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# Evolutionary Progression of the Iconic Australasian Kangaroos, Rat-Kangaroos, and their Fossil Relatives (Marsupialia: Macropodiformes)

WENDY DEN BOER



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**Abstract**

den Boer, W. 2018. Evolutionary Progression of the Iconic Australasian Kangaroos, Rat-Kangaroos, and their Fossil Relatives (Marsupialia: Macropodiformes). *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 1624. 105 pp. Uppsala: Acta Universitatis Upsaliensis. ISBN 978-91-513-0216-4.

The exceptionally diverse macropodiform's (kangaroos, rat-kangaroos and their fossil allies) currently have a fossil record that spans from the late Oligocene to the Holocene with an Australasian widespread fossil occurrence. The origins of the macropodiforms are believed to have been during the Eocene possibly having split from the Phalangeridae. This is largely based on molecular data as there is a complete lack of macropodiform fossil material prior to the late Oligocene leaving the origins of the macropodiforms to be largely speculative. Thus, late Oligocene rat-kangaroo dental fossil elements associated with *Palaeopotorous priscus* (which shares characteristics observed in both phalangerid and macropodiforms) were examined to get a better insight into the potential origins of the macropodiforms. The results obtained suggested that *P. priscus* is currently the most basal macropodiform known. Furthermore, due to the absence of adequate macropodiform post-cranial material, the functional eco-morphological interpretation of various macropodiform fossil taxa has been based largely on cranial and dental characteristics. Consequently, the examination of Miocene Balbaridae kangaroo's (*Balbaroo nalima* and an untaxonomised balbarid) post-cranial elements was undertaken, suggesting an array of locomotion types (similar to living macropodiforms) and a likely persistent arboreal and quadrupedal lifestyle. In addition, the Pleistocene *Protemnodon anak*'s post-cranial material are examined, proposing a probable combination of quadrupedal bounding and a slow walking gait alternative to the eminent fast bipedal saltation seen in almost all extant macropodiforms.

*Keywords:* macropodiforms, kangaroos, rat-kangaroos, fossil ancestors, post-cranial, eco-morphology, systematic, phylogeny

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*For Violetta - Lyza*



# List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I** Black, K.H., Travouillon, K.J., **den Boer, W.**, Kear, B.P., Cooke, B.N., & Archer, M. (2014) A New Species of the Basal “Kangaroo” Balbaroo and a Re-Evaluation of Stem Macropodiform Inter relationships. *PLoS ONE*, 9(11): 1 - 30.
- II** **den Boer, W.**, & Kear, B.P. (in press). Is the fossil rat-kangaroo *Palaeopotorous priscus* the most basally branching stem Macropodoid? *Journal of Vertebrate Paleontology*.
- III** **den Boer, W.**, Campione, N., & Kear, B.P. (submitted). Climbing adaptations, locomotory disparity and ecological convergence in ancient stem ‘kangaroos’. *Proceedings of the Royal Society B*.
- IV** **den Boer, W.**, & Kear, B.P. (manuscript still in draft format and was prepared for Journal of Vertebrate Paleontology). Comparative Postcranial Osteology of the Plio-Pleistocene ‘Giant Wallaby’ *Protemnodon anak*, and its Implications for Locomotion.
- V** **den Boer, W.**, & Kear, B.P. (manuscript still in draft format and was prepared for Australian Journal of Zoology). The Systematics of Fossil Kangaroos, Wallabies, Rat-Kangaroos, and their Related Stem Clades (Macropodiformes).

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## Introduction – What are the Macropodiformes?

The Macropodiformes (kangaroos, rat-kangaroos and their fossil relatives) are the most diverse radiation of marsupials on Earth, adopting various different ecological roles throughout Australia, Papua New Guinea, Indonesia, and on some surrounding islands (Burke et al. 1998). The current fossil record of the macropodiforms dates back to the Late Oligocene, as until now no macropodiform fossils prior to the Late Oligocene have been uncovered in Australasia (Rich 1996, Godthelp et al. 1999). This leaves the origins of the macropodiform super-family to remain relatively unrequited. However, based on molecular data, the origins of this mosaic super-family are believed to have occurred during the Eocene possibly having evolved from a possum-like ancestor and perhaps may have split from the phalangerid lineage (Phalangeridae: brush-tail possums, cuscuses, and close relatives) around this time (Westerman et al. 2004, Meredith et al. 2009). In addition to this, the Late Oligocene - Early Miocene Potoroidae (bettongs, rat-kangaroos, and potoroids) are often regarded as being the transitional step from the phalangerid-like form to the more macropodiform-like profile (Rich 1996). Conversely, as of the Late Oligocene ample fossil macropodiform material has been uncovered across Australasia (Australian mainland, Tasmania, Papua New Guinea, Indonesia and various surrounding islands) (Fig. 1 (See **Paper V** for description of the various fossil localities), suggesting a very successful and widespread occurrence during the Oligocene - Pleistocene, and perhaps may have had an even greater diversity than today (Archer et al. 1991, Archer et al. 2006).

The extant macropodiforms are renowned and acclaimed for their bipedal saltation. Although, within the modern Macropodidae (crown radiation of macropodids which have been divided into two main groups; the kangaroos and the wallabies (Macropodini), and the tree-kangaroos (Dendrolagini)) various eco-morphological adaptations exist; - These include: the largely arboreal tree-kangaroos (*Dendrolagus*) from Northern Queensland (Australia) and Papua New

Guinea; the diverse *Macropus* genus constituting of the famous bipedal hopping kangaroos; the medium sized wallabies constituting of the swamp wallaby (*Wallabia*), which occupy dense undergrowth swampy areas; the rock wallabies (*Petrogale*) which have adapted to inhabiting rocky terrain landscapes; the nail-tail wallabies (*Onychogalea*), that occur in semi-arid thick shrub woodlands; the pademelons (*Thylogale*), that inhabit thick vegetated forest-like environments; the quokka (*Setonix*), occur in semi-vegetated and semi-arid scrub environments; the lesser and greater dorcopsids (*Dorcopsis* and *Dorcopsulus*), found in highly vegetated tropical regions of Indonesia and Papua New Guinea; and finally, the banded-hare wallaby (Lagostrophinae), which is largely found in Acacia dominated areas (Groves 2005, Shorts and Turney 1992). Although, the placement of the living representative of the Lagostrophinae *Lagostrophus faciatius* within the Macropodidae is indecisive, as some believe it may be a living representative to the Pliocene - Late Pleistocene *Tropsodon* (Sthenurinae) kangaroos, based on analogous dental morphology (Archer 1981, Flannery and Archer 1983, Flannery 1989, Burk and Springer 2000, Prideaux 2004).

Nonetheless, also within the macropodiforms are the diverse, small to medium sized rat-kangaroos - the Potoroidae (crown group of the potoroids) constituting of the bettongs (*Bettongia*), the potoos (*Potorous*), the rufous rat-kangaroo (*Aepyprymnus rufescens*), and the desert rat-kangaroos (*Caloprymnus*) (recently extinct) of which the distribution was arid central Australia. The bettongs and the potoos adopt various different ecologies and occupy several different environmental types across the Australian mainland, Tasmania, near-by islands, and Papua New Guinea (Groves 2005). Additionally, within the modern macropodiforms there is the Hypsiprymnodontidae, which consists of only one (very genetically distinct) living species, the musky rat-kangaroos (*Hypsiprymnodon moschatus*), the only extant macropodiform that does not have the anatomical adaptations for bipedal saltation (Johnson and Strahan 1982, Burke et al. 1998). All other extant macropodiforms are capable of bipedal saltation, including the tree-kangaroos.

Initially, Hypsiprymnodontidae was believed to have been closely related to the Potoroidae (forming a monophyletic group), with the Macropodidae placed as a sister-taxon to Hypsiprymnodontidae and the Potoroidae (Fig. 2A) (Archer 1984, Flannery 1989). This was largely due to the similarity in the female reproductive systems of *H. moschatus* and the Potoroidae and other shared fea-

tures (such as; the frontal-squamosal contact on the cranium, a strongly developed masseteric canal and the condition of metatarsal V) (Burke et al. 1998). In later years, DNA testing was conducted which showed that *H. moschatus* is polyphyletic with the Potoroidae and the Macropodidae, with the two latter groups being monophyletic (Fig. 2B) (Burke et al. 1998).

The extinct macropodiforms currently include the following: the Late Oligocene Palaeopotoroinae, currently consisting of only one species - *Palaeopotorous priscus*, which may at present represent the most basal stem macropodiform (See **Paper II**); the Late Oligocene - Middle Miocene Balbaridae, comprising of quadruped (See **Paper I**) and possibly arboreal (See **Paper III**) kangaroos; the Late Oligocene – Late Miocene bulungamayine kangaroos, which are perceived as the ancestral grade of stem macropodids and potoroids (Flannery et al 1983, Cooke 1999); the medium to large (omnivorous and possibly carnivorous) Miocene - Pleistocene giant rat-kangaroos, the Propleopinae; and the extremely diverse large ice-age kangaroos, the Sthenurinae. The phylogenetic affinities of the extinct macropodiforms (Palaeopotoroidea, Balbaridae, bulungamayines, Propleopinae and the Sthenurinae) have been subjected to various different hypothesized phylogenies over the years (see **Paper V**). This has been largely due to gaps within the fossil record and because of insufficient post-cranial material for many macropodiform fossil taxa, as these phylogenies have been largely tested based on only cranial and dentrigenous material. This has further caused for the systematic placements of almost all extinct macropodiform clades to remain relatively indeterminate.

## The Cenozoic Climate, Environmental and Geographical History of Australia

The landmass of Australia broke off from Antarctica roughly 55 Mya (Early Eocene) and was geographically isolated up until roughly one Mya (Holocene) when it came into contact with Indonesia and Papua New Guinea (Fig. 3) (Martin 2006, Krebs et al. 2011). Being isolated from the other continents for such a long period of time allowed the flora and fauna on the Australian mainland and surrounding islands to flourish into the most fortuitous and unique



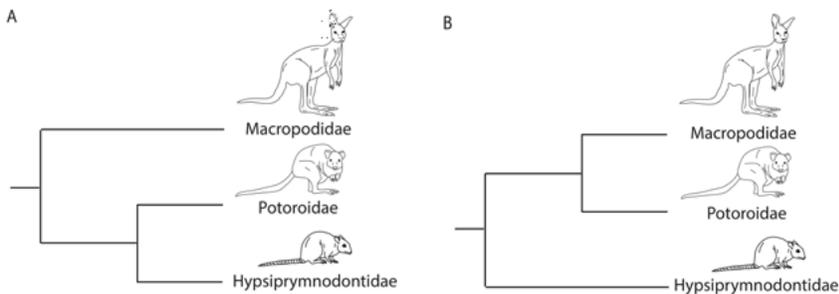
**Figure 1.** Distribution of fossil localities across Australia, Tasmania, Indonesia, Papua New Guinea and surrounding islands from which macropodiform remains have been uncovered.

fauna and flora found nowhere else on Earth. Australasia (combined with the Australian continent being geographically isolated for ca. 55-40 Mya) has also had various shifts in climatic and environmental conditions during the Cenozoic Era that had a strong influence on the fauna and flora residing in Australia (Fig. 4) (Also See **Paper V** Fig. 2). During the Oligocene Epoch, climatic conditions became warmer and more humid causing the distribution of numerous tropical riparian

ecosystems to occur (Flower and Kennett 1994). These riparian palaeo-environments caused the Oligocene macropodiforms, the Balbaridae, and stem macropodoids and potoroids, to have most likely adapted to quadrupedal (See **Paper I**), (semi) arboreal (See **Paper III**), and largely (mixed) browsing lifestyles (Fig. 4) (Flannery et al. 1983, Flannery and Rich 1986, Travouillion et al. 2016, Kear and Pledge 2007). During the Oligocene temperatures started to rise at an abrupt rate (Steppuhn et al. 2006, Micheels et al. 2007) causing semi-arid conditions to occur during the following epoch - the Miocene. Due to the alteration from warm and humid to hot and dry, the mosaic riparian palaeo-habitats started to gradually retract and more semi-arid open grassland environments started to develop during the Miocene (Wolfram et al. 2008). The macropodiforms during this time start to adjust, whereby we start to see more grazing dentition occurring in the fossil record, and the loss of many browsing quadrupedal bounding taxa (such as the balbarid kangaroos), and then the appearance of the Propleopinae giant rat-kangaroo *Ekaltadeta ima* (Archer and Flannery 1985), the early Sthenurinae forms (such as *Hadronamas puckeridgei* (Woodeburn 1967) and *Rhizosthenurus flanneryi* (Kear 2002), and some of the first Hypsiprymnodontinae (Flannery and Archer 1987, Flannery et al. 1992, Bates et al. 2014) start to occur in the fossil record. By the Late Miocene, alterations towards bipedal locomotion strategies start to emerge, due to the open grassland condition dominating. Bipedal movements may have occurred, as it was a faster and more effective way to cross open landscapes and to escape predators due to the increasing lack of coverage (Webster and Dawson 2004). By the Pliocene epoch, grasslands and Eucalyptus environments are the most dominant habitats, and the large grazing Sthenurinae kangaroos and macropodines (such as *Kurrabi* spp. (Flannery and Archer 1984, Flannery et al. 1992) and *Prionotemnus palankarinnicus* (Stirton 1955)) start to appear. Arid environments continue to spread during the Pleistocene (Bowler et al. 1976). Although, by the Middle - Late Pleistocene (ca. 5 - 7 Mya) some rainforest habitats re-occur in what is now northern Queensland (Prideaux and Warburton 2008), which caused some macropodiforms to revert back to an arboreal lifestyle (Bishop 1997), causing the appearance of the first tree-kangaroos (*Bohra*) (Flannery and Szalay 1982, Dawson 2004, Prideaux and Warburton 2008). By the Late Pleistocene, temperatures start to decline causing a glacial phase to take place (Tedford and Wells 1990). This event, coupled with the first humans to arrive in Australia (Webb 2008) caused 90% of the mega-fauna (such as the Sthenurinae) to go

extinct (Turney et al. 2008). The ice age event was over by the end of the early Holocene, when temperatures started to gradually increase again, causing ice caps to melt, sea levels to rise and islands to form around Australia (Pledge 1980). The Potoroinae and the Hypsiprym-  
 nodontidae still occupied medium-low semi-densely vegetated niches, and only the herbivorous, grazing and bipedal *Macropus* kangaroos start to diversify into various different habitats. During the Late Holo-  
 cene (ca. 5000 – 3000 ya) the dingo (*Canis lupis dingo*) is first intro-  
 duced to Australia, conceivably causing the decline and extinction of the thylacine (*Thylacinus cynocephalus*) and the Tasmanian devil (*Sarcophilus harrisii*) (on mainland Australia, as the Tasmanian devil's current distribution is only in Tasmania), most likely due to direct competition (Pledge 1980).

