Extinction implications of a chenopod browse diet for a giant Pleistocene kangaroo

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Kangaroos are the world's most diverse group of herbivorous marsupials. Following late-Miocene intensification of aridity and seasonality, they radiated across Australia, becoming the continent's ecological equivalents of the artiodactyl ungulates elsewhere. Their diversity peaked during the Pleistocene, but by approximately 45,000 years ago, 90% of larger kangaroos were extinct, along with a range of other giant species. Resolving whether climate change or human arrival was the principal extinction cause remains highly contentious. Here we combine craniodental morphology, stable-isotopic, and dental microwear data to reveal that the largest-ever kangaroo, *Procoptodon goliah*, was a chenopod browse specialist, which may have had a preference for *Atriplex* (saltbushes), one of a few dicots using the C_4 photosynthetic pathway. Furthermore, oxygen isotope signatures of *P. goliah* tooth enamel show that it drank more in low-rainfall areas than its grazing contemporaries, similar to modern saltbush feeders. Saltbushes and chenopod shrublands in general are poorly flammable, so landscape burning by humans is unlikely to have caused a reduction in fodder driving the species to extinction. Aridity is discounted as a primary cause because *P. goliah* evolved in response to increased aridity and disappeared during an interval wetter than many it survived earlier. Hunting by humans, who were also bound to water, may have been a more decisive factor in the extinction of this giant marsupial.

Australia | dietary ecology | extinct marsupial | stable isotopes | human hunting

Whether climate change, humans, or a combination of factors drove 90% of Australia's large animals ("megafauna") to extinction during the late Pleistocene has been disputed for well over a century (1–6). Recent studies have shown that most species were gone by approximately 45,000 years (kyr) ago (2–3), leaving over-hunting (1, 2), landscape burning (3, 4) by humans after their arrival approximately 50 kyr ago, and/or increased aridity since the penultimate glacial maximum (6) as the 3 most strongly championed hypotheses. Most arguments are fuelled by the same 3 problems: paucity of well-dated occurrences and knowledge of prehuman faunal change, difficulties distinguishing "absence of evidence" from "evidence of absence," and inadequate understanding of the ecologies of extinct taxa. Here we conduct the first multidisciplinary appraisal of the dietary ecology of a megafaunal marsupial and consider the potential roles of increased aridity, fire, and human hunting in its extinction.

All large extant kangaroos are grazers (specialist grass consumers), a handful of small to medium-sized species, or wallabies, are browsers (selective feeders on dicots), and the remainder are mixed feeders (browser-grazers) (7–9). Of the more than 40 kangaroo species that became extinct before the end of the Pleistocene epoch, at least two-thirds were apparently browsers based mainly on appraisals of craniodental morphology (10). However, no independent tests of this widespread assumption have been made, and so the precise nature of their diets, and the ecological basis for the local coexistence of up to 12 browsing kangaroo species, has remained speculative (1).

Sthenurines were a diverse group of robust kangaroos that originated in the late Miocene and by the Pleistocene had become one of the most diverse and widespread herbivore groups in Australia (1). *Procoptodon goliah* was the most robust, short-faced, and largest kangaroo ever to have evolved (Fig. 1, also see Figs. S1 and S2), with an estimated body mass of 230 kg and height of approximately 2.0 m (11). The species also appears to have been one of the last megafaunal survivors (2, 6). This has been used to argue that it was better adapted to Pleistocene aridity and climatic variability than many other megafaunal species (12). Its extreme brachycephaly, greatly enlarged masticatory muscles, near-cylindrical elephant-like mandibles, highly reduced incisors, deep maxillae, and bulbous molars (Fig. 1) suggest that *P. goliah* had a distinctive, tough diet relative to other kangaroos. By contrast, the hypertrophy of the molar crests of *P. goliah*, which resembles that seen in grazing macropodine kangaroos (e.g., larger *Macropus* species), and its wide distribution through open, drier regions (Fig. 2) have been used to infer a grazing habit (8). Although its remains have been extensively found through eastern and southern regions of mainland Australia, they have not been discovered in areas where modern mean annual rainfall exceeds 800 mm (13), which places a distinct limit on its preferred diet vegetation.

