# Prolonged coexistence of humans and megafauna in Pleistocene Australia

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**Recent claims for continent wide disappearance of megafauna at 46.5 thousand calendar years ago (ka) in Australia have been used to support a ''blitzkrieg'' model, which explains extinctions as the result of rapid overkill by human colonizers. A number of key sites with megafauna remains that significantly postdate 46.5 ka have been excluded from consideration because of questions regarding their stratigraphic integrity. Of these sites, Cuddie Springs is the only locality in Australia where megafauna and cultural remains are found together in sequential stratigraphic horizons, dated from 36–30 ka. Verifying the stratigraphic associations found here would effectively refute the rapid-overkill model and necessitate reconsideration of the regional impacts of global climatic change on megafauna and humans in the lead up to the last glacial maximum. Here, we present geochemical evidence that demonstrates the coexistence of humans and now-extinct megafaunal species on the Australian continent for a minimum of 15 ka.**

archeology | extinction | geochemistry | rare earth element | climate change

Late Quaternary extinctions of megafauna have been documented on all continents except Antarctica, and in North America and Australia, these extinctions have broadly coincided with human colonization (1, 2). In Australia, conservative estimates place human arrival on this continent at ≈43–45 thousand calendar years ago (ka), although some researchers argue for colonization up to 60 ka (3). Intense debate surrounds the timing and causes of megafaunal extinctions in Australia, especially in resolving the relative roles of humans and climate (1–6). The following three explanatory hypotheses (Fig. 1) dominate the discussion.

1. Human overkill, or "blitzkrieg," in which megafauna went extinct within 1,000 years of human arrival, with megafauna disappearing by 46.5 ka.
2. Habitat modification by humans through firing the landscape and associated hunting, with extinctions complete by 46.5 ka.
3. A paleoecological explanation in which climate change was the driving force in megafauna demise as factors such as increasing aridity, habitat reconfiguration, competitive exclusion, and possibly the added pressures of a new predator combined to suppress and ultimately drive to extinction a suite of Australian fauna.

Developing extinction chronologies has generally relied on the dating of sediments associated with megafaunal remains (2). Direct dating of skeletal material from Australian late Pleistocene contexts has been problematic, and few studies have produced unequivocal results (7, 8). The analysis of rare earth element (REE) contents in bone has emerged recently as a valuable test for stratigraphic associations (9–13). In buried bone, REEs are adsorbed rapidly from pore waters onto bone crystal surfaces and then locked in the bone crystal lattice during recrystallization (9). The relative abundances of REEs sequestered into bone are controlled by the immediate pore water chemistry. Therefore, bones in successive depositional units frequently inherit distinct REE patterns. Subsequent postdepositional mixing of fossils from different primary depositional localities may be detected by comparing REE signals within and between assemblages of bones (9–11, 13). Here, we apply REE analyses to a faunal assemblage from the late Pleistocene archeological site of Cuddie Springs, which is an ephemeral lake in southeastern Australia (see Fig. 2*A*) where megafauna and cultural material have been recovered from sediments that significantly postdate the proposed 46.5 ka extinction date (14). Specifically, we use REE analysis to test the hypothesis that faunal remains from the archeological horizons were secondarily derived from underlying noncultural bone-bearing units.

## Materials and Methods

**Study Site.** The sedimentary sequence at Cuddie Springs consists of ≥10 m of stratified, bone-bearing deposits, the upper levels of which also contain an archeological record (5, 14, 15) (from ≈1.7 m to surface, Fig. 2*B*) consisting of flaked and ground stone tools, charcoal, ochre, and bone with modifications that are consistent with butchering and burning (14). Luminescence, accelerator mass spectrometry, and conventional radiocarbon determinations on charcoal and sediments consistently place the human–megafauna overlap at ≈36–30 ka (16, 17). Although investigations of geomorphology, palynology, and the archeological record at Cuddie Springs suggest that the deposit is intact (14–16, 18, 19), luminescence dating studies have been used to argue that the sedimentary sequence is disturbed and that megafauna fossils in the archeological levels are derived from older, underlying buried horizons (20). To test whether archaeological horizons in the Cuddie Springs sequence contain bones from a variety of depositional sources, REE analysis was applied to assemblages from four stratigraphic units spanning the prehuman [stratigraphic unit (SU)9 and SU7] and archeological (SU6A and SU6B) horizons (Fig. 2*B*).

