

The family Macropodidae (kangaroos, wallabies, and their kin) is a diverse and charismatic group of herbivorous marsupials with a significant presence in Australia and New Guinea in the present day and a fossil record stretching back at least into the late Oligocene. Of these, the genus *Protemnodon* is among the most diverse and widespread yet poorly understood. Although *Protemnodon* was raised nearly 150 years ago, poor delineation of species and increasingly unclear generic identity have perpetuated taxonomic uncertainty and impeded research into their palaeobiology.

Here I clarify the systematics of this key group of kangaroos and shed light on their palaeoecological identities. Morphological descriptions, comparisons and measurements were taken from multiple newly prepared, semi-complete skeletons and from photographs and 3D surface scans of material of *Protemnodon* collected from 14 institutions in four countries. This research reveals that a major driver of past taxonomic confusion was an over-reliance on morphology of the cheek dentition, which is far less useful for differentiating the species than features of the postcranial skeleton. In total, seven species are recognised, three of them new, supported by a sound phylogenetic hypothesis. Three species are considered *nomina dubia*, and two are synonymised. The species “*Protemnodon*” *nombe* is reallocated to a monotypic genus, *Nombe* gen. nov., and in a cladistic analysis is placed in a basal position within Macropodinae. Unexpected variation between species of *Protemnodon* is highlighted in locomotory adaptations inferred from major differences in limb morphology and proportions. These are discussed in relation to species distributions and habitats. Species of *Protemnodon* are united by anatomical features that reflect stability and power in the limb joints during locomotion, exemplified in the enlarged ilium and broad femoral proximal end, which bear well-developed muscle attachments. One of the two new Pleistocene species was a robust, low-g geared, bipedal hopper likely adept in uneven, better-wooded habitats. In contrast, the other of the two new Pleistocene species was larger but more gracile, convergent in some attributes on high-g geared, modern red and grey kangaroos. This and their wide inland distribution imply adeptness in open terrain. I also find evidence to suggest sexual dimorphism was present in this species to a similar extent to that seen in red kangaroos. A third Pleistocene species, *Protemnodon anak*, was of intermediate proportions, a large, mid-g geared bipedal hopper of forests and woodlands of eastern Australia. The Pliocene *P. otibandus* of New Guinea and eastern Australia displays adaptations to slower hopping, while its Pleistocene successor, *P. tumbuna*, converges on the morphology of modern New Guinean forest wallabies, and was likely facultatively quadrupedal. A cladistic analysis supports the monophyly of *Protemnodon*,

finding the early Pliocene *P. newini* basal within the genus. This research reinforces and expands upon the emergent view that megafaunal kangaroos demonstrated a much greater diversity of locomotor adaptations than has generally been understood.