These conflicting inferences prompt questions which highlight an apparent contradiction. If *P. goliah* was a grazer, why do all other aspects of the craniodental system suggest that a capacity to generate large masticatory forces, seemingly befitting a tough-browse diet, was a major selective force in its evolution (1)? And with such small incisors and no trunk, how would it have harvested sufficient grass to satisfy its energy requirements? On the other hand, if *P. goliah* was a browser, what types of dicot vegetation would require processing in a manner similar to grass and be widely distributed through semiarid and arid Australia?

As one of the latest-surviving megafaunal species, elucidating the dietary ecology of *P. goliah* is critical for identifying key factors in the extinction process. We analyzed dental microwear patterns and stable carbon-isotope ratios (expressed as $\delta^{13}C$) in *P. goliah* tooth enamel to document its dietary ecology. In herbivore tooth enamel, $\delta^{13}C$ reflects the isotopic contents of dietary plants, which are

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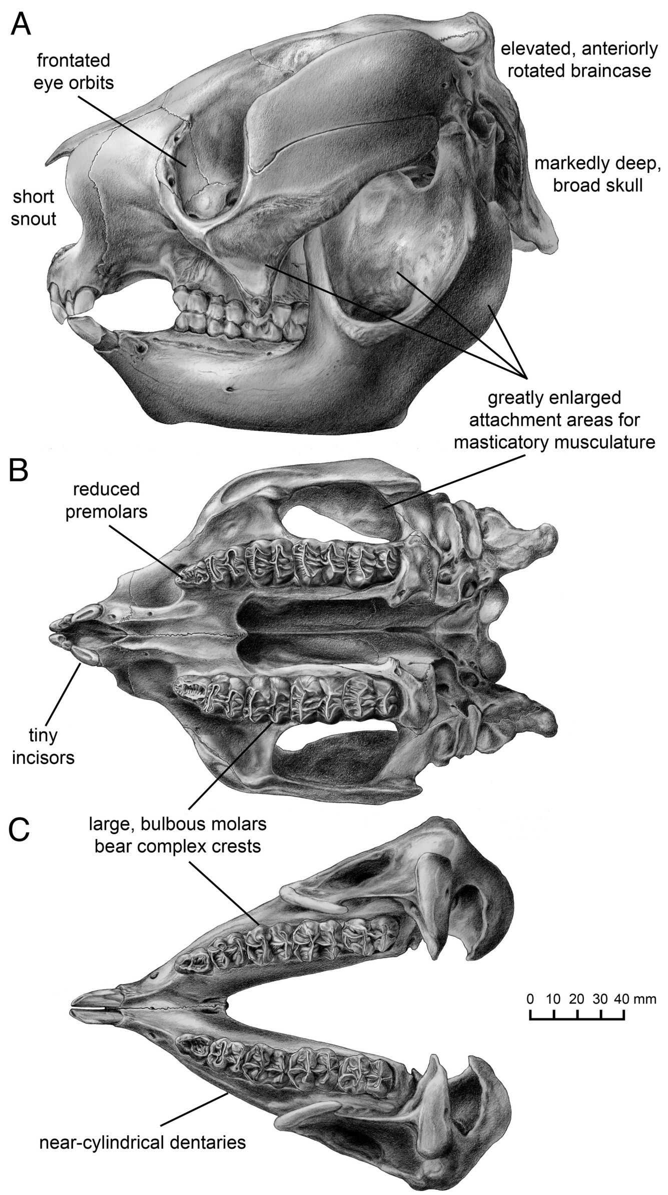

Fig. 1. Skull of *P. goliah*. (*A*) lateral view, (*B*) palatal view, (*C*) dentary in occlusal view.

determined by the photosynthetic pathways used. These, in turn, are influenced by climate (14). Today, isotopically lighter C$_3$ grasses dominate temperate southeastern Australia, seasonally variable dominance of C$_3$ and C$_4$ grasses characterizes subtropical and semiarid areas, and C$_4$ grasses dominate tropical and arid regions (15). Modern grazing kangaroo δ^{13}C values closely reflect C$_3$ and C$_4$ grass predominance (16).

