Kangaroos hop to a different beat: late response of tooth evolution to global aridification

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Perhaps none of Australia's remarkable endemic plants and animals are more iconic than the kangaroos and wallabies that constitute Macropodoidea. These pouched animals share a common ancestor with all the world's mammals, but like Australia's other marsupials, they evolved in isolation from small opossum-like founders that inhabited the southern supercontinent of Gondwana in the late Mesozoic (*1*). Australian clades offer comparative opportunities for understanding how global-scale processes like climatic change interact with the exceedingly contingent processes of evolution, adaptation, and extinction. In this issue of *Science*, Couzens and Prideaux show that dental evolution in kangaroos responded to global aridification much like in other mammalian herbivores around the world, but that in Australia tooth specialization was linked to a late spread of grasslands that postdated the onset of drier habitats.

Couzens and Prideaux's conclusions are based on analysis of the functional traits that link macropodoids to vegetation and thus to climate. Classically, paleontologists have studied biotic responses to global change by measuring taxonomic turnover (*2*). The analysis of taxonomic diversity documents mass extinctions, clade turnovers, and changes in global carrying capacity (*3*), but it is too coarse study how evolutionary adaptation contributes to these events. Ecometrics, the analysis of turnover in functional traits, atomizes organisms into form-function pairings between specific traits and associated environmental factors in order to more directly understand the processes by which taxonomic diversity changes (*4*). Couzens and Prideaux measured the evolution of tooth crown height (roughly the ratio of crown to root), which is proportionally higher in mammals that eat abrasive vegetation (*5*) and is thus linked via natural selection to aridity and vegetation cover, especially grasslands (*6*) (**Fig. 1**). To characterize the actual dietary demands on the teeth, the authors measured the wear on their occlusal surfaces. Using independent proxies for global climate (oxygen isotopes), the spread of grasslands in Australia (pollen and carbon isotopes), and air-borne grit (aeolian flux in nearby ocean sediment cores), they analyzed the interplay between tooth wear, crown height, and environmental change in the radiation of macropodoids.

Unlike in North America and Eurasia, global aridification was not accompanied in Australia by an increase in herbivore crown height. On the former two continents, hypsodonty (high crowned teeth) became increasingly common with the onset of drier global climates in the mid Miocene (10-15 Ma) (*7,8*). But in Australia, tooth wear and crown height did not increase until the Pliocene (3-4 Ma) when grasslands expanded and true kangaroos radiated. So what happened 10 million years earlier when Australia became more arid? Instead of browsers giving way to hypsodont grazers, browsing macropodoids got bigger. The sthenurines–giant kangaroo-like animals that weighed as much as 240 kg and strode instead of hopped (*9*) –radiated into the increasingly arid habitats of 14 Ma. Their low-crowned teeth, short faces, large body size, and presumably slower mass-specific metabolic rates allowed them to thrive by browsing the increasingly sparse vegetation during the early phase of aridification. Only later when abrasive, silica-rich grasslands replaced the earlier arid vegetation did high crowned, fast-moving true kangaroos replace their slow-moving sthenurine cousins via a combination of clade-replacement and trait evolution.

Evolution is a process that is often context specific, rife with contingencies. Gould wondered what would change if we could "replay life's tape" (*10*). While comparing evolution on isolated continents does not let us to play the tape again, it does at least allow us to listen in stereo as independent voices respond to the same global theme. Couzen and Prideaux's data demonstrate a disjunction between the onset of aridity and the evolution of high-crowned teeth in Australia that differs from the classic patterns in Eurasia and North America. The Australian transition illuminates a previously identified anomaly in South America where hypsodonty evolved in clades inhabiting humid forests predating the spread of grasslands by almost 20 million years (*11*). High crowned teeth in South America were favored because the vegetation was gritty from frequent ash falls from the nascent Andes, not because of the climate was arid. So too in Australia was hypsodonty favored by gritty vegetation, this time grasslands. The classic connection between hypsodonty and climate is at least one step removed from climate (C4 grasses are favored over many other plant groups in hot, dry climates) and sometimes completely decoupled (**Fig. 1**). Aridity, grasslands, and hypsodonty were entangled in classic North American data, but the comparative histories of mammals in Australia and South America help disentangle the mechanisms of biotic response to environmental change.

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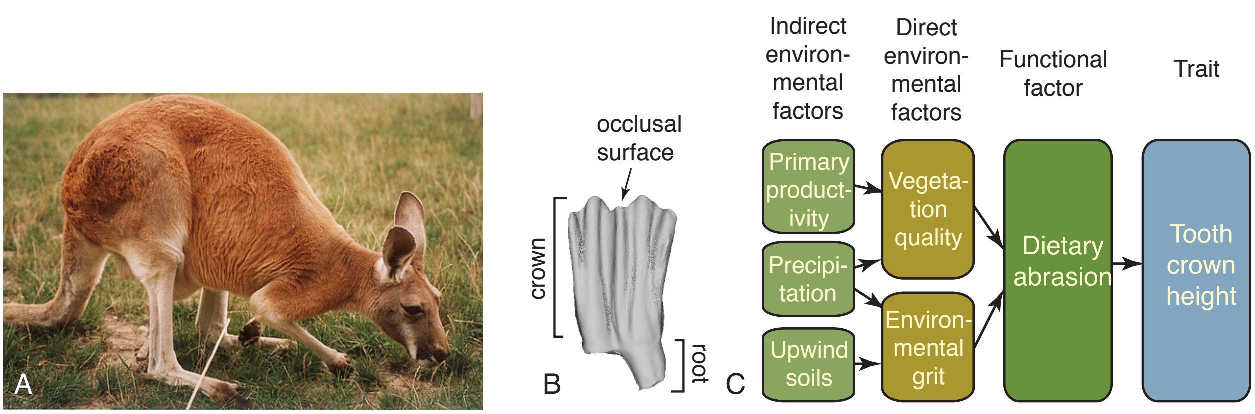

Fig. 1. Red kangaroo, *Macropus rufus*, grazing (A) (from Wikipedia.org). Lateral view of a bison tooth in which the crown is tall relative to the length of the root (B). Functional links between tooth crown height and environmental factors (C) (after *12*).