The lowest sampled layer, SU9, is a condensed horizon within >1 m of fine-grained, in places laminated, lacustrine sediments. SU9 contains abundant articulated and disarticulated remains of extinct and extant taxa. SU7 comprises ferruginized sands overlain by a coarse, compacted stone and nonartifactual bone conglomerate within a silty clay matrix that may reflect local flooding after a pluvial event. Compaction and cementation of this unit occurred during formation of a fragipan. SU6 (≈1.7 to ≈1.0 m in depth) is dated at ≈30–36 ka (16), and it contains an archeological record and the remains of extant and extinct taxa, the extinct taxa including species of *Diprotodon*, *Genyornis*, *Sthenurus*, and *Protemnodon* (14).

SU6 reflects a return to low-energy conditions and contains two distinct SUs: SU6A and SU6B (18). It is sealed at its upper and lower limits by old land surfaces, SU5 and SU7, respectively. SU6B (≈36 ka) is composed of manganese-coated peds, which together with the palynological evidence indicates extended lake full conditions (18). Complete bones of extinct and extant fauna are enclosed in horizontally bedded structured clays and silts and concentrated toward the base of the unit. Extinct taxa constitute ≈20% of the

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Abbreviations: ka, thousand calendar years ago; REE, rare earth element; SU, stratigraphic unit.

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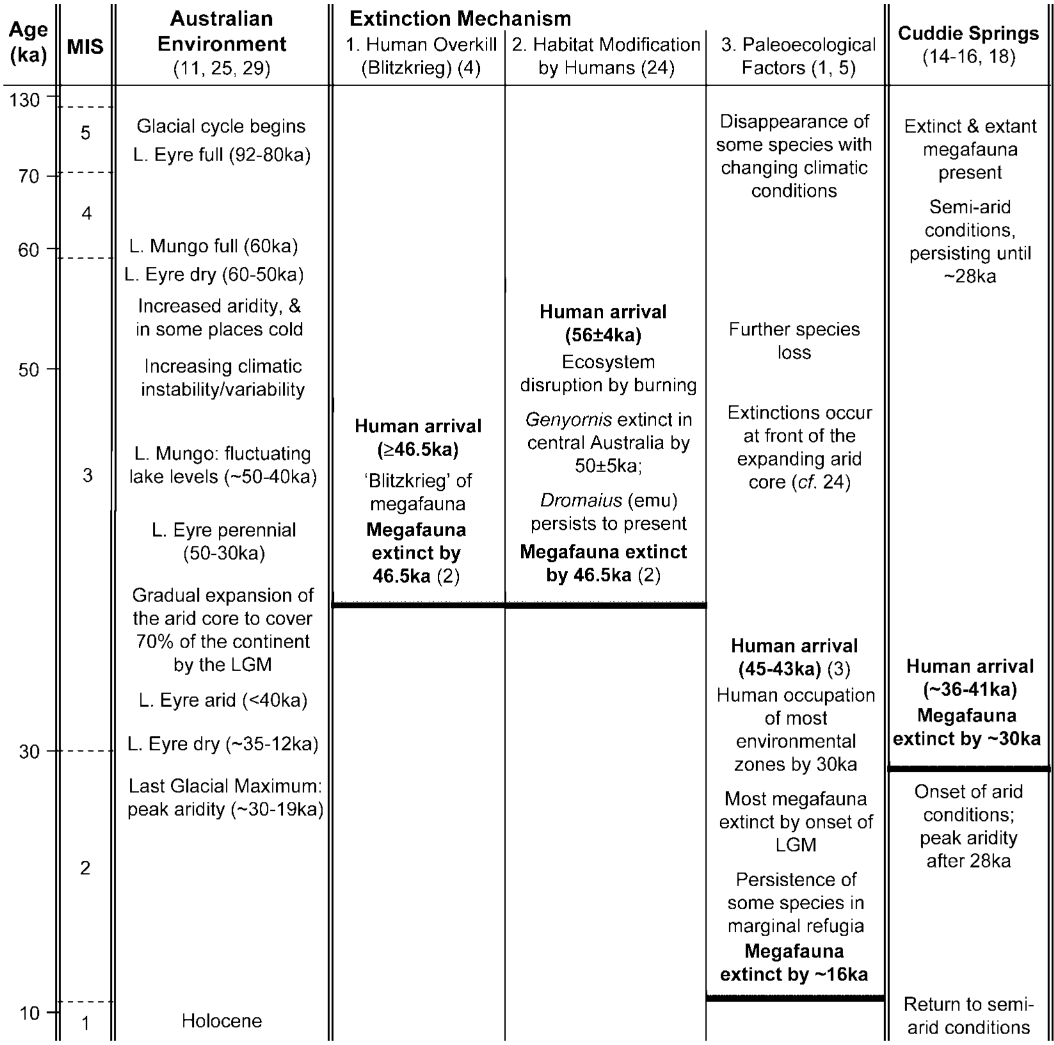