Results and Discussion

Enamel Microwear. Dental microwear texture analysis (17, 18) was applied to specimens from 3 distinct climate zones (Fig. 2 and Table S1) to test whether *P. goliah* was a browser, mixed-feeder, or grazer. The extant browser *Wallabia bicolor* and the grazer *Macropus giganteus* differ significantly in several surface parameters, including anisotropy and heterogeneity (see Table S2). *P. goliah* is also distinct from *M. giganteus*, and similar to *W. bicolor*, in most features (Fig. 3), which indicates that specimens of *P. goliah* studied were consuming browse vegetation immediately before their death.

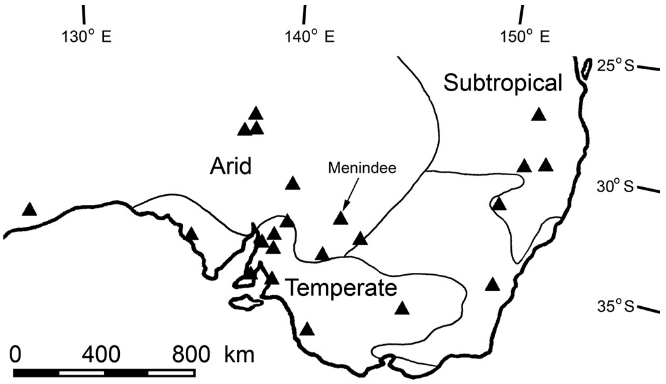

Fig. 2. Map of southeastern Australia showing localities yielding *P. goliah* and major climatic zones (37). Arid, warm temperate to subtropical, seasonally variable rainfall, 100–300 mm/yr; Subtropical, mainly summer rainfall, 400–1,200 mm/yr; Temperate, mainly winter rainfall, 300–1,200 mm/yr.

Carbon Isotopes and Diet. The isotope data demonstrate that *P. goliah* had a diet comprising a large fraction of C$_4$ vegetation (Fig. 4 and Tables S3 and S4). At first glance, this would appear to support the grazer hypothesis (8), given that the vast majority of C$_4$ plants are grasses, and all prior palaeoecological studies have equated C$_4$ enamel signatures with a grass diet (14). However, enamel δ^{13}C averages indicate that *P. goliah* consumed significant quantities of C$_4$ vegetation in each region. In the temperate southeast, where C$_4$ grasses are rare or absent, the δ^{13}C values for *P. goliah* are surprisingly high (-4.0 ± 2.1‰, $n = 15$), indicating a predominantly C$_4$ diet. The lack of temperate C$_4$ grasses is reflected in grazing kangaroos from the same fossil sites, which yield isotopic signatures indistinct from those of browsing/mixed-feeding kangaroos (δ^{13}C grazers -12.1 ± 1.1‰, $n = 69$; browser/mixed feeders -12.3 ± 1.7‰, $n = 66$) (Fig. 4). The δ^{13}C values for *P. goliah* in the arid (-4.4 ± 4.1‰, $n = 13$) and subtropical (-6.0 ± 2.9‰, $n = 16$) regions are also consistently higher than those for grazing kangaroos in the arid (-7.5 ± 3.7‰, $n = 51$) and subtropical (-8.6 ± 2.5‰, $n = 25$) regions (Fig. 4). The relatively high δ^{13}C values for *P. goliah* across 3 distinct climatic zones suggest it was largely a C$_4$ browser, the first to be identified worldwide.

Globally, C$_4$ dicots are much rarer than C$_4$ grasses (14); however, 23 of 24 Australian species of the xeromorphic chenopod genus *Atriplex* (saltbushes) use the C$_4$ photosynthetic pathway (19). Species of *Atriplex* and the C$_3$ chenopod *Maireana* (bluebushes) dominate large tracts of shrubland through semiarid and arid Australia (Fig. S3) and are common elsewhere in woodland understories (20). However, they are markedly underexploited by modern native mammals as a food resource (1). The combination of stable-isotope and dental microwear analysis indicates that *P. goliah* was a browser of tough chenopod leaves and stems, which would account for its robust craniodental morphology, large body size, and mobile forearms with grappling hook-like claws (21). These may have been used for feeding clumps of herbage directly onto the heavily buttressed molars, bypassing the highly reduced incisors (1) (Fig. 1). The δ^{13}C values of chenopod samples collected from throughout the former range of *P. goliah* (Fig. 2) are consistent with the proposed diet (Fig. 4).