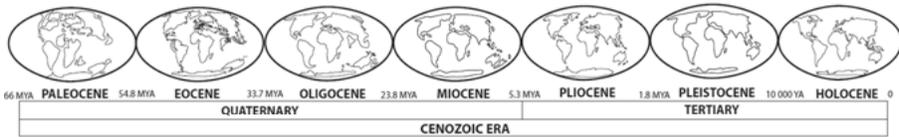
Then, roughly, around 1700 - 1790, the first Europeans arrived in Australasia, accompanied by rats, cats, foxes and rabbits (Dickman 1996) that had devastating impacts on the local fauna. Later, in the early 19<sup>th</sup> century (ca. 1935) the cane toad (*Rhinella marina*) had been introduced onto the Australian mainland as an effort to control the native beetle population (*Dermolepida albohirtum* and *Lepidiotia frenchi*). This too, caused native Australian species to become outcompeted, and due to *R. marina* capability of toxin excretion, the local biodiversity often became poisoned (Cabrera-Guzman et al. 2012).



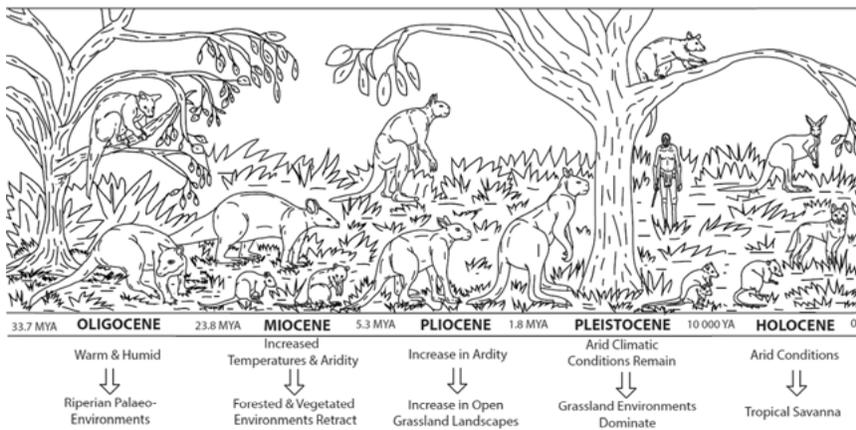
**Figure 2.** Traditional (A) and current placement (B) of Hypsiprym-  
 nodontidae, Potoroidae and Macropodidae. A. Hypsiprym-  
 nodontidae and Potoroidae form a monophyletic group and Macropodidae is poly-  
 phyletic. B. Macropodidae and Potoroidae are monophyletic and  
 Hypsiprym-  
 nodontidae is polyphyletic (Image after Burke et al. 1998).

Unfortunately, numerous members of the modern  
 macropodiforms are either vulnerable, endangered, critically endan-

gered or some even subject to near extinction, with many having reduced abundances and distributions due to the introduction of exotic species (such as the fox, cat, rabbit and the dingo) (Pledge 1980, Dickman 1996) and the arrival of the first Europeans in Australasia roughly 200 years ago. The loss of many unique Australasian species in the last two centuries has not been limited to the macropodiforms, as the loss of many different taxa from various other Australasian clades has also taken place from these devastating events. Although, within the past few decades much conservation efforts have taken place to preserve the remaining species, including the re-establishment of lost distributions for many species (Short et al. 1992, Dickman 1996). Alas, a lot more effort needs to take place in order to conserve and prevent any further needless extinctions of the Australasian distinctive and exceptional fauna.



**Figure 3.** Geographical Location of Australia throughout the Cenozoic Era.



**Figure 4.** Adaptations of the Macropodiforms due to Climate and Environmental Shifts from the Oligocene up until the Holocene.

## Research Aims

Due to macropodiform post-cranial fossil material being exceptionally poor and often completely lacking, the principal research objectives was to investigate the scanty availability of various post-cranial elements of a number of fossil macropodiforms in order to stipulate a conceivable morphological aptitude and ecological function. This was attained by preliminary examination of the Middle Miocene balbarid '*Balbaroo nalima*' post-cranial components (**Paper I**) and auto-pedal elements belonging to an unspecified Miocene balbarid (**Paper III**). Furthermore, the Pleistocene *Protemnodon anak* (and other members of the *Protemnodon* genus), has since its first description by Owen (1859, 1873) continuously been recognized as a 'giant wallaby' due to shared and analogous dental morphologies to wallabies (Stirton 1963). However, the post-cranial material of the type species *Protemnodon anak* within this genus is considerably incongruent to wallabies. *P. anak* is also the most skeletal complete *Protemnodon*. However, never before has the post-cranial material of *P. anak* been thoroughly studied. Therefore, for the first time, the post-cranial material of *P. anak*'s is examined to provide a feasible functional eco-morphology (**Paper IV**). Moreover, the Late Oligocene rat-kangaroo *Palaeopotorous priscus* had upon its first description by Flannery and Rich (1986) believed to have been a probable ancestral state to the whole macropodiform radiation. This however, has never been verified. Therefore, the phylogenetic assignment and morphological similarity of *P. priscus* to other macropodiforms was tested (**Paper II**).

# PAPER I

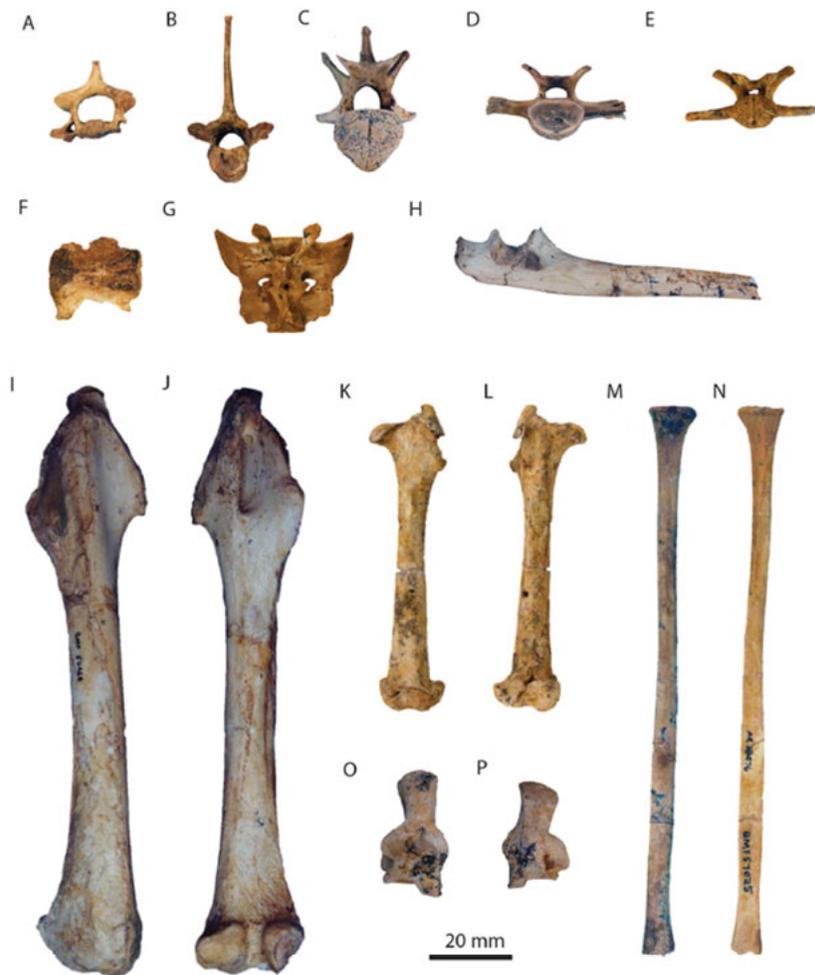
## Post-Cranial Fossil Remains of a Miocene Kangaroo *Balbaroo nalima* (Balbaridae, Balbaroo) Suggesting Quadrupedal Locomotion Strategies

Various post-cranial fossil elements associated with a balbarid (Balbaridae, Balbaroo) kangaroo *Balbaroo nalima* were uncovered at the Riversleigh World Heritage Area located in north-western Queensland (Australia) (Fig. 1) preserved in Middle Miocene limestone and freshwater deposits, and consists of a number of isolated vertebrae (QMF41234) (one largely complete cervical vertebra (Fig. 5A), three complete thoracic vertebrae (Fig. 5B), one complete lumbar vertebra (Fig. 5C), one intact caudal vertebra (Fig. 5D-E), one considerably worn but complete mid-series caudal vertebra (Fig. 5F)), one fragmented sacrum element (QMF41270) (Fig. 5G), one proximal ulna fragment (right) (QMF52809) (Fig. 5H), one largely intact femur (QMF50468) (Fig. 5I-J), one almost complete juvenile femur (QMF41270) (Fig. 5K-L), one almost complete fibula (QMF57025) (Fig. 5M-N), and one calcaneum (QMF41234) (Fig. 5P-Q). Found in association with the post-cranial material was also a well-preserved cranium (QMF36295), two dentaries (QMF31446 and QMF52809) and various isolated dental remains (QMF52811, QMF41271, QMF52809, and QMF57025) (These fossil elements are depicted and described in **Paper I**). The post-cranial material was uncovered together with the dental and cranial remains. Henceforth, they were ascribed with certainty to *Balbaroo nalima*.

The balbarids were initially believed to have possibly been the ancestral stock to the modern macropodiform radiation upon their first description by Flannery et al. (1983). In more recent studies, the balbarids were suggested to be a monophyletic basal and a diverse

grade of Late Oligocene - Middle Miocene kangaroos (Cooke and Kear 1999), currently comprising of thirteen different species assigned to five different genera, which are *Nambaroo*, *Ganawamaya*, *Balbaroo*, *Wururoo* and *Galanarla* (Cooke, 1992, Cooke, 1997, Flannery et al. 1983, Kear and Pledge 2007, Kear et al. 2007) (See **Paper V** for a further description of the different Balbaridae genera). They comprised of small to medium sized browsing kangaroos, and are the most common macropodiform fossils uncovered during the Late Oligocene and the Early to Middle Miocene (Prideaux and Warburton 2010). Their fossils indicate a relatively wide range across Australia, with remains having been uncovered from various fossil localities located in the Northern Territory, Northeastern Queensland, and South and Central Australia (Black et al. 2014). By the end of the Miocene, the balbarids became extinct, possibly due to their browsing and quadrupedal/arboreal nature, which would have made them less prosperous in an environment that is becoming increasingly more arid and a further diminishing of dense vegetation (Cooke 1997, Prideaux and Warburton 2010).

The Late Oligocene - Early Miocene balbarid *Nambaroo gillespieae* from Riversleigh (Fig. 1) (Kear et al. 2007) is currently the oldest macropodiform fossil of which there is post-cranial material available. The interpretation of the post-cranial remains associated with *N. gillespieae* by Kear et al. (2007) suggested a probable quadrupedal form of locomotion, and limited features that would have suggested some arboreal capabilities. This was the first time that morphological interpretations were undertaken of a balbarid not solely examining cranial and dental components but also skeletal elements. The conceivable quadrupedal nature of *N. gillespieae* was a new milestone in macropodiform evolution. As, due to the semi-dense, vegetated palaeo-environments, and warm, humid climatic conditions during this time, previous hypotheses had suggested a potential quadrupedal lifestyle for Oligocene macropodiforms (Warburton et al. 2011). However, before the discovery of *N. gillespieae* this was only speculative. *Balbaroo nalima* is the second balbarid of which post-cranial material is available and is essential in providing a better insight into the eco-morphology of these ancient Oligo - Miocene kangaroos. The post-cranial material associated with *B. nalima* is described here and a comparative and plausible functional morphology is implemented. Since, *N. gillespieae* is the only other balbarid of which post-cranial fossil material is available, *B. nalima*'s post-cranial material shall be principally compared to *N. gillespieae*.



**Figure 5.** Post-cranial fossil elements associated with *Balbaroo nali-ma*. **A.** Cervical vertebra in anterior view (QMF41234), **B.** Thoracic vertebra in anterior view (QMF41234), **C.** Lumbar vertebra in posterior view (QMF41234), **D, E.** Caudal vertebrae in anterior view (QMF41234), **F.** Mid-series caudal vertebra in dorsal view (QMF41234), **G.** Sacral fragment in dorsal view (QMF41234), **H.** Proximal ulna fragment in medial view (QMF52809), **I, J.** Adult Femur in anterior and posterior view (QMF50468), **K, L.** Juvenile femur in posterior and anterior view (QMF41270), **M, N.** Fibula in posterior and anterior view (AR18476), **O, P.** Calcaneum in dorsal and ventral view (QMF41234). Scale bar is equal to 20 mm.

## Description and Functional Eco-Morphological Interpretation of *Balbaroo nalima*'s Post-Cranial Material

**Cervical vertebrae** - One almost complete cervical vertebrae (Fig. 5A), lacking the neural spine and one fragmented post-zygapophyses. The neural arch has a triangular-like contour, and the centrum is large bearing an opisthocoelous form. The neural canal is exceptionally large. The pre-zygapophyses are enlarged, distal-horizontally inclined and have a semi-rectangular-like outline. The post-zygapophyses extends out slightly further than the pre-zygapophyses, being well developed and prominent. The post-zygapophyses extend out distally along the proximal part and then orient proximally towards the distal region. The cervical vertebrae associated with *Nambaroo gillespieae* also bear an oblong-like shaped neural arch, large neural canal and a playcoelous centrum (Kear et al. 2007). However, *N.gillespieae*'s cervical vertebra is dorso-ventrally wider and the neural arch is smaller in comparison to *B. nalima*. Both balbarids have ovoid-like pre and post-zygapophyses, though the pre-zygapophyses are larger in *B. nalima*, and the post-zygapophyses are more elongated in *N. gillespieae*.

