age. This midden was recognized as Pleistocene in the field by the presence of extinct ground sloth faeces; extralocal plant macrofossils were not evident on the surface of the midden. A more concerted, systematic effort will be needed to recognize and recover the rare Pleistocene midden in Argentina and Bolivia and a more synoptic approach will be needed to identify sensitive transitions in vegetation that may yield significant palaeoclimatic inferences.

In Australia, progress has been highly intuitive and opportunistic. The field and laboratory methods used in the U.S. have been transferred only through the imperfect medium of publications, rather than actual exchange of scientists and their students. Problems with accessibility and funding have also blunted the research. We think stick-nest rat midden research needs a decisive program to identify the optimum sites to provide information about vegetation using the full temporal range of middens and to build useful spatial resolution. Synoptic lines of inquiry, survey work, computer models, climate data, biological databases, ecology and biogeography will help optimize site selection. Midden analysis, however, like most palaeoecological work, will remain constrained by opportunities, so the development of more efficient research methods needs to have scope for intuitive and creative approaches. We also recognize the necessity of sufficient resources and training for searching, macrofossil analysis and dating to determine the vegetation, underlying processes and palaeoclimate.

Australia has already established computer-based ecological models such as BIOCLIM (Nix, 1982) that relate the databases of species distributions with a multivariate climatic envelope (e.g. Nix & Austin, 1973) to predict and (re)construct biological responses of species to climatic environments (e.g. Kershaw & Nix, 1988; Graetz *et al.*, 1988). These ideas developed into ERIN, the meta-database linked to the Australian Biological Resources Study, to provide high-quality spatial biodiversity information to decision-makers (Hawke, 1989). It has mapping and modeling capabilities that could, until recently, be accessed on the web (e.g. http://www.environment.gov.au/search/mapper.html). Gap-analysis programs within ERIN interrogate databases to build sets of predictive environmental factors for individual species. With modifications, this system may allow researchers to predict how species have responded to palaeoenvironmental changes and direct attention to areas that are likely to exhibit species turnover under specific climatic scenarios. This is particularly useful in Australia where suites of variables account for a species distribution and there is no simple latitudinal–elevational framework as in the U.S. However, there are problems with assuming that the modern situation heavily modified by humans, imperfectly understood and incompletely recorded in databases, can be projected with accuracy into the darkened past.

Systems like ERIN are based on biogeographic principles that explain the spatial distributions of life in relation to environmental gradients. Other biogeographic phenomena such as patch heterogeneity, habitat connectivity, migration, vegetation and taxa inertia and models of metapopulation dynamics can be added to site and midden selection protocols (Mensing *et al.*, 2000). Processes underlying the distributions described by biogeography, or modeled by ERIN, are built into ecological models that predict the response of species to changing environments. The problem with the current theories for Australian arid areas is that they are largely untested due to their qualitative nature and enormous spatial and temporal variability. For example, the pulse-reserve models proposed by Ludwig *et al.* (1997) and the concepts of refugia used in biodiversity management (e.g. Morton *et al.*, 1995) are widely applied but not well understood. We are concerned how these theories and environmental envelopes interact with non-linear reponse curves for individual species (Austin & Gaywood, 1994) and also how difficult it will be to include species–species interactions. However, used cautiously, these theories can be used to guide research into palaeoclimatically sensitive locations where variables such as substrate can be controlled and into places with expectations of high or low species turnover (migration and refugia signals, respectively). This will increase the efficacy of the midden and radiocarbon analyses. Iteratively, data from these longer-term records from spatially and temporally constrained sites may provide a better understanding of modern ecosystem process and variability (Clark, 1990; Foster *et al.*, 1990).

Conclusion

Efficacy could be measured with reference to quantities such as publications, funding and citations; however, in this paper we compared the history and qualitative results of midden-based research in two continents. Our aim was to review the achievements and to suggest ways to achieve further advances in Australia and in other areas with midden records. The paper was not intended to prescribe a straitjacket of uniformity on midden research; we are aware of the importance of individual interests and serendipity in scientific breakthroughs. Our purpose was to highlight the routes that have worked well and review what we found in the research *cul de sacs* on the way.

Most North American midden researchers were not palynologists by training, but it has been palynologists who have keenly pursued midden research in Australia and Africa. The result was a surprising neglect of macrofossil analysis, precisely the most successful aspect of midden research in North America. In Australia, where vegetative changes in macrofossils were unremarkable and the midden records were short, it should have been no surprise that pollen only reflected modern levels of natural variability. The focus on pollen rather than macrofossils has also produced a preoccupation with quantification of taxa recorded in middens and in dating of presumed stratigraphic sequences in middens. As an aside, these issues were debated and largely resolved in the U.S. during the 1970s and early 1980s. Consequently, based on both packrats and stick-nest rats, the taphonomy of the middens is now relatively well known. Finally, expectations of recovering Pleistocene and early Holocene middens should have been lower in Australia given the LGM history of the arid zone and the limited research effort.

There are three obvious directions for Australian midden research suggested by this comparative review. Firstly, the search for middens of great antiquity needs to be restarted. Secondly, the sampling needs to use a more synoptic perspective to select prospective sites. Thirdly, the middens that have already been collected need to be systematically reanalysed for additional information, such as macrofossil remains, using adequate reference materials. We have suggested that the biological database ERIN provides an excellent framework for deriving testable ecological and biogeographic hypotheses about the vegetation and climate of arid Australia. There is value in exporting the research methods developed on U.S. packrat and Australian middens to other arid areas as a part of the growing need for global environmental information. In both continents the lack of formal training mechanisms, comprehensive databases, archives of midden materials and publications may need attention before the current cohort of midden analysts become inactive. The middens that have already been dated will continue to be used by researchers who need relatively inexpensive access to organic and inorganic materials that have been radiocarbon dated. Organizational and procedural steps should be in place to facilitate this sort of analysis. Our final comment is that in arid environments the palaeoenvironmental record of the last few thousand years preserved in rodent middens is innately valuable because it addresses issues such as short-term climatic oscillations and long-term ecological changes that affect humans but are beyond our ready understanding.

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