Water Relations. Saltbushes have long been exploited by Australian sheep pastoralists due to their abundance and nutritional value (22, 23). Like sheep, the arid-adapted red kangaroo (*Macropus rufus*) is principally a grazer but is forced to exploit *Atriplex* during drier months and droughts, when young or mature grasses and green forbs are unavailable (9). Despite the high moisture content of

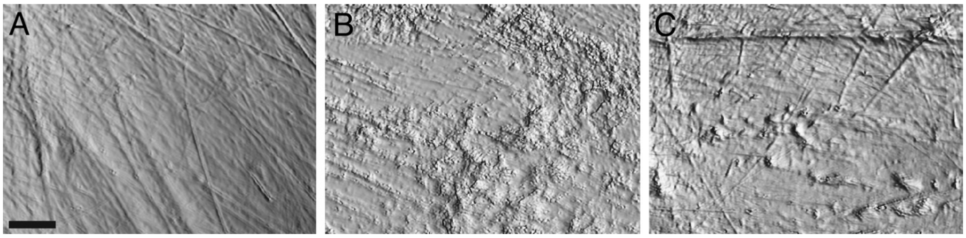

Fig. 3. Photosimulation of typical microwear surfaces of 3 kangaroo species. (*A*) extant C_4 grazer (*M. giganteus*, FU2003.8.27–13). (*B*) extant C_3 browser (*W. bicolor*, AM M36793). (*C*) extinct giant kangaroo (*P. goliah*, AM F105983). (Scale bar = 20 μm.) The grazer is characterized by a more anisotropic surface (more parallel striations), while the browsers have a more complex array of surface features (including those traditionally termed ''pits''). (see *SI Text*).

Atriplex (24), heavy reliance on it by sheep dictates greater free-water consumption to counteract high sodium concentrations (22, 23), and this can only be facilitated by frequent access to artificial watering points. Red kangaroos survive on saltbush by increasing water removal from feces to produce more concentrated urine, thus achieving a net water gain on a saltbush diet (9). Given the greater absolute water requirements of larger mammals, *P. goliah*, as a year-round saltbush specialist 3–5 times heavier than the red kangaroo or sheep, must have had both a highly efficient osmotic physiology and the ability to travel long distances to exploit semipermanent or ephemeral water bodies. This is reflected in the hind foot of *P. goliah*, which was reduced to one broad digit with a hoof-like distal phalanx and bore prominent ligament scars reflecting enhanced spring flexion, a morphology strikingly convergent on that of "open-plains" horses (21).

