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

Billie Jones, Christine M. Janis, Emily J. Rayfield
School of Earth Sciences, University of Bristol, Life Sciences Building, Bristol, BS8 1RJ, UK

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 **limit 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 sthenurines, 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 *Protemnodon* (fig. 1b), 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*.

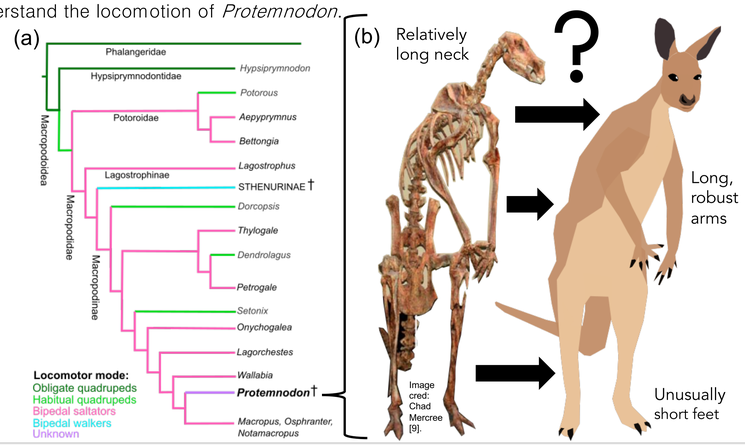

Figure 1: (a) Schematic phylogenetic tree of Macropodoidea modified from a molecular phylogeny by Llamas *et al.* [10] showing locomotor groups. (b) Images of *Protemnodon* highlighting its unusual anatomy.

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 "Unknown" for *Protemnodon*.

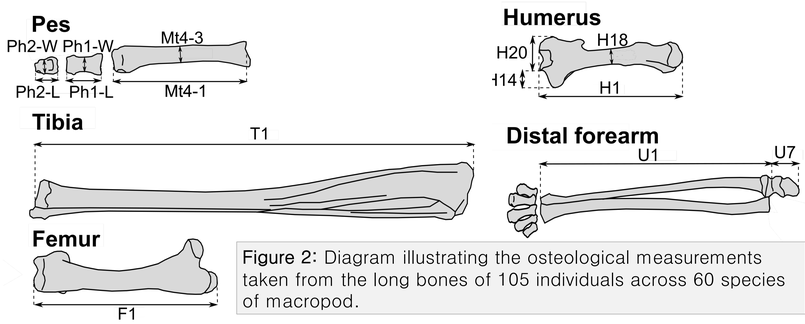

Figure 2: Diagram illustrating the osteological measurements taken from the long bones of 105 individuals across 60 species of macropod.

- **The following osteological indices were calculated (all ratios multiplied by 100):** **BI**, Brachial Index (U1/H1); **CI**, Crural Index (T1/F1); **EI**, Epicondyle Index (H20+H14/H1); **HRI**, Humeral Robustness Index (H18/H1); **IM**, Intermembral Index (H1 + U1/F1+T1+Mt—1); **IPI**, Intermediate Phalanx Index (Ph2-L/Ph2-W); **OPI**, Olecranon Process Index (U7/U1); **RI**, Radial Index (Maximum/minimum diameter of the radial head); **MI**, Metatarsal Index (Mt4-1/Mt4-3); **MFI**, Metatarsal-Femur Index (Mt4-1/F1); **MHI**, Metatarsal-Hindlimb Index (Mt4-1/F1+T1+Mt4-1); **PPI**, Proximal Phalanx Index (Ph1-L/Ph1-W); **UFI**, Ulna-Femur Index (U1/F1).
- Indices were subject to ANOVA and Kruskal-Wallis tests.
- Finally, a **Principal Components Analysis (PCA)** of the indices was run in RStudio using the package FactoMineR [11].

3. Results

- 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 hindlimb 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 inefficient 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 macropod morphospace (fig. 4) due to this unusual combination of morphological features.