**Fig. 1.** The three principal explanatory models for the extinction of the Australian megafauna showing the various colonization and extinction timelines for each scenario. The evidence from Cuddie Springs shows the timing of the arrival of humans at this site and the last appearance of megafauna. A (nonlinear) time scale and marine isotope stages (MIS) are given.

bone assemblage (21), and flaked stone artifacts and charcoal occur in low concentrations throughout.

SU6A (≈30 ka) is composed of horizontally bedded lacustrine sediments and accumulated after the onset of extended dry lake phases. Extinct taxa constitute ≈6% of the faunal assemblage (21). The bones are more fragmented than those in SU6B, and there are significantly higher concentrations of stone artifacts and charcoal in this horizon (14). SU6 is capped by a pavement of stone, bone, and charcoal (SU5), which was formed by deflation of sediments over a long time period and is dated to ≈27 ka (16). The upper surface of the stone in SU5 shows marked weathering, whereas the undersides of these stones are relatively fresh and sharp.

**Analysis.** Cortical bone samples were collected from securely provenanced and identified elements of extant and extinct fauna, as well as from small, unidentified bone fragments that were recovered on site during sieving. The outer surface of the bone (≈1 mm in thickness) was removed, and subsurface cortical bone samples were collected (≈0.5 g of bone powder per specimen). Trace element concentrations (REE, U, and Th) were determined by using an Elan 5100 inductively coupled plasma mass spectrometer (Perkin–Elmer) at the University of Technology Sydney. National Institute of Standards and Technology 120C phosphate rock was used to monitor accuracy, and it was assayed consistently within 5% of expected values. REE concentrations were normalized to shale (post-Archean Australian shale) values. Log-transformed, shale-normalized REE ratios ($La_n/Sm_n$; $La_n/Yb_n$; and $Dy_n/Yb_n$; $n$ refers to shale-normalized values), redox sensitive elemental ratios $U/Th$ and the cerium anomaly (defined as $Ce/Ce^*$, where $Ce^* = 2/3La_n + 1/3Nd_n$) in bone were analyzed by using multiple ANOVA (Systat, Evanston, IL) to test for effects of depositional layer on trace element composition of bones (22). Difference-between-groups tests were used to test for significant differences in populations between layers (Hotelling–Lawley trace). Univariate ANOVA was used to test for significant differences in means and variances of untransformed elemental ratios between groups.

## Results and Discussion

Total REE contents in bones from Cuddie Springs range from <1 ppm to >1,000 ppm (Table 2, which is published as supporting information on the PNAS web site). The total concentrations are not a function of age, consistent with observations that REE are incorporated into bone rapidly postmortem and reflect immediate postdepositional pore water chemistry (9, 12). Elemental profiles of REE in bones from each sampled stratigraphic horizon determined by laser-ablation inductively coupled plasma mass spectrometry