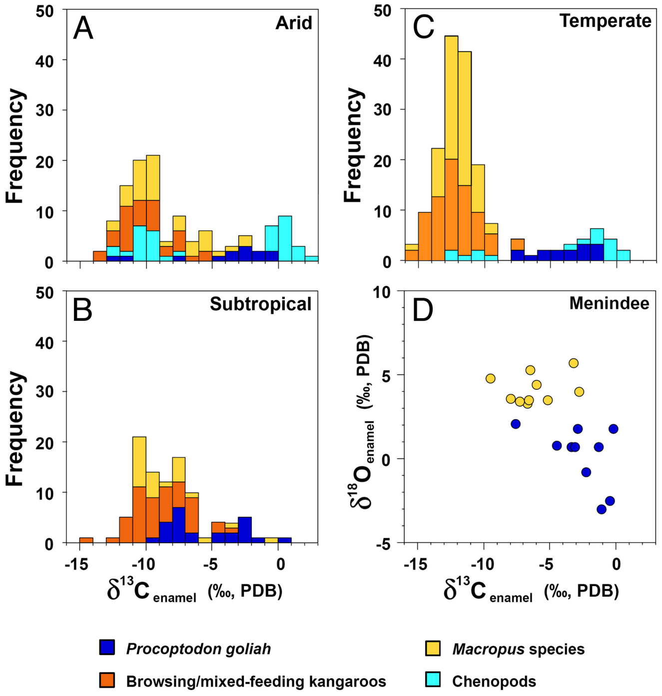

Fig. 4. Carbon-isotope data (δ^{13}C) for Pleistocene kangaroos from south-eastern Australia. (*A–C*) Frequency histograms of enamel δ^{13}C values of *P. goliah*, grazing kangaroos (*Macropus* species), browsing/mixed-feeding kangaroos and modern chenopods (e.g., *Atriplex, Maireana*) from Arid, Subtropical and Temperate climate zones. Chenopod vegetation samples are expressed as equivalent enamel δ^{13}C values (ε = 13.3%; see *SI Text*) and have been corrected by +1.5‰ for the effects of fossil fuel burning over the past century. (*D*) Enamel δ^{13}C vs. δ^{18}O for Menindee fossil grazing kangaroos. Enamel δ^{13}C and δ^{18}O averages for grazing kangaroo teeth (–6.2 ± 2.1‰, n = 10; δ^{18}O: 4.2 ± 0.9‰, n = 10) differ significantly ($P < 0.002$) from those of *P. goliah* (δ^{13}C: –2.7 ± 2.2‰, n = 10; δ^{18}O: 0.2 ± 1.8‰, n = 10).

If *P. goliah* consumed more free-water than grazers from the same sites and time intervals, one would expect this to be borne out by a comparison of enamel δ^{18}O values. Due to the enrichment of ^{18}O in leaf-water, herbivores that are less reliant on free-water and live in drier environments generally have higher enamel δ^{18}O values than those which obtain a larger fraction of their ingested water directly from waterholes and streams (25). The relationship between enamel δ^{18}O values and environmental parameters (e.g., local meteoric water δ^{18}O, relative humidity) is very similar for a broad range of extant species (4). Since *P. goliah* is a member of the same family as modern kangaroos, it is likely that it had a similar physiology. It is therefore significant that the average enamel δ^{18}O value for *P. goliah* (0.2 ± 1.8‰, n = 10) is markedly lower ($P <$ 0.001) than that for grazing kangaroos (4.2 ± 0.9‰, n = 10) from the same stratigraphic horizons in our arid locality (Fig. 4*D*). This result supports the hypothesis that *P. goliah* was a more committed drinker than contemporaneous grazing kangaroos.

Potential Environmental Impacts. At a local scale, episodic droughts undoubtedly impacted *P. goliah* populations given individuals' need to drink regularly, and this is consistent with its presence in a drought assemblage that accumulated 55 kyr ago at Lake Menindee in the arid southern interior of Australia (26). However, droughts have characterized the Australian interior for at least 7 million years (27) and *P. goliah* (and many other Pleistocene megafaunal species) survived multiple Pleistocene periods of higher aridity, including the penultimate glacial and last interglacial (5, 6, 28, 29). Moreover, effective rainfall in southern, eastern, and inland Australia was not markedly diminished until after 40 kyr ago (30–32). This is well after the demise of *P. goliah* and many other megafaunal taxa (including water-efficient grazing species) 50–45 kyr ago (2, 6) and well before the onset of arid conditions marking the last glacial maximum 27–17 kyr ago (29). Consequently, we consider it unlikely that *P. goliah* was driven to extinction in 3 distinct climatic regions solely or primarily by reduced water supply.

Landscape burning by humans, who arrived in Australia approximately 50 kyr ago, has been advocated as a more likely explanation than hunting or aridity for the late Pleistocene extinction of Australia's megafauna by means of replacement of nutritious fire-sensitive plants with nutrient-poor, fire-adapted shrub/grassland mosaics (3, 4, 27). In the case of *P. goliah*, however, a major component of its diet (chenopods including a large proportion of *Atriplex*) was less affected due to its relatively lower flammability (20, 24, 28, 33). Also, the paucity of combustible grasses typically dispersed between saltbushes in chenopod shrublands greatly inhibits the spread of fire (20). Furthermore, chenopods tend to increase in abundance in some areas 50–40 kyr ago (28, 29, 34), which implies that the demise of this giant kangaroo is unlikely to have been precipitated by a reduction in food supply due to fire. While it is conceivable that the incipient increase in aridity that favored an increase in chenopod abundance 50–40 kyr ago (28, 34) also reduced free-water sources, increasing concentrations of individuals around water, this alone is unlikely to have driven *P. goliah* to extinction.