A significantly large neural canal on *B. nalima*'s cervical vertebra proposes a large insertion area for the ep-axial and nuchal ligament muscles. These muscles assist the animal with increased flexion in the neck region (Finch and Freedman 1988, Kear et al. 2007). However, the enlarged pre-zygapophyses resemble modern macropodids that frequently utilize bipedal saltation. Yet, the post-zygapophyses are relatively reduced in bipedal hopping extant taxa, while this condition in *B. nalima* is strongly developed, similar to *Hypsiprymnodon moschatus* (Johnson and Strahan 1982) and members of *Dendrolagus* (Flannery and Szalay 1982, Prideaux and Warburton 2008, Prideaux and Warburton 2010).

**Thoracic vertebrae** - Three complete thoracic vertebrae (QMF41234) (only one depicted in Fig. 5B), lacking the parapophyses characteristic. The neural canal has a gracile outline and is projected inwards. The centrum is dorso-ventrally elongated and bears a slightly opisthocoelous morphology and medially and ventrally a tubular nature. The pre-zygapophyses are enlarged, lobed and distally and posteriorly oriented. This feature on the pre-zygapophyses is observed in all consecutive vertebrae. The post-zygapophyses are considerably reduced in comparison to the pre-zygapophyses. However, they too are of a lobated nature and are horizontally displaced. The thoracic vertebrae of

*N. gillespieae* has a similar morphology to *B. nalima*'s thoracic vertebrae, with a dorso-ventrally elongated and cylindrically shaped centrum that has a partially opisthocoelus surface when observed medially or laterally, and enlarged and lobated pre and post-zygapophyses. Yet, the post-zygapophyses of *N. gillespieae*'s thoracic vertebrae decreases in size in successive vertebrae, while in *B. nalima* the post-zygapophysis appears to remain of relatively equal size in succeeding vertebrae. Elongation and the outwardly sloping of the pre-zygapophyses on both balbarids might be an indication for restriction of movement within the vertebral column (in particular within the thoracic area) (Christian and Preuchoft 1996, Kear et al. 2007).

**Lumbar vertebrae** - One complete lumbar vertebra (QMF41234) (Fig. 5C) depicting an opisthocoelous centrum, semi-circular shaped neural canals and reduced anapophyses. The transverse processes are obliquely displaced, relatively compressed and are blade-like. The post-zygapophyses are strongly developed (being larger than the pre-zygapophyses) and are distally and diagonally located. The pre-zygapophyses have a lobated morphology and are laterally oriented. *N. gillespieae*'s lumbar vertebrae's centrum has an opisthocoelous morphology and has a relatively rounded profile when viewed in the ventral aspect. This feature is larger and has a distally triangular-like profile in *B. nalima*'s lumbar vertebrae. Furthermore, the neural canal has a semi-circular outline in each balbarid although it is less compressed in *B. nalima* than in *N. gillespieae*. The transverse processes are largely broken off in *B. nalima* however, appear to have been oriented in a similar manner to *N. gillespieae*, although in *N. gillespieae* the transverse processes are more ventrally-medially displaced and face downwards, while in *B. nalima* the transverse processes are directed in a more upwards manner. In both *B. nalima* and in *N. gillespieae* the anapophyses are considerably abated, although these features appear to have been more developed in *B. nalima* than in *N. gillespieae*. The pre- and post-zygapophyses are lobated, obliquely oriented and well developed in both balbarids, although the pre-zygapophyses are larger and end in a sharp point in *B. nalima*, and the post-zygapophyses are more elongated in *N. gillespieae*. The reduction of the transverse processes in *B. nalima* is similar to *Sthenurus* spp., which were walking ice-age giants (Janis et al. 2014), which might suggest limited flexibility within the lumbar region.

**Caudal vertebrae** - Two unfragmented caudal vertebrae (QMF41234) (Fig. 5D-E) and an intact but considerably worn away mid-series caudal vertebra (QMF41234) (Fig. 5F). Center in each caudal vertebra is ovoid in cross-section and dorso-ventrally compacted. The central canal is semi-circular in shape. The transverse processes are horizontally conformed and considerably elongated. The pre-zygapophyses and post-zygapophyses are strongly developed, narrow, slender and blade-like. The pre-zygapophyses are laterally and medially oriented and the post-zygapophyses are anteriorly adjusted. The caudal vertebrae belonging to *N. gillespieae* has (similar to *B. nalima*), an ovoid and compressed centrum in cross-section. The neural canal in *N. gillespieae* appears to be reduced and somewhat enclosed, and in *B. nalima* the neural canal is larger. Although, the caudal vertebrae in both specimens suggests a semi-circular outline of the neural canal.

The dorso-ventrally compressed condition of the center in both *B. nalima* and *N. gillespieae* caudal vertebrae, may propose improved dorso-ventral agility within this region, which might further suggest the employment of a combination of quadrupedal and pentapedal habits (Kear et al. 2007), a feature also seen in *Dorcopsis* spp. and *Dendrolagus* spp. (Flannery and Szalay 1982).

The mid-series caudal vertebra has a dorso-ventrally compressed centrum and considerably waisting occurring in the mid-section. The transverse processes are well developed and are of an oblong profile. Mid-section waisting and strongly developed ovoid-like transverse processes is also observed in *N. gillespieae*'s mid-series caudal vertebra. However, the mid-section of *N. gillespieae*'s mid series caudal vertebra is distinctly more waisted than the mid-series caudal vertebra belonging to *B. nalima*. The compressed mid-section may suggest for some dorso-ventral flexion in the tail (Flannery and Szalay 1982, Kear et al. 2007).

**Sacral Fragment** - One almost complete, transversely wide sacral element (QMF41234) lacking the coccyx (Fig. 5G). Extremely large sacral foramina, with restricted but wide transverse processes. The superior articular surfaces are strongly developed and point out ventrally in a slanting manner. The sacral canal is extremely large and well developed. The sacral tuberosities are distally sharp and protrude out along the medial and lateral sides and towards the proximal end of the sacrum. The sacrum remnant associated with *N. gillespieae* is largely fragmented, although still reveals a similar morphology to the

sacrum belonging to *B. nalima*; such as the strong developed, enlarged and upward facing sacral tuberosities, large sacral foramina, and well developed superior articular facets. The robust and wide morphology of *B. nalima*'s sacral component is very different to the sacral condition in modern-day saltating kangaroos, where the sacral is more of a gracile nature (Janis. et al. 2014). This might suggest improved mobility between *B. nalima*'s pelvis and sacral regions.

**Ulna** - One proximal right ulna fragment (QMF52809) (Fig 5H), with a shaft depicting a straight-ventral edge and lacking the supraspinatus fossa. The coronoid process and the radial notch are distinct and well developed. The olecranon process is dorso-ventrally shallow and is poorly developed. The semilunar notch is dorsally bilobed and enlarged. The proximal ulna fragment of *N. gillespieae* has a reduced and abate supraspinatus facet, and in *B. nalima* this feature appears to have been either significantly more reduced or completely absent. The shafts of the ulnas reveal a straight, ventral-edge morphology in both *B. nalima* and *N. gillespieae*. Both *N. gillespieae* and *B. nalima* bear a dorso-ventrally shallow olecranon facet, although the olecranon facet has a rounder and smoother nature in *B. nalima* than in *N. gillespieae*. Furthermore, on the ulnas of both balbarid species there is a narrow, shallow, dorsally oriented coronoid process. These features (shallow olecranon process, narrow coronoid process, a laterally oriented radial notch) are commonly seen in the tree-kangaroos (*Dendrolagus, Bohra*) (Warburton et al 2011), which suggests some degree of flexibility in the elbow region. This may further suggest that *B. nalima* was more prone to quadrupedal bounding (and perhaps some arboreal behaviors) than to fast bipedal saltation. However, the relatively shallow olecranon facet in *B. nalima* would suggest a reduced attachment region for the M. anconeus and M. triceps brachii muscles, which are muscles that assist the bending in the animal's ulna during quadrupedal movements (Kear et al. 2001a). This feature on *B. nalima*'s ulna would therefore suggest some limited bending mobility in the elbow region. Nevertheless, the ulna of *B. nalima* is large and strongly developed in comparison to the other available post-cranial material, which does propose a higher probability of a habitual quadrupedal posture. In extant macropodiforms that predominantly adopt a bipedal form of locomotion (such as *Macropus* spp.), the ulna (and other fore-limb elements) are small and reduced in comparison to the hind-limb elements, facilitating a faster bipedal locomotion type.

**Femur** - One almost complete left femur (QMF50468) (Fig. 4I-J) and one largely intact juvenile femur (QMF41270) (Fig. 5K-L), in each the femoral heads are absent. A relatively semi-deep attachment area for the *M. quadratus femoris* muscles is present in both adult and juvenile femoral shafts, in combination with a well-developed and obliquely oriented spherical-like midline boss. The patellar groove is deep and strongly developed. The trochanteric neck is relatively constricted, and the greater and lesser trochanter elements are enlarged and well developed. On *N. gillespieae*'s femoral shaft the mid-line boss is strongly developed, similar to *B. nalima*. However, in *B. nalima* the mid-line boss is significantly raised. A relatively large attachment area for the *M. quadratus femoris* muscles seems to be present on the femurs of both balbarid species, although this feature is larger in *B. nalima*. A deep patellar groove, a dorso-ventrally reduced trochanteric neck, and the raised lesser and greater trochanter facets are present on the femurs of both *B. nalima* and *N. gillespieae*. An averaged sized antero-posteriorly displaced distal epiphysis is also a feature that is present on both femurs of the two balbarids. A reduced distal epiphysis is common amongst extant kangaroos that largely bipedal hop, as this increases stability in the hind limbs during hopping (Kear et al. 2007), and in extant tree-kangaroos the distal epiphysis is large and broad, increasing the rotational ability in the knee region which is advantageous during climbing. Therefore, the medium size of the distal epiphysis on *B. nalima*'s femur may be suggestive of neither climbing nor saltation, but perhaps quadrupedal bounding. Furthermore, the strongly developed mid-line boss along the femoral shafts in both balbarids, suggesting an enlarged attachment area for the *M. quadratus femoris* muscles, is a condition also seen in the quadrupedal *Hypsiprymnodon moschatus* (Johnson and Strahan, 1982), possibly suggesting a similar locomotion type. Although, this feature in *B. nalima* is also significantly raised, which is a condition also seen in saltating macropodiforms (Wells and Tedford 1995). This might suggest that *B. nalima* may have been capable of limited bipedal hopping, and that *N. gillespieae* may have been more adapted to quadrupedal bounding than *B. nalima*.

**Fibula** - A single proximal fibula fragment (AR18476) lacking the distal epiphysis (Fig 5M-N). The fibula head is oblong-like, and the proximal epiphyses bears a broad posteriorly displaced tibial facet. The medial malleolus fossa is wide, concave and is anteriorly-posteriorly oriented. Distally the fibula flattens out laterally and shifts

into gradual increased posterior broadening. In cross section, the shaft is distally D-shaped. The shaft itself is slender and flattened in cross-section with thickening occurring near the proximal end, somewhat depicting a convex-concave outline. A distinct and deep groove runs along the shaft suggesting a large attachment area for the *M. fibularis longus et brevis* muscle. In cross-section the fibula of *N. gillespieae* has a D-shaped contour, similar to *B. nalima*. The fibular shafts in both balbarids are transversely flattened and are proximally wide and oblong-like. A broad proximal tibial facet on the fibula is also seen in members of *Dendrolagus* (tree-kangaroos) as this would permit non-restrictive motion between the tibia and the fibula (Bishop 1997, Kear et al. 2001a). If the tibial facet were gracile and elongated, this would be indicative of restricted mobility between the tibia and the fibula elements, which is characteristic of extant kangaroos that predominantly utilize a bipedal form of locomotion.

**Calcaneum** - One left calcaneum (QMF41234) (Fig. 5O-P). The calcaneum lacks its epiphysis, which exemplifies that the individual had not reached adulthood. The tuber calcanei is short, robust and non-sinuuous. The calcaneum-cuboid facet is significantly stepped, and the sustentaculum tali is semi triangular-like, enlarged and posteriorly conformed. The astragalus-calcaneum and talar facet are distinctly divided and both are strongly developed. The calcaneum of *N. gillespieae* is elongated, expands posteriorly and is dorso-ventrally narrow, whilst in *B. nalima* the calcaneum is broader and more robust. The tuber calcanei in both balbarid's calcaneums have a rather slanting appearance, being slightly more prominent in *N. gillespieae*. A similar sustentaculum tali in both *N. gillespieae* and *B. nalima* is present depicting a horizontally displaced, oblong-like morphology. In addition, in both balbarids the calcaneums reveal a markedly ascended and medially protruding talar facet. However, the astragalus-calcaneum facet is separated in *B. nalima*, in contrast to *N. gillespieae*. Furthermore, the plantar rugosity in *N. gillespieae* is elongated with a shallow plantar sulcus. The plantar rugosity in *B. nalima* is more compact and flattened, and the plantar sulcus on *B. nalima*'s calcaneum is even more reduced than the plantar sulcus in *N. gillespieae*. Furthermore, the dorso-lateral facet in *B. nalima* is dorso-ventrally oriented while in *N. gillespieae* the dorso-lateral facet is obliquely oriented. The cuboid-calcaneum facet is of a shallower and smoother nature in *N. gillespieae* than in *B. nalima*, where this feature is slightly deeper and more robust.

The robust and shortened calcaneum condition and the stout-like calcanei are traits commonly observed in the calcanea belonging to extant tree-kangaroos (*Dendrolagus*) and rock-wallabies (*Petrogale*). As these characteristics in the calcaneum are reminiscent of a broad foot, and a broad foot is beneficial when needing to maneuver over unequal sub-terrains and/or when required to uphold a balance while standing on branches (Prideaux and Warburton 2010). A more slender and elongated calcanei on the calcaneum is a condition common amongst *Macropus* spp. that regularly bipedal bound, as this feature would indicate an elongated pes that allows for enhanced stability during saltation (Kear et al. 2007). Therefore, the calcaneum morphology of *B. nalima* may indicate at movements through dense, uneven substrates, and possibly the frequent need to move through low-hanging or fallen branches. However, the deeply stepped calcaneum-cuboid articulation condition in *B. nalima*, may have be indicative of some restricted movements between the calcaneum and the cuboid elements, a characteristic favorable for bipedal saltation (Bishop 1997). Nevertheless, the transversely broad sustentaculum tali in *B. nalima*'s calcaneum, is also another feature that is commonly observed on the calcanea of tree-kangaroos, which is a trait that allows for some flexibility between the pes.