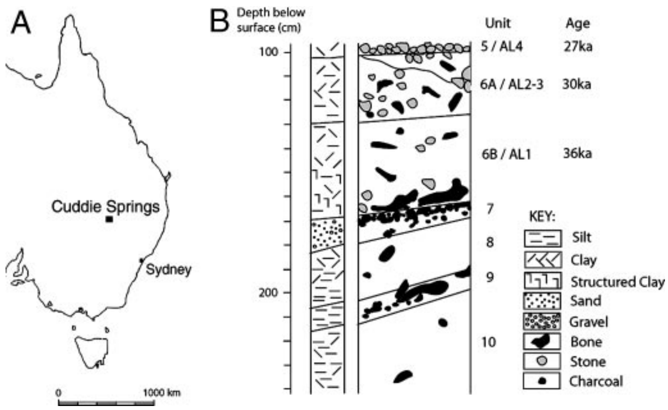


**Fig. 2.** Site location and stratigraphic context of the fossil and archeological assemblages investigated in the REE study. (*A*) Map of eastern Australia showing the location of the Cuddie Springs site. Cuddie Springs lies within the current semiarid zone (defined by average annual rainfall of 250–500 mm). (*B*) Stratigraphy of the Cuddie Springs claypan deposits showing the SUs (SU5–10) and the archeological levels (AL1–4) for the central excavation trench. No age determinations are available for the deposits greater than SU6B.

typically show steep, U-shaped concentration profiles consistent with single-event introduction of REE occurring over a time scale on the order of 1 ka and controlled by a diffusion–adsorption mechanism (23). Bones are enriched in all REE with respect to shale (post-Archean Australian shale) values, with more pronounced enrichment in middle–heavy REE and a smooth decline in light REE concentrations. All bones possess a minor, positive cerium anomaly. Multiple ANOVA of bone trace element compositions indicates that SU has a significant effect on trace element composition ($f = 8.58$; df = 20, 450; $P < 0.001$; Hotelling–Lawley). Bones from each unit form populations that differ significantly in terms of their trace element composition (Table 1 and Fig. 3). Based on multiple ANOVA results, there is a <0.1% probability that bone assemblages recovered from dated archeological layers were derived from underlying horizons. Clearly, each depositional unit contains an assemblage of bones with a discrete chemical signature and, therefore, a discrete and distinct postdepositional history.

The variation in REE signals within bone assemblages can be used as a relative measure of the number of source localities contributing bones to the assemblage and, hence, the relative amount of mixing (12, 13). Thus, REE analyses may be used to test the following taphonomic hypotheses to explain the formation of the Cuddie Springs assemblages. (*i*) Bones from SU6A and SU6B are *in situ* and paraautochthonous (contain bones from the immediate burial locality and from a narrow temporal spread); if so, these assemblages will show internally consistent REE patterns with low variability. (*ii*) Bones in SU6A and SU6B are at least in part derived from older deposits in the sequence; if so, REE compositions in SU6A, SU6B, and underlying deposits will be similar. (*iii*) Bones from SU6A and SU6B include allochthonous (not in their original depositional context) material from older deposits not in this sequence; if so, REE variability within each stratigraphic group will be high.

The bone samples from the time-averaged deposit SU7 and from the interface between SU7 and SU6B (termed SU6/7) show relatively high levels of variation in geochemical signals (Fig. 3). However, bones from SU6B are significantly less varied in REE content, suggesting derivation from a limited range of sources (i.e., less time- and space-averaged) compared with either SU6/7 ($La/Yb$; $f = 3.1$; df = 12, 14; $P = 0.04$) or SU7 ($La/Yb$; $f = 6.8$; df = 31, 14; $P < 0.001$). Bone assemblages from SU6A, which include megafaunal remains, yield REE signals with distinctive high $La/Sm$ ratios (two-sample $t$ test, pooled variance, $t = 5.1$, df = 55, $P < 0.001$, Fig. 4), and show low levels of chemical variation. Consequently, REE patterns indicate that bones from SU6A and SU6B are *in situ* and paraautochthonous. The low variance in trace element composition of bones from SU9 and SU6 is consistent with their accumulation during a low-energy lacustrine phase (18), whereas the relatively high variance in SU7 and SU6/7 reflects a more complex fluvial regime.

These results demonstrate that pore water chemistry varied during deposition of the Cuddie Springs sequence, and these stratigraphically distinct pore water signatures were inherited by the interred bones. Subsequent mixing of bones from different sources produced geochemically varied assemblages in SU7 and in the interface between SU7 and SU6. The homogeneous and distinct trace element compositions of bone assemblages from SU9, SU6B, and SU6A argue strongly against any postdepositional movement and mixing of bone between stratigraphic horizons and, thus, indicate low temporal averaging. Our findings demonstrate that fossil material (including megafaunal remains) in SU6A is autochthonous (i.e., remained in the original depositional context), and that material in SU6B is likewise *in situ*, clearly affirming an association between the megafaunal fossils and surrounding sediments dated at 36–30 ka.

