Limb proportions indicate *Protemnodon*’s locomotion was divergent from modern large macropodines.

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1. Introduction
Kangaroos (Macropodoidea) encompass a range of body masses from 500 g to over 70 kg [1]. The most well-known form of kangaroo locomotion is hopping or “bipedal saltation” however, at slow speeds kangaroos employ either a quadrupedal bound or a pentapedal walk where the tail is used as a fifth limb [2]. Some kangaroos are habitually quadrupedal and hop very infrequently. The tree kangaroos (*Dendrolagus* spp.) employ a quadrupedal bound at all speeds, hopping only occasionally when on the ground. The only kangaroo that does not hop at all is the musky rat-kangaroo, *Hypsiprymnodon moschatus* (fig. 1a) [3]. The primary type of locomotion employed by a kangaroo is reflected clearly in its morphology. Optimum body mass for hopping is 50 kg [4], with a shift to hopping predicted at 160 kg due to tendon strain [5], but many Pleistocene kangaroos exceeded this. Evidence suggests a group of extinct giant kangaroos, the thylacines, adopted a bipedal walking locomotion that may have released them from these body mass constraints, allowing them to reach up to 233 kg (*Procoptodon goliah*) [6]. The extinct giant kangaroo (*Protemnodon* fig. (b), however, also frequently grew above the optimum body mass for hopping, reaching up to 166 kg [7]; but its locomotion is currently not understood. Some evidence points to *Protemnodon* being more quadrupedal than any known extant large kangaroo [8], but this has not been studied in any depth. Therefore, we applied a set of osteological indices known to reflect locomotor mode to a comprehensive dataset of macropod limb measurements in order to try to better understand the locomotion of *Protemnodon*.

2. Material & Methods
- **Dataset of long bone measurements** (fig. 2) from 105 individuals across 60 species of macropod, encompassing the entire taxonomic, body mass and locomotor range of Macropodoidea.
- **Species divided into four locomotor categories:** Bipedal saltators, Bipedal walkers, Quadrupedal (either obligate *(H. moschatus)*, or habitual quadrupeds that hop very infrequently) and "*Uniped*" for *Protemnodon*.

3. Results

![Figure 1: (a) Schematic phylogenetic tree of Macropodoidea modified from a molecular phylogeny by Llamas et al. [10] showing major groups. (b) Images of *Protemnodon* highlighting its unusual anatomy.](image)

- **For 7 out of 13 indices, *Protemnodon* and the quadrupedal group were significantly different to the bipedal saltators.**
- **E.g. bipedal saltators typically have MFI values of around 40–60 (fig. 3a) – reflecting elongated metatarsals that elongate the hindlimbs for a more effective stride length and allow longer flexor tendons.** Our results follow this trend but both quadrupedal taxa and *Protemnodon* fall below this range, reflecting much shorter feet that would be efficient during hopping.
- **Overall, compared to extant large hopping species, *Protemnodon* has much shorter feet and longer, more robust forelimbs that are more similar in length to the hindlimbs (fig. 3b). This is anatomically more similar to quadrupedal macropods. However, *Protemnodon* has a long tibia and ulna like that of large extant macropod species (bipedal saltators).**
- ***Protemnodon* occupies a vacant area of morphospace (fig. 4) due to this unusual combination of morphological features.**

![Figure 3: Clustered column plots showing the osteological indices: (a) Metatarsal–Femur Index (MFI) – (b) Intermembral Index (IMI) reflecting the relative lengths of the fore- and hindlimbs. Colours indicate locomotor groups. The dark green bar indicates the only obligate quadrupedal macropod species, *Hypsiprymnodon moschatus*.](image)

![Figure 4: Principal Components Analysis (PCA) of 13 osteological indices calculated for Macropodoidea. Variable factors map shows the loadings of each index within the morphospace.](image)

4. Discussion & Conclusions
- **Osteological indices are a good reflection of primary gait among extant members of Macropodoidea, with locomotor groups clustering together despite the more quadrupedal forms being distributed through the phylogeny (see fig. 1 & 4).**
- ***Protemnodon* possesses an unusual suite of morphological features similar to that of both quadrupedal and large bipedal saltating kangaroos.**
- ***Protemnodon* represents an unknown ecomorph to which there are no extant analogues and its locomotion was clearly divergent from modern large macropods (bipedal saltators).**
- ***Protemnodon* offers a unique opportunity to test our understanding of the locomotion of this group.**

**Acknowledgements**
Would like to thank my co-authors, Professor Christine Janis and Professor Emily Rayfield for their continued support and contribution to this project. I would also like to thank the University of Bristol for supporting this project and PAUSA for the opportunity to present my work to a wider audience.

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