## Conclusion

The post-cranial bones of *B. nalima* resemble *N. gillespieae* post-cranial remains to a large degree, with often only slight differences. This might suggest a similar functional morphology and lifestyle akin to *N. gillespieae* for *B. nalima*. Kear et al. (2007) suggested that the post-cranial material associated with *N. gillespieae* closely resembled the skeleton of the extant *Hypsiprymnodon moschatus* (which is the only modern macropodiform that cannot bipedal hop, but can only quadrupedal bound), and proposed a likely similar locomotion type of *N. gillespieae* to *H. moschatus*. Therefore, provided that the post-cranial material associated to *B. nalima* bears a resemblance to *N. gillespieae*'s post-cranial remains, a similar probable gait may perhaps also be suggested for *B. nalima*. Although, the deeply stepped calcaneum-cuboid facet on the calcaneum, a short antero-posteriorly distal epiphysis on the femur, and the pre-zygapophyses condition on the thoracic vertebrae in *B. nalima* are all features seen in macropodiforms that have adapted to utilizing bipedal hopping as a main form of locomotion. However, despite these various bipedal

adapted features, various structures of *B. nalima*'s post-cranial material resemble characteristics also seen in the extant tree-kangaroos. These features include; the comparatively large and strongly developed ulna, the short and robust condition of the tuber calcanei and the broad sustentaculum tali on the calcaneum, and the fibula's wide tibial facet. All these traits may imply a consistent utilization of quadrupedal movements and possibly some arboreal capabilities. Furthermore, modern kangaroos and rat-kangaroos (except for the strictly quadrupedal musky rat-kangaroo *Hypsiprymnodon moschatus*) utilize various different forms of locomotion, from bipedal progression when needing to reach high speeds, to quadrupedal and pentapedal locomotion habits (use of the tail as a fifth limb for stability) when foraging and browsing, to even climbing (scansorial habits only observed in the tree-kangaroos) (Bennett 1999, Bennet 2000, Warburton et al. 2011). When examining the post-cranial material belonging to *B. nalima* and *N. gillespieae* it appears that the combination of various quadrupedal, some limited arboreal, and some selective bipedal traits may indicate that the balbarids may also have been capable of adopting various different locomotion strategies, which may further imply that considerable disparity in locomotion types was present in the Oligo-Miocene balbarid kangaroos.



**Figure 6.** Reconstruction of the Miocene balbarid kangaroo – *Balbaroo nalima*.

## PAPER II

### Phylogenetic and Morphometric Assessment of the Late Oligocene Rat-Kangaroo *Palaeopotorous* *priscus*

A number of Late Oligocene peculiar dental remains (Fig. 7) were uncovered from the Tarkarooloo local fauna (Namba Formation (see **Paper V** for description of fossil locality)) in South Australia (Fig. 1) (See **Paper II**). The teeth had first been described by Flannery and Rich (1986), suggesting close affiliation to potoroids due to the presence of the potoroid uniting feature - an antero-posterioly oriented metaconid-protocristid crest. However, the direct placement with macropodiforms was uncertain due to the presence of an elongated and antero-posteriorly displaced protoconid-metaconid crest (a feature common in all species of possums (Phalangeridae)). However, other features common to possums such as joining of the anterior crest to the paracristid - protocristid cusps, presence of a buccal convexity, and the equal height of the talonid and the trigonid were lacking in the dentigenous remains. Consequently, Flannery and Rich (1986) established a monotypic subfamily Palaeopotorinae placing the dental elements into it and diagnosed the teeth as belonging to *Palaeopotorous priscus* (Fig. 8) Flannery and Rich (1986) further suggested that due to the primitive nature of the dental remains, *P. priscus* might have been the base to the macropodiform radiation. In later years, Cooke (1997) highlighted the following features in *Palaeopotorous priscus* dentition; the presence of a fore-link paraconule (this feature Flannery and Rich (1986), suggested was a metaconule), another stylar cup on the stylar cusp C, and the presence of a post-link on the molars. Because of these features, Cooke (1997) suggested that *Palaeopotorous priscus* may have been affiliated with the Oligo - Miocene paraphyletic stem group Bulungamayinae instead of with the early potoroids. However, whether *P. priscus* may have been the base

to the macropodiform radiation, or associated with either the Bulungamayinae or early potoroids has never been investigated. For this reason, a geometric morphometric (2D landmark based Principal Component Analysis) in order to visualize morphological consistency and a phylogenetic analysis (utilizing backbone constraints) from published Oligocene – Miocene macropodiform morphological character matrices (Kear and Pledge 2008, Butler et al. 2016, Meredith et al. 2008, Philips et al. 2013), were employed to determine the placement of *Palaeopotorous priscus* within the macropodiforms.



**Figure 7.** Lower first molar (m1) holotype of *Palaeopotorous priscus* (SAMP24243) SAM abbreviation = South Australian Museum, Adelaide, Australia. Scale bar = 20mm.

## Material and Methods

**Geometric Morphometrics** - The morphological similarity of *P. priscus* to other macropodiforms was determined using a Principal Component Analysis (PCA) using 2D digital non-homologous landmarks. Photographs (some images were from published papers (See **Paper II** Supplementary Data)) of 40 extinct, 41 modern macropodiforms specimens and two species of extant phalangerids (See **Paper II**, Supplementary Table 1 for the list of specimens) were taken in the dorsal (occlusal) aspect of the lower first molars (m1). The holotype SAMP24243 of *P. priscus* was utilized for the PCA analysis (Fig. 6). The landmarks were placed and digitized in tpsDIG (v2.16) (Rolf 2010), and the PCA was run in R-Studio (v.3.2.2) utilizing the

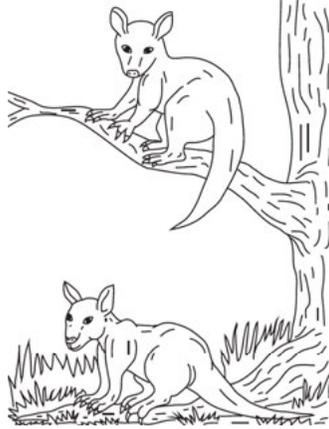
‘MASS’ (7.3-45) and ‘geomorph’ (3.03) packages (Venables and Ripley 2002, Adams et al. 2015, R Development Core Team 2015). In tpsDIG, a total of 6 landmarks were utilized of which one landmark was placed on each lophid (metaconid, protoconid, entoconid and hypoconid), one landmark was placed on the anterior termination of the paracristid and one landmark was placed on the termination of the lingual cristid oblique (Fig. 9). The four landmarks that were placed on each of the molar lophids were undertaken in order to differentiate between bunodont, lophodont and bunolophodont dental morphology. The landmark placed on the lingual cristid oblique, were used to distinguish whether this feature terminates on the lingual or buccal side of the molar. The landmark placed on the paracristid was used to discriminate between specimens that exhibited either a strongly or poorly developed paracristid.

**Phylogenetic Analysis** - A parsimony/Bayesian analyses was utilized to determine the placement of *P. priscus* to other macropodiforms. The dataset employed was taken from Butler et al. (2016), as this dataset is currently the most inclusive. The dataset was then expanded by including the matrices from Kear and Pledge (2008) and from Prideaux and Warburton (2010). Any missing data in the dataset was accommodated for by priori screening using TAXEQ3 (Wilkinson 2001) to allow for the taxonomic reduction (due to missing entries from lack of fossil materials) to be conducted safely (Wilkinson 1995).

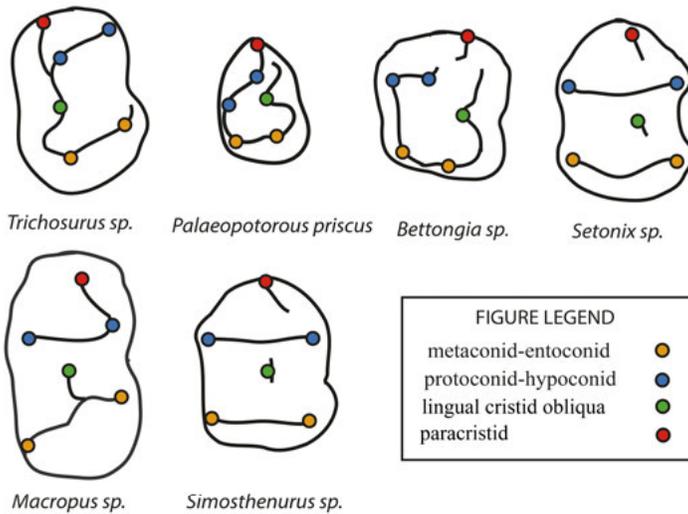
## Results and Conclusion

**Geometric Morphometrics** - 87% of the variance was explained in the first two principal component axes (PC1: 82%, PC2: 22,5%) (Fig. 10). The first principal component explains the variation in the metaconid-protoconid crest and the second axis describes the variation in the shape of the molars. The results showed clear separation between the bunolophodont/lophodont and the bilophodont macropodiforms. Furthermore, the phalangerid (*Trichosurus*) are distinctly segregated from both the extant and extinct macropodiform specimens. *P. priscus* loaded within the bunolophodont/lophodont morpho-space, plotted closest to extant and fossil potoroids (such as *Wakiewakie lawsoni* and *Gumardee pascuali*). These results suggest that the m1 of *P.*

*priscus* is possibly closer in morphology to members of the Potoroidae than to Phalangeridae.

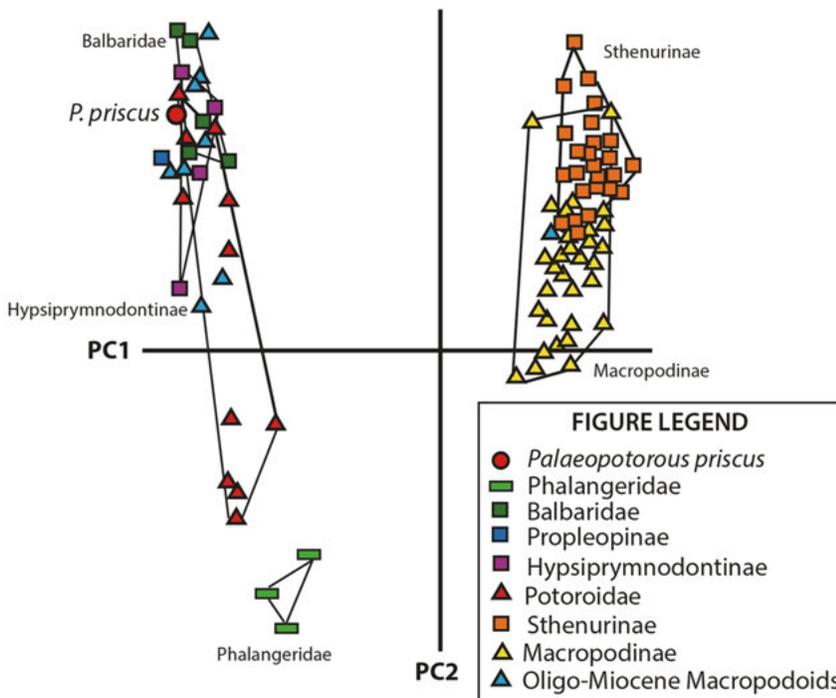


**Figure 8.** Reconstruction of the Late Oligocene rat-kangaroo *Palaeopotorous priscus*.

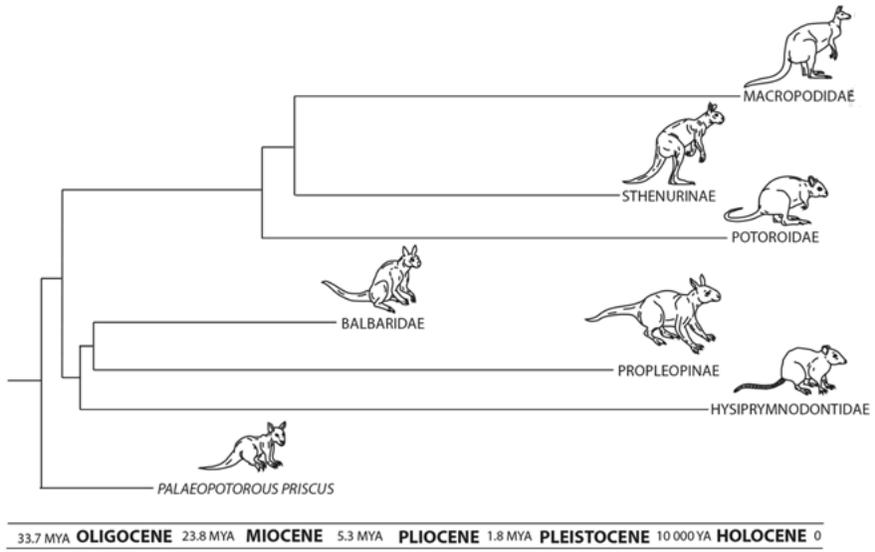


**Figure 9.** Placement of the non-homologous landmarks on the lower first molars in occlusal view.

**Phylogenetic Analysis** - The phylogenetic results suggested that *P. priscus* is an exceptionally pleisiomorphic macropodiform and clearly falls outside of the crown Macropodidea. Furthermore, the results also suggested a likely sister-relationship of *P. priscus* to all other macropodiforms (Fig. 11). The sister-taxon placement of *P. priscus* to other macropodiform clades would also suggest that *P. priscus* is currently the oldest described stem macropodiform and may potentially represent an early transitional stage from a possum-like being to the onset of displaying more rat-kangaroo-like features.



**Figure 10.** Principal Component Analysis (PCA) results to determine morphological similarity of *Palaeopotorous priscus* to other Macropodiforms.



**Figure 11.** Phylogenetic placement results of the fossil rat-kangaroo *Palaeopotorous priscus* amongst the Macropodiforms.