The verification of late survival for at least some Australian megafauna has broad ramifications. Although prolonged persistence of the megafauna after human arrival certainly does not rule out a role for humans in their extinction, it does demonstrate that the extinction of the megafauna occurred over a time scale of many thousands of years. In Australia, there is no evidence for either megafaunal kill sites or contemporaneous technologies typically associated with big-game hunting (such as spear-throwers or stone-tipped projectile points) (1). Arguments for human-mediated megafaunal extinction have commonly rested on the strength of a circumstantial case (i.e., that extinctions preceded significant climate change); therefore, humans must have been responsible (1, 24,

**Table 1. Results of between-groups multiple ANOVA test for significant difference in geochemical composition between bone assemblages from different layers**

| Stratigraphic unit | 6A | 6B | 6/7 | 7 | 9 |
|---|---|---|---|---|---|
| 6A | — | $La/Sm$; $Dy/Yb$ | $Dy/Yb$; $La/Sm$ | $La/Sm$; $Ce/Ce^*$ | $La/Sm$; $La/Yb$ |
| 6B | <0.001 | — | $La/Sm$; $U/Th$ | $La/Yb$; $Ce/Ce^*$ | $La/Sm$; $U/Th$ |
| 6/7 | 0.001 | 0.02 | — | $La/Yb$; $La/Sm$ | $La/Sm$; $La/Yb$ |
| 7 | <0.001 | <0.001 | 0.004 | — | $La/Sm$; $La/Yb$ |
| 9 | <0.001 | <0.001 | <0.001 | 0.01 | — |

Dependent variables that are used here are log-normalized values of $La/Sm$, $La/Yb$, $Dy/Yb$, $Ce/Ce^*$, and $U/Th$. The probability (Hotelling–Lawley) that each pair of assemblages was derived from a single population is shown in the lower half of the matrix, and the principle discriminating variables (variables giving highest $f$ values) are given in the upper half. Note that there is a <0.1% probability that bone assemblages recovered from SU6B and SU6A (including megafaunal remains in association with archeology) are secondary deposits derived from underlying assemblages.