Conclusions

P. goliah is one of an increasing number of Australian megafaunal species for which there is no dispute over chronological overlap with humans (2, 6, 12, 35), who were present in southeastern Australia, well within the geographic range of *P. goliah*, by 50–46 kyr ago (31). Still, there is no direct evidence from Australia to show that humans ever hunted megafauna, a fact used to bolster arguments against human hunting as an extinction cause (6, 35). Nevertheless, demonstrating a link between the two is inherently difficult because individual death and species extinction occur at different scales that only converge as the last individual dies. Likely mechanisms of prehistoric mass extinctions tend to be inferred from their temporal proximity to extinction events and the weighing of evidence for each hypothesis. In the case of *P. goliah*, we argue that its diet and the timing of its disappearance are more consistent with human hunting as a primary driver than increased aridity or a fire-induced reduction in fodder, although we cannot discount the possibility that such factors may have played ancillary roles. As the largest hopping animal ever to have evolved (11), high hind limb tendon stresses would have rendered *P. goliah* much slower to accelerate from a standing start than other kangaroos (36). It is conceivable, therefore, that its height and prevalence in open shrublands made *P. goliah* relatively conspicuous to humans from a distance, thus increasing its vulnerability to hunting by humans who were likewise bound to water. Clarification of the ecologies and precise extinction chronologies for different megafaunal species in different regions of Australia will help test this hypothesis.

Materials and Methods

Sample Collection. Tooth enamel from *P. goliah* and other Pleistocene specimens were obtained from museum collections. These include still-extant taxa that today are obligate grazers (e.g., larger *Macropus* species) and obligate browsers (e.g., *Wallabia*), and a range of extinct taxa very likely covering a broad dietary spectrum. Modern samples of kangaroo teeth (used to calculate enamel-diet enrichment factor, ε; see *SI Text* and Tables S5 and S6) and diet/plant samples were either collected directly from the field or sourced from museum collections. Time-averaging (confounding of signals due to mixing of samples from different intervals) was addressed by multiple sampling from within sedimentary units and between closely associated stratigraphic horizons. Site ages cross a time span from approximately 500 kyr (e.g., Nullarbor Thylacoleo Caves) to 55 kyr ago (Lake Menindee).

Dental Microwear. Dental microwear texture analysis quantifies enamel surface features using a combination of scanning confocal microscopy and scale-sensitive fractal analysis (17, 18). All specimens were examined and analyzed using a Sensofar Plμ white-light scanning confocal microscope (100× objective) and scale-sensitive fractal analysis (17, 18). Molar facet analysis was based on scans from 4 adjacent areas measuring $204 \times 276\ \mu m^2$ in total. This method does not rely on manually counting pits and scratches (traditional microwear) but is based on automated quantification of the following textural categories: anisotropy, complexity, heterogeneity, scale of maximum complexity, and texture fill volume (17, 18; see *SI Text*). These variables were compared between all taxa using nonparametric Kruskal-Wallis tests.

Stable Isotope Analysis. To test the dietary hypotheses for *P. goliah* we analyzed δ^{13}C in 53 enamel samples from 44 individual teeth from 3 distinct climate zones (Fig. 2). Values were compared with those of known grazing *Macropus* kangaroos and other kangaroo species contemporaneous with *P. goliah*, as well as with those of modern chenopod vegetation from the same climate zones (see *SI Text* and Fig. S4). Powdered samples of fossil enamel were first pretreated with 3% H_2O_2 to remove soil organics then with 0.1M CH_3COOH to remove secondary carbonates. Enamel samples were reacted at 90 °C in a common acid bath and analyzed on a Finnigan MAT 252 mass spectrometer. Isotope results were standardized to the Pee Dee Belemnite scale by in-run comparison of enamel standards calibrated against NBS-19. δ^{13}C, δ^{18}O ‰ = (Rsample/Rstandard −1) × 1000, where R is the ^{13}C/^{12}C or ^{18}O/^{16}O ratio. The δ^{13}C of finely ground plant specimens were determined by either analysis on a Costech Elemental Combustion System coupled to a Finnigan MAT 252 mass spectrometer operating in continuous flow mode or by off-line closed-tube combustion on a Finnigan MAT 251. Internal standards run in parallel with the unknown plant samples enabled conversion to the PDB scale.

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