## PAPER III

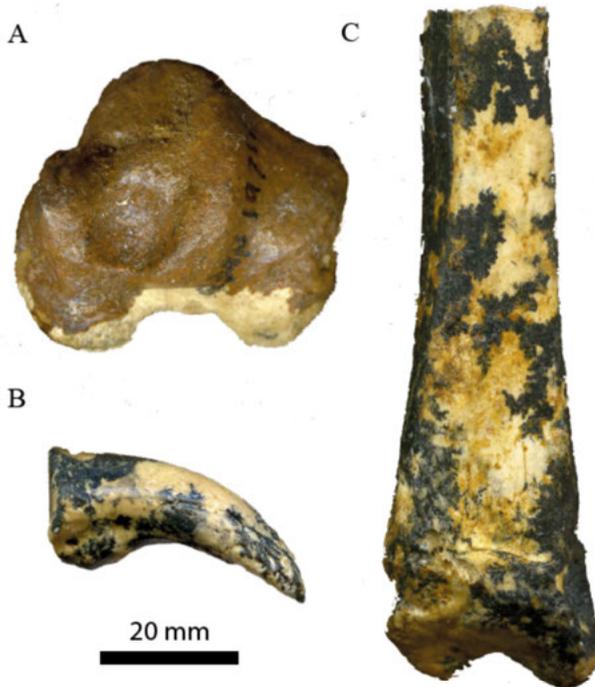
### Arboreal Features Revealed in Miocene Balbarid Kangaroo Post-Cranial Fossil Elements

Isolated fossil post-cranial material constituting of one complete astragalus (QMF19717) (Fig. 12A), one fragmented astragalus (QMF19718) (not depicted here), a pedal phalange (QMF19719) (Fig. 12B) and a fragmented distal fibula (QMF19719) (Fig. 12C) (See **Paper III**) were uncovered from Miocene freshwater and limestone deposits at the Riversleigh World Heritage Area (Fig. 1) (See **Paper V** for description of the Riversleigh Fossil Site). These post-cranial remains are associated with the Balbaridae due to the presence of the synapomorphic character state; an antero-posteriorly displaced, successive and considerably thickened malleolar fossa border on the astragalus. The bones reveal intriguing traits that may suggest a probable habitual arboreal lifestyle. These features include; reduced lateral trochlear crest, enlarged medial trochlear crest an obliquely oriented, strongly developed navicular facet on the astragalus as well as a transversely wide astragalus. Furthermore, the large (in comparison to the other available post-cranial elements), D-shaped (when viewed in cross-section), tapering and downwards curvature of the pedal claw is another suggestive characteristic that could possibly indicate climbing abilities. In addition, the distal fibula fragment reveals a short tibia-fibula contact, implying high mobility (in combination with the astragalus traits highlighted above) in the ankle region of this balbarid specimen.

The discovery of these fossil bones suggests that an arboreal way of life may have already been present in Oligocene macropodiforms, and that climbing re-emerged again in the tree-kangaroos (*Bohra*) during the Pliocene - Pleistocene. The tree-kangaroos are not direct descendant to the Oligocene - Miocene Balbaridae as they clearly reveal features within the pes that indicate at having adjusted from a bipedal-like nature to a more arboreal lifestyle (Bishop 1997). Hence, these balbarid remains may indicate that climbing may have evolved twice within the macropodiforms. Furthermore,

these bones may also indicate at a lot of disparity in balbarid locomotion abilities as well as niche occupation.

To test the functional similarity and probable gait utilization of these peculiar balbarid fossil bones, a 2D morphometric approach (Principal Component Analyses (PCA)) and Canonical Variate Analyses (CVA)) were employed. In addition, an array of modern macropodiform taxa was included into the analyses, to obtain a diverse assortment of locomotion strategies. Only utilization of the non-fragmented astragalus and the claw were undertaken, as only these elements were complete. Furthermore, the only other balbarid specimen of which an astragalus and pedal digit are available belongs to the Late Oligocene *Nambaroo gillespieae* (Kear et al. 2007). Hence, *N. gillespieae* was included into the analyses and utilized as a comparator to the balbarid fossil remains.



**Figure 12.** Balbarid post-cranial fossil remains from Riversleigh World Heritage Area, northwestern Queensland, Australia. **A.** Complete astragalus in dorsal view (QMF19717), **B.** Distal phalange in medial view, **C.** Distal fibula in ventral view.

## Description and Functional Interpretation of the Balbarid Fossil Elements

**Fibula** - One distal fibula element, fragmented proximally (QMF19719) (Fig. 12C). The fibula has a notably reduced fibula-tibia contact, which might suggest high mobility within the ankle and foot region. The reduction of the contact between the fibula and tibia is also observed in the Oligocene balbarid *N. gillespieae* (Kear et al. 2007), in extinct (*Bohra*) and extant (*Dendrolagus*) tree-kangaroos (Flannery and Szalay 1982). A deep groove runs along the lateral malleolus suggestive of a deep insertion area for the peroneal muscle. When viewed anterior-laterally the distal fibula has a broad and relatively deep attachment area for the flexor digitorum profundus muscles. The shaft of the fibula is ovate in cross-section, the tibial facet on the distal epiphysis and the lateral malleolus are poorly developed, which are also features seen in *Dendrolagus* species (Prideaux and Warburton 2008, Prideaux and Warburton 2010). These characteristics are all indicative of increased rotational movement in the lower hind-limb region, which would further suggest the aptitude for arboreal habits.

**Astragali** - Two right astragali (QMF19717, QMF19718), of which one is largely fragmented, the other complete (Fig. 12A (only complete astragalus depicted)). The astragali are transversely wide with an elongated, elevated, and strongly developed medial trochlear fossa, and a significantly reduced lateral trochlear crest are observed. The medial trochlear crest orientates laterally and is continuous into a broad astragalus-calcaneum facet. The trochlear sulcus is shallow and transversely narrow. The navicular facet has a condyle morphology, is particularly large, is diagonally displaced and extends out antero-posteriorly.

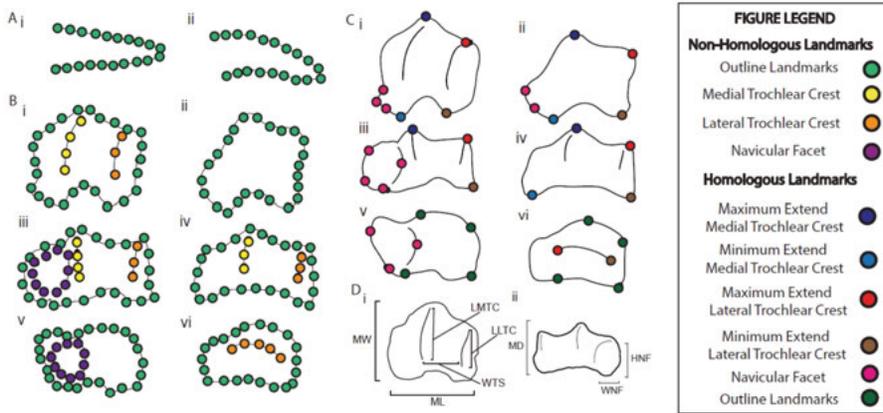
The poorly developed lateral trochlear crest and an enlarged medial trochlear crest is also observed in the exclusively quadrupedal bounding extant musky rat-kangaroo (*Hypsiprymnodon moschatus*), in *N. gillespieae* (Kear et al. 2007), in modern-day phalangerids (such as *Trichosurus vulpecula* – the common brush-tail possum), and tree-kangaroos (*Dendrolagus*) (Flannery 1982). Furthermore, the condition of the navicular facet is also commonly seen in species belonging to *Dendrolagus*, *H. moschatus*, and phalangerids. The combination of these traits may suggest an increase in lateral mobility between the ankle and the foot (Kear et al. 2001a, Kear et al. 2007), and a high degree of elasticity in the metatarsals (Kear et al. 2001b).

**Pedal Phalange** - One intact distal pedal phalange (QMF19719) (Fig. 12B). The pedal claw when viewed dorsally is proximally wide and increases in tapering distally. Medially and laterally the claw's morphology is D-shaped and curves downwards. In comparison to the available astragali and the distal fibula fragment, the claw is relatively large. A large, D-shaped and highly curved claw is seen in tree-kangaroos, phalangerids and rock-wallabies (*Petrogale*), as this condition would allow the animal to grip and hold onto branches and uneven terrains (Kear et al. 2001, Prideaux and Warburton 2008, Prideaux and Warburton 2010).

## Material and Methods

Two types of 2D geometric morphometrics was utilized; homologous and non-homologous (outline) landmarks, on the pedal phalange and the astragalus of the balbarid remains and compared to a series of modern macropodiform taxa (See **Paper III**, Table 2 and 4 for list of specimens utilized) to determine the bio-mechanical similarity and probable locomotory habit. The specimens were placed into three locomotory bins; frequent bipedal hoppers (facultative quadrupeds), quadrupedal, and largely arboreal (facultative quadrupeds and bipeds). In total, 28 extant species were used, of which 6 were placed into the arboreal group, 21 species were placed into the bipedal saltating assembly, and only 1 species had been placed into the quadrupedal bin - the extant musky rat-kangaroo (*Hypsiprymnodon moschatus*) (See **Paper III** – supplementary material Table 2 and 3 for the specimen utilized and the different locomotory grouping). In addition to this, *Nambaroo gillespieae* (Kear et al. 2007) was utilized as a fossil comparator in the analyses as it is the only other balbarid of which an astragalus and pedal claw is available.

The assortment of pedal claws and the claws associated with the balbarid remains and *Nambaroo gillespieae* were captured and outlined in the dorsal and lateral aspects. The dorsal aspect of each claw was obtained to capture the tapering nature of each claw. The lateral aspects of the claw were digitized to obtain the D-shaped and curved morphologies of each of the claws (Fig. 13A). These particular characters were selected due to these traits being largely commonly seen in climbing and quadrupedal bounding macropodiform taxa. Only an outline (non-homologous analysis was obtained on the pedal phalange as the main interest was to obtain the outlines of the claws in order to capture various levels of curvature. The claw's outlines in dorsal and lateral view were obtained in tpsDIG (Version 2.17)



**Figure 13.** Placement of the landmarks on the pedal phalange and the astragali for the Principal Component Analysis (PCA) In addition, the traits measured on the astragali for the linear measurement analysis. **Ai.** Placement of the non-homologous landmarks along the dorsal aspect of the pedal claws, **Aii.** Placement of the non-homologous landmarks along the lateral aspect of the pedal claws, **Bi.** Placement of the non-homologous landmarks along the dorsal aspect of the astragali, **Bii.** Placement of the non-homologous landmarks along the ventral aspect of the astragali, **Biii.** Placement of the non-homologous landmarks along the lateral aspect of the astragali, **Biv.** Placement of the non-homologous landmarks along the medial aspect of the astragali, **Bv.** Placement of the non-homologous landmarks along the anterior aspect of the astragali, **Bvi.** Placement of the non-homologous landmarks along the posterior aspect of the astragali, **Ci.** Placement of the homologous landmarks along the dorsal aspect of the astragali, **Cii.** Placement of the homologous landmarks along the ventral aspect of the astragali, **Ciii.** Placement of the homologous landmarks along the lateral aspect of the astragali, **Civ.** Placement of the homologous landmarks along the medial aspect of the astragali, **Cv.** Placement of the homologous landmarks along the anterior aspect of the astragali, **Cvi.** Placement of the homologous landmarks along the posterior aspect of the astragali, **Di.** measurements taken of the astragali in dorsal view, **Dii.** measurements taken of the astragali in lateral view. MW=Maximum Width, ML=Maximum Length, MD=Maximum Depth, LMTC=Length Medial Trochlanter Crest, LLTC=Length Lateral Trochlanter Crest, WTS=Width Trochlanter Sulcus, WNF=Width Navicular Facet, HNF=Height Navicular Facet.

and utilizing the pencil tool, 20 evenly spaced landmarks were placed around each claw. Then the tpsDIG files were converted to a 'tpsXY outline to landmarks' file in tpsUTIL (Version 1.54). The files were then run as a Principal Component Analysis (PCA) in R-Studio (Version 1.0.136), using the 'MASS' (7.3-45) and 'geomorph' (3.03) packages (Venables and Ripley 2002, Adams et al. 2015, R Development Core Team 2015).

Different assortments of species were utilized for the astragali analyses, due to not having either a pedal phalange or an astragalus available for each specimen (See **Paper III**, Table 2 and 4 for list of specimens). The same (non-homologous) landmark outline approach was used for the astragali as was done for the pedal claws. Only, instead of 20 landmarks, 25 equally spaced landmarks were used to obtain the shape of the astragali in the dorsal, ventral, medial, lateral, posterior and anterior aspects (Fig. 13B). In addition to the outline of each side of the astragali, in dorsal, lateral, and medial view, 3 landmarks were placed on the medial trochlear fossa and 3 were placed on the lateral medial trochlear fossa. No extra features were outlined on the astragali in ventral view, as no required features were present in this aspect. In lateral and anterior view 10 landmarks were used to portray the position and size of the navicular facet. In the posterior aspect of each astragalus 5 landmarks were used to digitize the outline of the lateral trochlear crest (Fig. 13B, **Paper III** Table 3). These features were highlighted due to these contrasting considerably in the largely arboreal (*Dendrolagus*) and largely bipedal (such as *Macropus*) species.

In addition to the outline analysis of the landmarks, the use of homologous landmarks were utilized on the astragali as well. Whereby, 7 landmarks were placed on the dorsal, anterior, and lateral aspect of the astragali, 6 on the ventral and posterior aspect of each astragalus, and 4 landmarks on the medial aspect of the various astragali (Fig. 13C). Each tpsDIG file of each aspect of the astragali, both non-homologous and homologous landmark approaches were converted to a tpsXY file in tpsUtil and were run as a PCA in R-Studio.

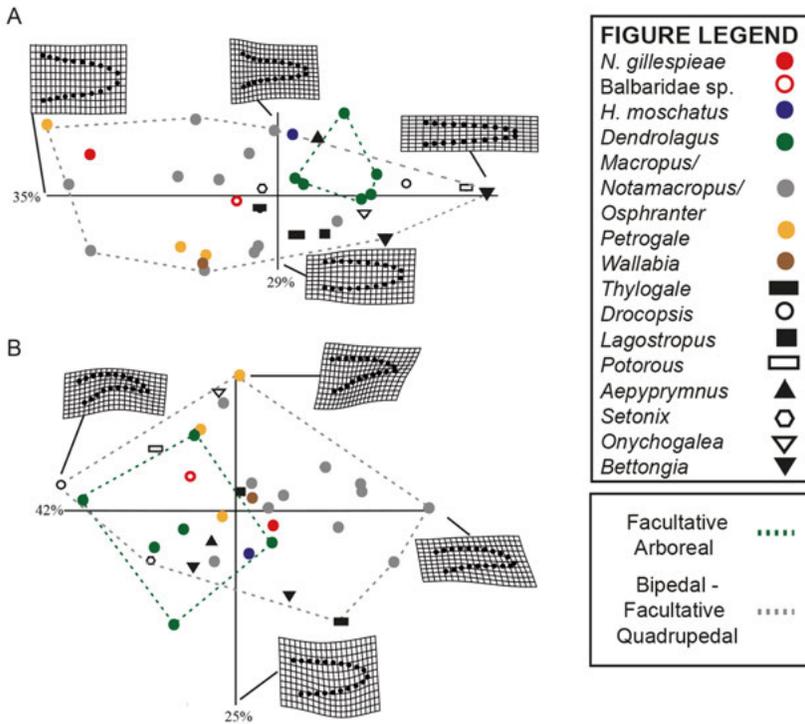
Lastly, a linear morphometric analysis was undertaken of the astragali, whereby using digital calipers, measurement (in mm) were taken of the entire length, width and height of each astragalus in dorsal, anterior and posterior view (Fig. 13D). From the dorsal aspect of each astragalus the width of the trochlear sulcus were taken, the lengths of the lateral and medial trochlear crests, and the height and width of the navicular facets (Fig. 13D). The measurements were log transformed (base 10) and were then run as a PCA in R-Studio (Version 1.0.136). Of these various measurements, a Canonical Variate

Analysis (CVA) was performed in R-Studio. A CVA was also undertaken of the astragali landmark analyses. A CVA approach was employed in order to estimate the plausible assignment of locomotory ability of the balbarid astragalus and pedal phalange to the various modern macropodiform taxa. Unfortunately, a CVA was not possible for the outline (non-homologous landmarks) analyses of the astragali and pedal claws, due to the number of variables exceeding the number of specimens utilized.