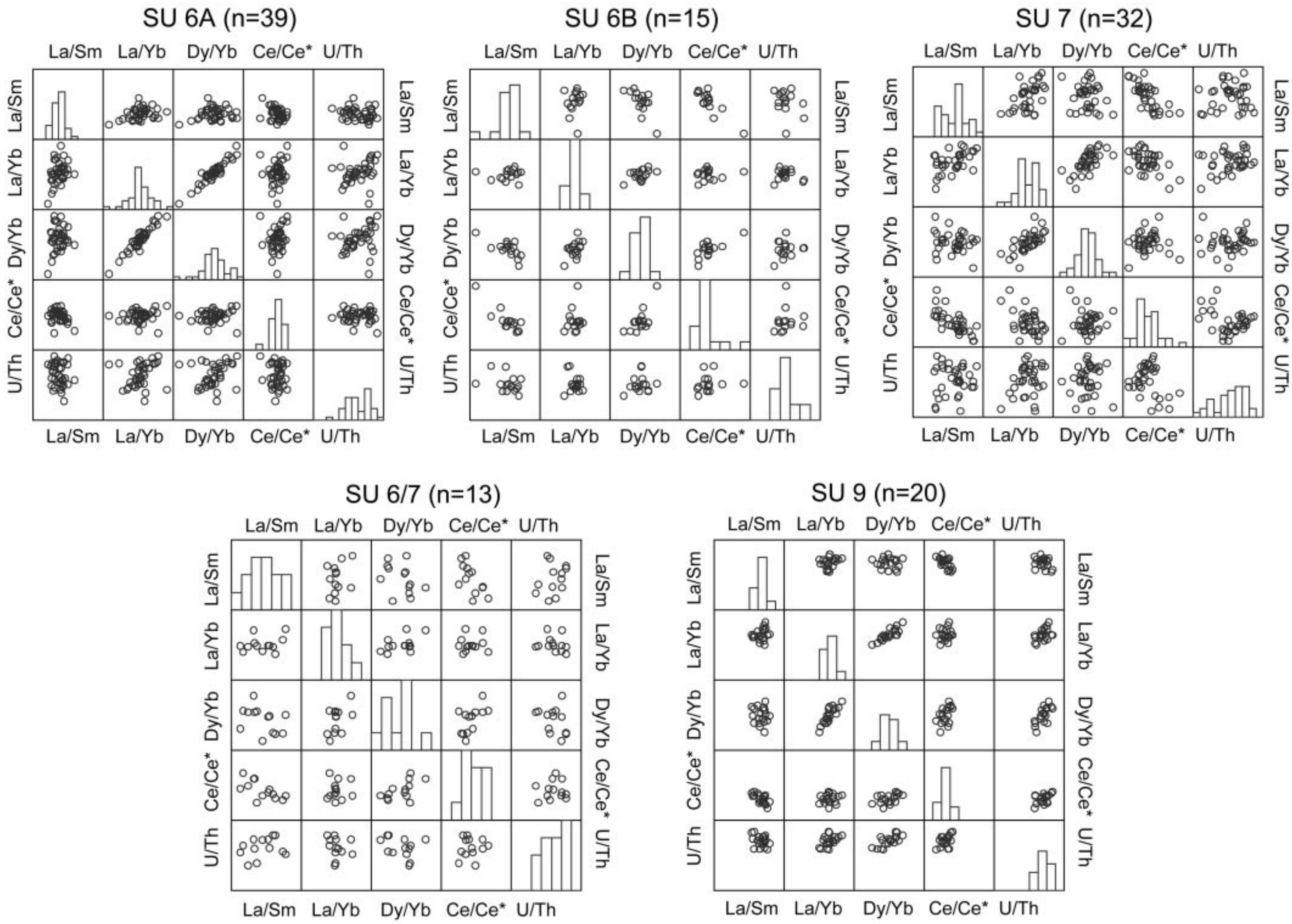


**Fig. 3.** Scatterplot matrix displaying cross correlations of all log-transformed trace element ratios used in multivariate analyses in bones from SU9, SU7, SU6/7, SU6B, and SU6A from Cuddie Springs. Central histograms show the frequency distribution of each variable within each population. Note relatively high within-group variability in all variables in bones from SU7 and SU6/7, and low within-group variability in SU9, SU6A, and SU6B.

25). However, sites other than Cuddie Springs have yielded megafauna remains that are significantly younger than 46.5 ka (26–28), and an increasing body of evidence attests to the onset of climatic instability in Australia from ≈50 ka (8), culminating in full glacial conditions as early as 30 ka (29). Climatic instability is characteristic of the late Pleistocene and is coincident with faunal extinctions on all continents.

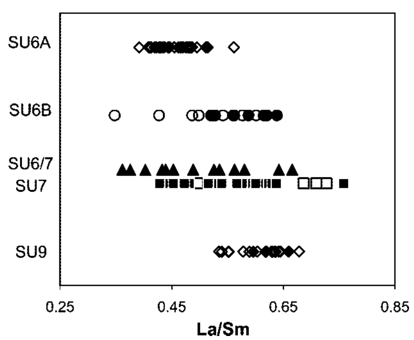


**Fig. 4.** Scatterplot showing shale normalized *La*/*Sm* ratios in bones from all sampled SUs from Cuddie Springs. Filled symbols indicate identified megafauna, and open symbols indicated extant fauna. Mean *La*/*Sm* values are significantly different between SU6B and SU6A (two-sample $t$ test, pooled variance, $t = 5.1$, df = 55, $P < 0.001$), between SU9 and SU6A ($t = 12$, df = 57, $P < 0.001$) and between SU9 and SU6B ($t = 3.2$, df = 32, $P = 0.003$).

## Conclusions

Cuddie Springs contains a rich record of megafauna and people in a secure stratigraphic context, with a human–megafauna overlap enclosed in sediments dating from ≈36 to ≈30 ka. This period coincides with significant environmental shifts, key technological developments in the archeological record (e.g., seed-grinding), and the loss of megafauna taxa (5, 14, 18, 30). The evidence from Cuddie Springs clearly rebuts the notion of a continent wide faunal extinction event at 46.5 ka (2). Furthermore, a prolonged coexistence of humans and megafauna refutes blitzkrieg as an explanatory model for megafaunal demise (1). The fossil record at Cuddie Springs documents the persistence of some megafaunal species to at least 30 ka in southeastern Australia and indicates that Pleistocene megafaunal extinctions occurred gradually against a backdrop of climatic deterioration.

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