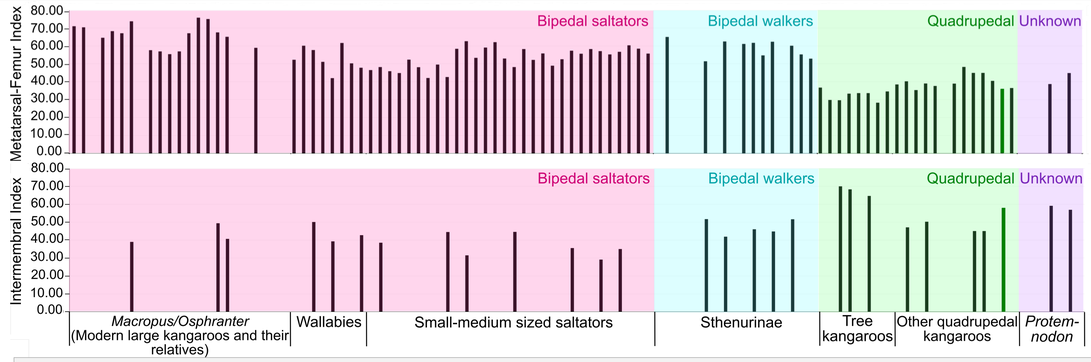

Figure 3: Clustered column plots showing the osteological indices: (a) Metatarsal-Femur Index (MFI) ; (b) Intermembral Index (IM), reflecting the relative lengths of the fore- and hindlimbs. Colours indicate locomotor groups. The dark green bar indicates the only obligate quadrupedal macropod species,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

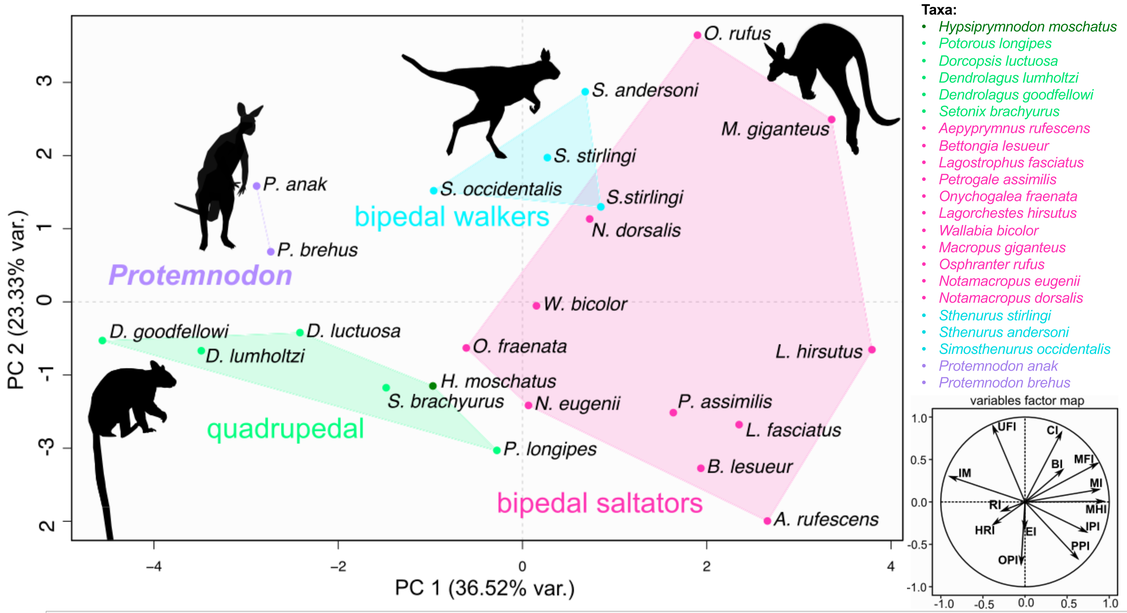

Figure 4: Principal Components Analysis (PCA) of 13 osteological indices calculated for Macropodoidea. Variable factors map shows the loadings of each index within the morphospace.

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).**
- Forelimb anatomy of *Protemnodon* reflects more reliance on quadrupedal locomotion than any large extant kangaroo.

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