## Results

**Pedal Phalange:** The dorsal aspect of the pedal digit's output showed 35% of the variation being explained in the first principal component axis (PC1) and 29% of the variation being explained in the second principal component analysis (Fig 14A, **Paper III** - supplementary material Table 6). PC1 depicts the variation from a dorsally convex claw to a more dorsally concave shaped claw. PC2 reveals the variation from a dorsally stout claw to a dorsally gracile claw. Significant overlap between the bipedal (facultative quadrupedal) and the facultative arboreal taxa is revealed, suggesting high disparity in modern macropodiform pedal phalanges. In the dorsal claw results, the balbarid pedal phalange loaded closest to *Thylogale* and *Setonix*. The pedal claw in dorsal view of *Nambaroo gillespieae* loaded within the bipedal hopping (facultative quadrupedal) grade, closest to *Petrogale* specimen.

The lateral outline analysis of the pedal phalange had PC1 displaying 25% of the variation and PC2 had 42% of the variation (Fig. 14B, **Paper III III** - supplementary material Table 6). The first axis shows the variation in the sharpness and bluntness of the mid-distal parts of each claw. The second axis demonstrates the various levels of tapering within the lateral aspects of the claws. Similar to the outputs of the pedal phalange in the dorsal aspects, the lateral aspects of the claws also reveal a high degree of overlap between the mostly arboreal and the bipedal (facultative quadrupedal) modern macropodiform taxa. *Nambaroo gillespieae* loaded notably close to the arboreal grouping, a *Dendrolagus* species and near *Hypsiprymnon moschatus*. Additionally, *N. gillespieae* pedal phalange in lateral view, loaded within the intermediate curved claws morpho-space. The balbarid loaded within the facultative arboreal grouping closest to extant specimens such as tree-kangaroos and rock-wallabies. Furthermore, the lateral aspect of the balbarid claw loaded within the sharply tapering and curving morpho-space.

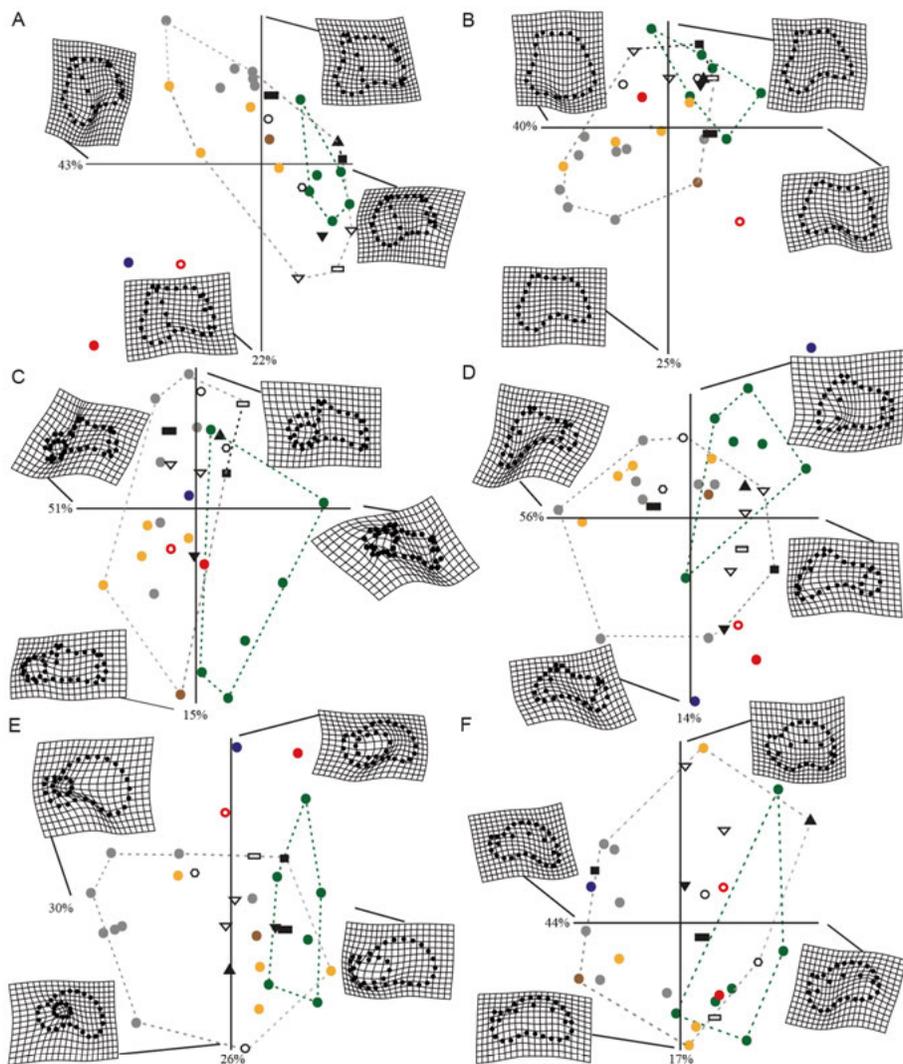


**Figure 14.** Pedal phalange Principal Component Analysis (PCA) results. **A.** PCA of the pedal phalanges in dorsal view, **B.** PCA of the pedal phalanges in lateral view.

**Astragali non-homologous landmark PCA results:** The outline PCA analysis of the astragali in dorsal view (PC1=22%, PC2=43%) (Fig 15A, **Paper III** - supplementary material Table 4), had the two balbarids loading as outliers, together with *H. moschatus*. In ventral view of the astragali outline PCA results (PC1=2%, PC2=40%) (Fig. 15B, **Paper III** - supplementary material Table 4), *H. moschatus* loaded as an outlier to the rest of the taxa, with the balbarid astragalus loading closest. *N. gillespieae* loaded closest to *Dorcopsis* sp. and inside the facultative quadrupedal morpho-space. In the medial aspect of the astragali outline PCA analysis (PC1=15%, PC2=51%) (Fig. 15C, **Paper III** - supplementary material Table 4), the balbarid loaded amongst the rock-wallabies (*Petrogale*) and *N. gillespieae* loaded closest to *Bettongia*. Notably, the balbarid's astragalus loaded within the morpho-space depicting a laterally situated navicular facet, and a

medial trochlear crest that is larger than the lateral trochlear crest. *N. gillespieae* loaded inside the morph-space with a medially broader astragalus with an aligned navicular facet. In the lateral aspect of the astragali outline PCA analysis (PC1=14%, PC2=56%) (Fig. 15D, **Paper III** - supplementary material Table 4), *H. moschatus* is once again an outlier, suggesting different astragalus morphology in comparison to other extant macropodiforms. The two balbarids load close to one another, closest to *Bettongia*, and within a larger medial trochlear crest and a significantly reduced lateral trochlear crest morphospace. In the anterior aspect of the astragali (Fig. 15E) the outline PCA outputs (PC1=26%, PC2=30%) (**Paper III** - supplementary material Table 4), the balbarids and *H. moschatus* load away from all other taxa, within a morpho-space exhibiting an enlarged and slightly less anteriorly displaced navicular facet, and a smaller anterior aspect of the astragali. The posterior aspect of the astragali outline PCA results (PC1=17%, PC2=44%) (Fig. 15F, **Paper III** - supplementary material Table 4), the balbarid astragali loaded closest to *Dorcopsis* sp. in a posteriorly robust astragali morpho-space. *N. gillespieae* loaded closest to tree-kangaroos and *Potorous* sp. within a morphospace of a more posteriorly elongated astragalus.

**Astragali homologous landmark PCA results:** The dorsal aspect of the astragali utilizing the digital landmarks (PC1=20%, PC2=40%) (Fig. 16A, **Paper III** supplementary material Table 5), both balbarids and *H. moschatus* fell outside of everything else, similar to the outline analysis of the dorsal aspect of the astragali (Fig. 15A). However, *N. gillespieae* loaded closest to *H. moschatus* in this analysis, and the balbarids astragali loaded closest to the bipedal (facultative quadrupedal) modern taxa nearest to *Onychogalae* sp., *Dorcopsis* sp. and *Aepyprymnus rufescens*. The ventral aspect of the astragali landmark analysis (PC1=25%, PC2=29%) (Fig. 16B, **Paper III** - supplementary material Table 5), *H. moschatus*, *N. gillespieae*, and the balbarids astragali loaded outside of the locomotion morpho-spaces. The balbarid loaded closest to *H. moschatus* and *N. gillespieae* loaded within a larger navicular facet morpho-area. The landmark analysis of the medial aspect astragali PCA results (PC1=26%, PC2=33%) (Fig. 16C, **Paper III** - supplementary material Table 5), had *H. moschatus*, and the balbarids loading outside the locomotory grades once again. However, *H. moschatus*, loaded as an outlier and the balbarids loaded closest to *Petrogale* species. The lateral astragali landmark PCA analysis (PC1=37%, PC2=53%) (Fig. 16D, **Paper III** - supplementary material Table 5), the balbarids and *H. moschatus* loaded within the same morphological region, loaded closest to *H. moschatus*, and *Lagostrophus faciatus* and a potoroid. The posterior aspect of the

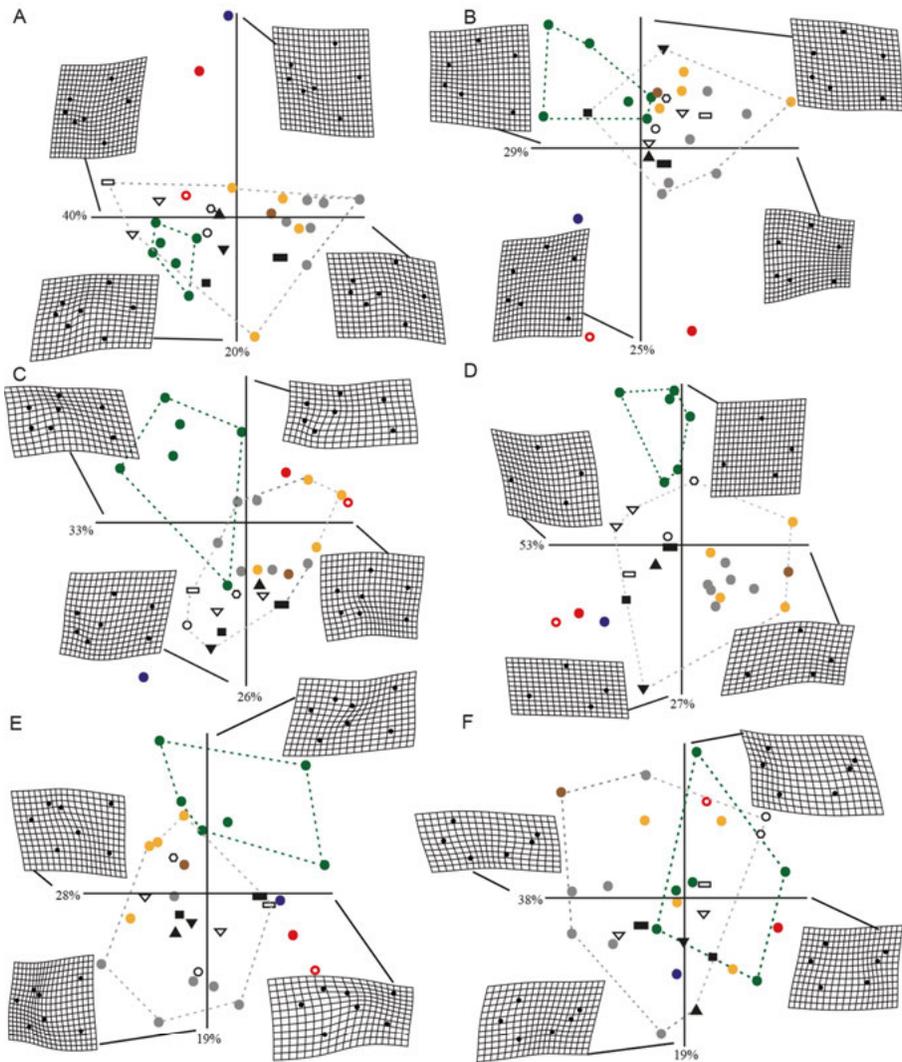


**Figure 15.** Principal Component Analysis (PCA) results of the non-homologous landmarks (outline) analyses of the various astragali. **A.** Dorsal aspect of the astragali, **B.** Ventral aspect of the astragali, **C.** Lateral aspect of the astragali, **D.** Medial aspect of the astragali, **E.** Anterior aspect of the astragali, **F.** Posterior aspect of the astragali. For legend see Figure 14.

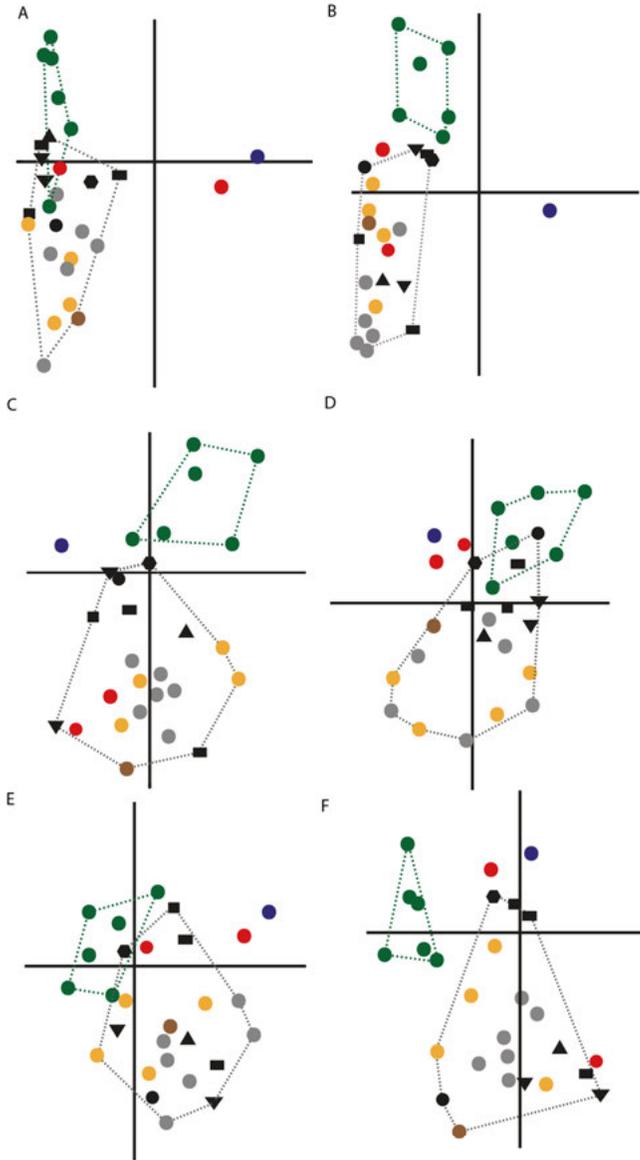
astragali digital landmark outputs (PC1=19%, PC2=28%) (Fig. 16E, **Paper III** - supplementary material Table 5), the balbarids and *H. moschatus* once again fall outside of everything else, with the closest loading specimen being a potoroid. In the anterior aspect of the astragali landmark analysis (PC1=19%, PC2=38%) (Fig. 16F, **Paper III** - supplementary material Table 5), the balbarid loaded within the arboreal grade, but close to a *Petrogale* species. *N. gillespieae* loaded closest to the facultative arboreal grade, with closest loading species associated with *Dendrolagus*. Peculiarly, here *H. moschatus* loaded within the bipedal (facultative quadrupedal) morpho-space.

**Astragali homologous landmark CVA results:** The astragali CVA outputs in dorsal view (Fig. 17A, **Paper III**), had the balbarids loading inside the facultative arboreal morpho-space but closest to *Onychogalea* species. *N. gillespieae* loaded as an outlier together with *H. moschatus*. The ventral CVA results (Fig. 17B, **Paper III**), the balbarid loaded inside the bipedal (facultative quadrupedal) bin closest to *Petrogale* species. *N. gillespieae* loaded outside of the grades, but closest to *Dorcopsis* and *Onychogalea* species. *H. moschatus* loaded as an outlier. The medial CVA results (Fig. 17C, **Paper III**) the balbarid loaded within the largely bipedal morpho-space, closest to *Petrogale* and *Macropus* species. *N. gillespieae* loaded within the same morphological area but closest to *Bettongia*. *H. moschatus* is once again an outlier. The lateral CVA results (Fig. 17D, **Paper III**) had *H. moschatus* and both balbarids loading close to one another, outside of the locomotory grades. The anterior CVA results (Fig. 17E, **Paper III**), *N. gillespieae* loaded closest to *H. moschatus*, and the balbarid's astragalus plotted nearby *Setonix*. In the posterior CVA results (Fig. 17F, **Paper III**), the balbarid loaded outside of the allocated gait bins, however neighbouring *Onychogalea* and *Thylogale*. *H. moschatus* and *N. gillespieae* loaded closest to one another, outside of everything else, with closest loading species being *Setonix* and *Lagostrophus faciatus*.

The percentage of the extant taxa being correctly assigned to their locomotion type had been calculated for the CVA's of the landmark data of the astragali in each aspect (**Paper III** - supplementary material Table 7). The results suggested that in the dorsal aspect 50% of the specimens had been correctly assigned to the arboreal (facultative quadrupedal and bipedal) group, 63% to the bipedal (facultative quadrupedal group) and in total of the specimens 60% had been correctly assigned. In ventral view of the astragali, 66% was



**Figure 16.** Astragali homologous landmarks Principal Component Analysis (PCA) results. **A.** Dorsal aspect of the astragali, **B.** Ventral aspect of the astragali, **C.** Lateral aspect of the astragali, **D.** Medial aspect of the astragali, **E.** Anterior aspect of the astragali, **F.** Posterior aspect of the astragali. For legend see Figure 14.



**Figure 17.** Canonical Variate Analysis (CVA) of the homologous landmark astragali analysis. **A.** Dorsal aspect of the astragali, **B.** Ventral aspect of the astragali, **C.** Lateral aspect of the astragali, **D.** Medial aspect of the astragali, **E.** Anterior aspect of the astragali, **F.** Posterior aspect of the astragali. For legend see Figure 14.

estimated that the arboreal specimens had been correctly allocated, the bipeds has an estimate of 73% and in total all specimens has a 72% probability that they had been correctly assigned. The lateral, medial and anterior view of the astragali had an 83% probability that the arboreal taxa were placed correctly, the bipedal specimens had a 95% (94% in anterior) and a 92% that all specimens had been correctly assigned. The posterior aspect of the astragali showed that 67% of the arboreal taxa, 68% of the bipedal taxa, and in total 63% of the specimens had been placed into the correct locomotion bin.

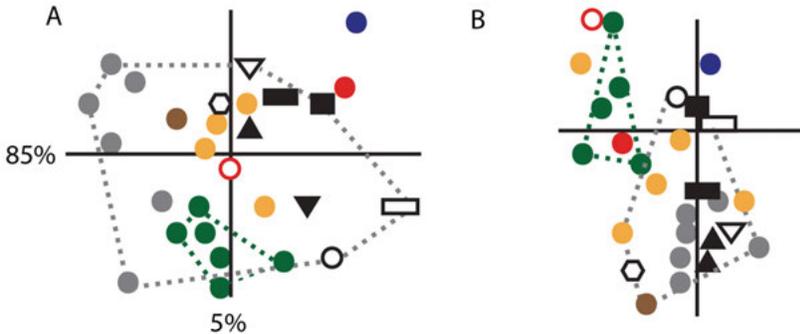
**Astragali Linear PCA and CVA Results:** The PCA results of the various astragali measured features (Fig. 18A, **Paper III** – supplementary material Table 9) had *H. moschatus* plotting away from all other modern taxa and *N. gillespieae* loading closest. The balbarid loaded inside the bipedal grade, although closest loading species are tree-kangaroos. In the CVA linear measurement results (Fig. 18B), the balbarid loaded closest to living tree-kangaroos, although outside of the grade. *N. gillespieae* loaded inside the tree-kangaroo's grouping, and *H. moschatus* loaded as an outlier.

The estimations made of *N. gillespieae* and the balbarid's astragali from the various measurements, to determine the probable locomotory group they are closest associated with (**Paper III** –supplementary material Table 11), had a 98% probability that the balbarid may have utilized arboreal strategies. *N. gillespieae* had 73% estimated that it may have been quadrupedal. Also tested was the percentage of extant specimens that had been correctly assigned to each of the locomotion bins (**Paper III** - supplementary material Table 10), where the arboreal group had been estimated at 65% of the species had been assigned correctly, despite each individual being a tree-kangaroo. This might be due to the modern tree-kangaroo's being capable of adopting various forms of locomotion types. The bipedal grouping had been estimated that 82% of the specimens had been correctly assigned, and the quadrupedal grouping (which consisted of only *H. moschatus*) had an estimation of 73% that it was correctly assigned to the quadrupedal bounding bin.

## Conclusion

Both the balbarids and *N. gillespieae*'s pedal claw and astragalus in all analyses, loaded within and amongst scansorial (*Dendrolagus*) (but capable of quadrupedal and bipedal bounding), and largely bipedal (but facultative quadrupedal) loading extant specimens. Furthermore, often the exclusively quadrupedal extant *H. moschatus* loaded within

close proximity or within similar morph-spaces as the two balbarids. These results could suggest considerable plasticity within the Oligo - Miocene Balbaridae lineage. Additionally, the significantly reduced lateral trochlear crest, the enlarged medial trochlear crest, and the strongly developed and obliquely displaced navicular facet on the balbarid transversely broad astragali (Fig. 12A), combined with the reduced tibia - fibula contact on the distal fibula fragment (Fig. 12C), the high curvature and comparatively large size of the pedal phalange (Fig. 12B) are all features suggestive of increased mobility within this animals ankle and pes, likely permitting some ability to climb and hence the possibility of the occupation of low-medium canopy niches (Fig. 19). Henceforth, the presence of the unmistakable arboreal features on the distal fibula, astragali and pedal digit (Fig. 12A-C) of the Balbaridae fossil remains hints at Oligo - Miocene kangaroos already having adapted towards an arboreal lifestyle and that the capability of climbing re-occurred again when the Pliocene – Pleistocene tree-kangaroos (*Bohra*) occupied the Pleistocene’s newly formed forested habitats in what is today Northern Queensland and Papua New Guinea (Bishop 1997, Prideaux and Warburton 2008).



**Figure 18.** Principal Component Analysis (PCA) and Canonical Variate Analysis (CVA) of the astragali measurements. **A.** Principal Component Analysis (PCA) results, **B.** Canonical Variate Analysis (CVA) results. For legend see Figure 14.



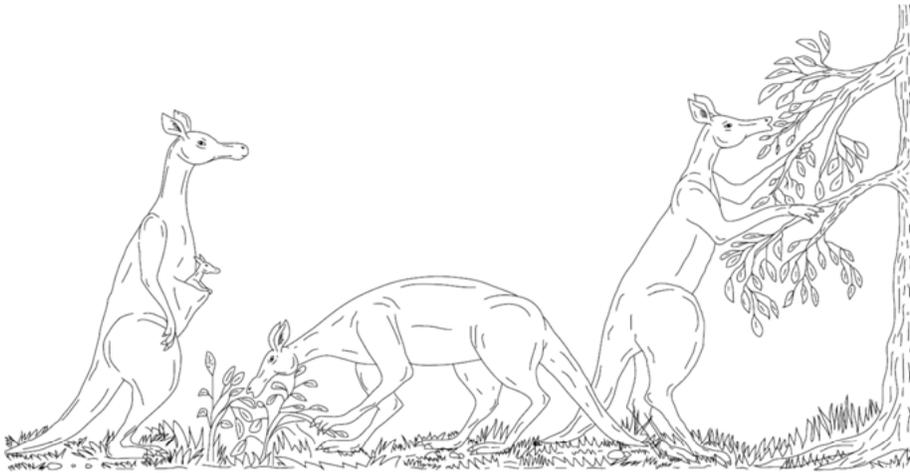
*Figure 19.* Reconstruction of the balbarid fossil elements.

## PAPER IV

### Description and Functional Interpretation of New Cranial and Post-Cranial Fossil Material of the ‘Giant Extinct Wallaby’ *Protemnodon anak*

Owen (1859) was first to describe the giant Pleistocene ice-age kangaroo *Protemnodon anak* (Fig. 19). In the initially description *P. anak* was referred to as *Macropus anak*. Later, in 1873, Owen erected the *Protemnodon* genus and in 1874, Owen changed *Macropus anak* to *Protemnodon anak*. Currently, *Protemnodon anak* is the most completely known taxon within the *Protemnodon* genus. Despite this, no previous attempts to describe and interpret, the functional eco-morphology of *P. anak*'s post-cranial material has ever been embarked on. Unfortunately, *Protemnodon anak* (like many other currently described *Protemnodon* species) has always been compared to wallabies based on dental similarities (Owen 1874, Raven and Gregory 1946, Kreft 1873, Kreft 1874, Trouessart 1905, Raven 1929, De Vis 1895, Simpson 1930) causing the members of the *Protemnodon* genus to commonly be referred to as ‘Giant Wallabies’ (Stirton 1963). However, the skeletal fossil elements belonging to *Protemnodon anak* appear to bear no resemblance to members of *Wallabia*. Upon closer inspection of *P. anak*'s skeletal elements a number of palpable distinguishing features emerge; such as an elongated neck, a short and stout pes, elongated hind limbs, lengthened and robust fore limbs, and a comparatively short and broad tail. These features are clearly disparate to wallabies, which have a completely different body-plan (Fig. 20). Furthermore, the cranium of *P. anak* is of a more gracile nature to wallabies and the base of the cranium in *P. anak* is wider and more compact than in wallabies (Bartholomai 1973). For this reason, for the very first time, post-cranial elements associated with *P. anak* from Morwell Local Fauna (Victoria) (Fig. 1) (See **Paper IV** for description of the fossil locality) are described, investigat-

ed, and compared to provide a plausible insight into this extinct kangaroo's bio-mechanical ability and ecological role. Furthermore, a linear morphometric method utilizing various measurements (femur, tibia and metatarsal IV) (See **Paper IV** Table 2) of a number of extant and extinct macropodiform specimens, was conducted in order to provide an eco-biological comparison of members belonging to *Protemnodon*.



**Figure 20.** Reconstruction of the Pleistocene Kangaroo *Protemnodon anak*.

## Material and Methods Linear Morphometric Analysis

The *Protemnodon*'s eco-morphological similarity to other members of the macropodiforms were assessed by the utilization of a linear morphometric analysis approach. Measurements were obtained from the femurs, tibias, and fourth metatarsals (IV) of an assortment of extant (32 specimens) and extinct (12 specimens) macropodiforms and three non-macropodiform Australian marsupials (See Table 2 in **Paper IV** for list of specimens and the measurements). All measurements were taken in millimeters (mm) with the use of a digital caliper and were log transformed (base 10) before the analysis was run. With the use of the MASS 7.3-45 (Venables and Ripley, 2002) and the geomorph 03 (Adams et al., 2015) packages a Principal Component Analysis (PCA) of the data was run in R-Studio (Version 1.0.136) (R Development Core Team, 2015). Of the currently known *Protemnodon* species, the only post-cranial material available belongs to *Protemnodon anak*,

*Protemnodon buloloensis* (Plane, 1967, Bartholomai, 1973, Flannery et al., 1989), *Protemnodon otibandus* (Stirton, 1963, Plane, 1967), *Protemnodon snewini* (Archer and Wade, 1976, Bartholomai, 1978). Other post-cranial material of *Protemnodon* is available which has either not yet been associated with known *Protemnodon* taxa or not yet been provided with a taxonomic name. Nevertheless, of these specimens, only *P. anak*, *P. baloloensis*, *P. otibandus* and *Protemnodon* spp. were accessible to us. Unfortunately, *P. snewini*'s post-cranial material was not available for this analysis and therefore could not be included.

## Results and Conclusion Linear Morphometric Analysis

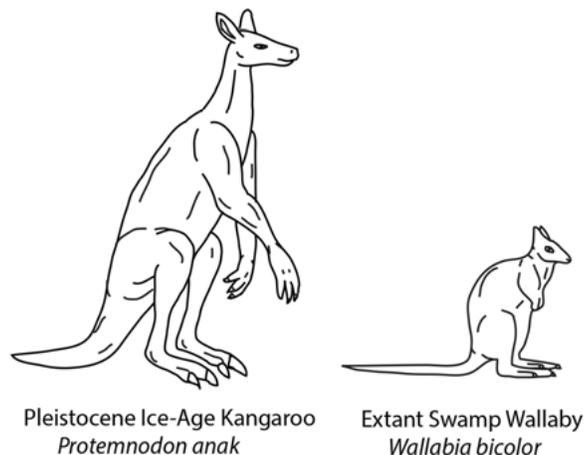
The Principal Component Analysis (PCA) utilizing linear morphometrics of the various *Protemnodon* taxa, extinct and extant macropodiform and the non-macropodiform Australian marsupial's hind limb measurements are depicted in Fig. 22. The results show an 81% of variation explained in the first principal component axis (PC1) and only 5% of the variation is explained in the second principal component axis (PC2). The results reveal a wide morpho-space for the Macropodinae. The balbarid, bulungamayine, and *Hypsiprymnodon moschatus* loaded as outliers away from most of the other macropodiform taxa. Along the second axis, the koala, - *Phascolarctos cinereus* (Phascolarctidae), the common wombat, - *Vombatus ursinus* (Vombatidae) and the common brush-tail possum, - *Trichosurus vulpeculata* (Phalangeridae) loaded away from the macropodiform species, similar to the *Protemnodon* taxa. These non-macropodiform specimens often utilize a combination of quadrupedal and pentapedal movements (apart from *T. vulpeculata*, which is largely arboreal). Nevertheless, along the first axis, the *Protemnodon* taxa loaded closest to the Sthenurinae morpho-space. These results may suggest a possible slow, walking-type gait for the *Protemnodon* spp. similar to the Sthenurinae.

## Description of *Protemnodon anak*'s Cranial, Dentary and Dental Fossil Material

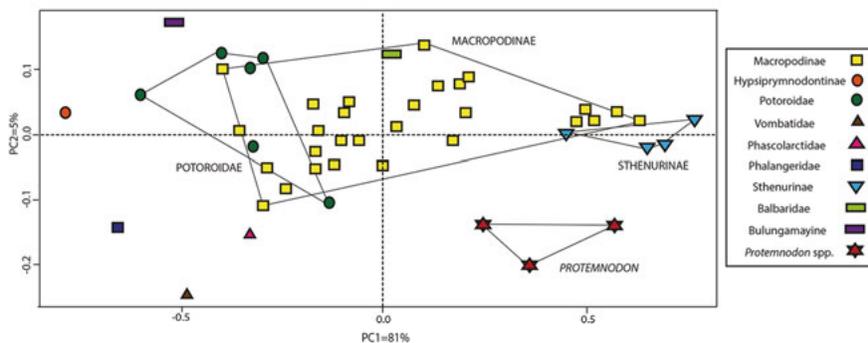
**Cranium and dentary** – One slightly crushed, fragmented and notably gracile cranium (P231103) (Fig. 23A - B) with an associated largely undamaged right dentary (P231103) (Fig. 23C - D). Due to the fragmentary nature of the cranium the zygomatic arch and various

occipital elements along the antero-posterior region of the skull are either absent or difficult to construe. The nasal and maxillary were also difficult to interpret due to the level of fragmentation. The rostrum is significantly slender and elongated. The anteorbital sulcus is lacking. The jugal and the masseteric canal are strongly developed. Minor downward flexion along the rostrum and the incisors are located slightly below the molar rows. Non-partition of the frontal and sagittal crest along the dorsal aspect of the cranium are present. Along the ventral aspect of the cranium the medial and anterior palatal vacuity are absent. All upper dentition (M1-M4, P3, I1-I3) are present along the maxilla and pre-maxilla and follow into an almost imperceptible bow. On the associated dentary the lower teeth (m1-m4, p3) and incisor (i1) are present. The condyle and coronoid processes are absent. The diastema is conspicuously elongated. The alveolar process is enlarged and horizontally displaced. The masseteric foramen is reduced. The ramus is steep, with the mental foramen inconspicuous (or possibly absent).

The upper and lower molars have a low-crowned and bilophodont morphology. Crenulation on the molars appears unobtrusive or perhaps may be worn away. Distinct and well developed metalophs and protolophs are present on each of the molars (being more enlarged in the fourth molars and gradually reduce in size



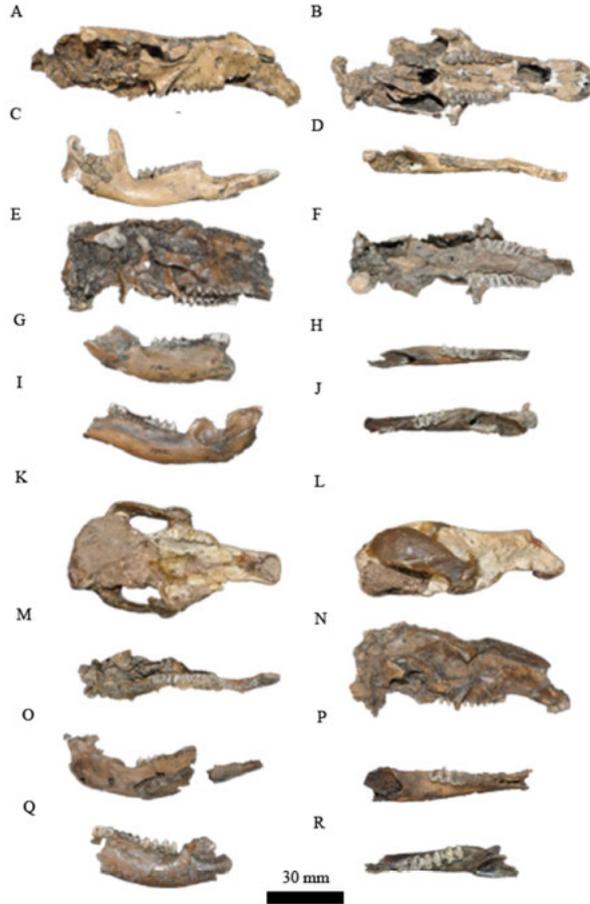
**Figure 21.** Comparison of *Protemnodon anak* to the extant swamp wallaby *Wallabia bicolor*.



**Figure 22.** Principal Component Analysis (PCA) of the hind limb measurements.

towards the first molars). The molars are all of relatively equal size, with an almost square-like outline and are occlusally U-shaped. The post-protocrista is weakly developed and extends into the mid-line section of each tooth on the upper molars. The upper molars (M1-M4) have a non-kinked condition and the pre-protocrista is either significantly reduced or possibly completely absent. The post-metacrista, pre-protocrista and post-paracrista are under developed. Three deeply grooved ridgelets are present on the P3. The post-metacristas are semi-developed. The upper incisors (I1-3) are bucco-lingually deep, elongated and blade-like. The first upper incisors (I1) are larger than the second (I2) and third upper incisors (I3). Distinct buccally placed enamel is present on the antero-laterally oriented I1. The lower molars (m1-m4) have the cristid obliqua and paracristid divided. The cristid obliqua has a linear morphology and terminates at the mid-line. The post-metacristid is successive and ceases at the mid-line and the vale of the interloph. The postentocristid and the posthypocristid are strongly developed and the posterior cingulum is significantly reduced. The lower incisors (i1) are significantly enlarged, strongly developed and robust with a procumbent blade-like morphology. The p3 have three or less shallow cuspules. Both the P3 and p3 lack a broadened base, are narrow and elongated, have a under developed lingual cingulum, have a non-arcate morphology, are of equal height to the molars, and align directly with the molar rows.

**Cranium and dentaries** – An extremely distally fragmented cranium (P39101) (Fig. 23E - F) associated with two partially complete dentaries (P39101) (Fig. 23, G - J). The dentaries are largely disintegrated



**Figure 23.** Cranial and dentary material of *Protamnodon anak*. **A.** Cranial (P231103) in right lateral view, **B.** Cranial (P231103) in ventral view, **C.** Dentary (P231103) in lateral view, **D.** Dentary (P231103) in occlusal view, **E.** Cranial (P39101) in right lateral View, **F.** Cranial (P39101) in ventral view, **G.** Right dentary (P39101) in lateral view, **H.** Right dentary (P39101) in occlusal view, **I.** Left dentary (P39101) in lateral view, **J.** Left dentary (P39101) in occlusal view, **K.** Cranium (P159918) in ventral view, **L.** Cranium (P159918) in right lateral view, **M.** Cranium (P42532) in ventral view, **N.** Cranium (P42532) in right lateral view, **O.** Left dentary (P209939) in lateral view, **P.** Left dentary (P209939) in occlusal view, **Q.** Right dentary (P209939) in lateral view, **R.** Right dentary (P209939) in occlusal view.

along the beginning of the diastema, and lack the posterior condyle and coronoid processes. The left dentary lacks half of the ramus and has the m4, m3 and p3 available. The right lower jaw is slightly fragmented along the ramus with the m4, m3 (significantly worn) and p3 present. Nevertheless, due to the fragmentary condition of the cranium there is lack of many occipital features, the nasal and the zygomatic arches. All dentition are present on the maxilla (M1-M2, P3) except for the upper incisors.

The upper dental rows advance into a semi-curved line. The masseteric canal is deep, elongated and strongly developed. The frontal crests perpetuate deeply into the parietal crest. The lower mandibles both have the rami rise up steeply and the angular processes are curved and considerably protrusive. The condyloid process and the mandibular foramen are weakly developed. The masseteric canals and fossae are located anteriorly to the molar rows. The alveolar processes are shallow, horizontally displaced with a wide buccinators concavity. The pterygoid fossa and the masseteric fossa are deep and enlarged, while the pterygoid shelf is broad and shallow.

The molars have almost a complete square-like shape, although are buccally and lingually slightly longer, giving a more rectangular morphology. Both the upper and lower molars slightly decrease in size from the fourth molar to the first molar. The lopheids on the upper molars are sharp, and are more developed in M4 and M3 and are comparatively smaller in the M2 and M1. Both the P3 and the p3 align with the molar rows, and each bears a weakly developed lingual cingulum, a narrow base, three deep ridgelet grooves, are non-kinked and elongated. The metalophs and protolophs on both upper and lower molars are well developed and become larger and wider in the second and first molars. On the upper dentition the postprotocristids are narrower in M4 and M3 becoming wider in M2 and M1. On both upper and lower molars, the post-protocristas are separated, the post-metacrista and post-metacrista are reduced and the cristid oblique is non-kinked, wide and shallow. The cristids (postprotocristid, prematacristid, postentocristid, posthypocristid) are weakly developed, although the postentocristid and the posthypocristid are a bit more distinct.

**Cranium** – Note; - Specimen was used in the reconstruction of *P. anak* by T. Flannery 16/1/1981). One mostly fragmented and worn isolated cranium (P159918) (Fig. 23K - L) lacking the upper incisors, the masseteric canal, infraorbital foramen and the paroccipital process.

Many missing features on the cranium have been reconstructed with the use of clay. All upper left and right molars are present (with the left M1 being significantly worn), and only the right P3. The reconstructed zygomatic arches, jugal and squamosal on the cranium are strongly developed. The zygomatic arches extend out dorsally. The nasal is elongated and medial-laterally wide. The maxilla and pre-maxilla are reduced and narrow. The maxillary processes are enlarged. The parietal is divided by the sagittal crest. The rostrum is less elongated and wider than the rostrum in the P231103 and P42532 crania, however still exhibits a relatively gracile exterior. Meek flexion occurs in the rostrum. Division of the medial palatal cavity is absent. Due to the significantly worn condition of the dentition the characteristics were difficult to interpret and so are not discussed here. However, despite the worn nature of the molars, a low-crowned and almost square-like morphology is observed. Furthermore, a slight decrease in size from M4 to M1 occurs and the P3 is aligned with the molar row.

**Cranium** – Significantly fragmented cranium (P42532) (Fig. 23M - N) lacking the lateral side of the skull with only the medial aspect and right upper molars, right P3 and right pre-maxilla incisors available. The skull is gracile with a large and elongated masseteric process, rostrum flexes downwards and shortly below the molar row's plane. Anteorbital sulcus absent, zygomatic process, jugal, zygomatic arch and masseteric process are distinct and robust. The infraorbital is enlarged. There is a slight decrease in size from M4 to M1, however relatively minuscule. The molars are also slightly longer than they are wide. The P3 is non-arcuate, longer than it is wide, and has three deep ridgelets and a poorly developed lingual cingulum. The molars are low-crowned, and the metalophs and protolophs appear to be more developed in the first and second molars than in the third and fourth molars. The lophids on the molars are almost cone shaped being slightly larger in M4 and then decreasing marginally along the molar row. The preprotocristas in the molars are distinct and well developed, and the postparacristas in each of the molars are reduced in size. The postprotocristas are distinctly divided into two different components, and they extend into the interloph valley close to the mid-line in each of the teeth. The postmetacrista and postmetaconulecrista are more strongly developed here than in the P231103 cranium described above. The postprotocrista is low, shallow and weakly developed.

**Dentaries** - Fragmented left and right, lower mandibles (P209939) (Fig. 23O - R). Left mandible relatively intact with only the ramus broken off, fourth, third molars and incisor present. Right lower mandible lacking the ramus and broken off before the diastema, between the first molar and second molar, m4-m2 present with m1 significantly worn. Mental foramen lacking, alveolar process sinuous in appearance, whereby concave along m4-m3, and then a convex appearance along m2-m1-p3. Left mandible has an elongated and shallow symphyseal plate. Mandibles reveal a broad but shallow buccinators concavity. Incisor on the left mandible is enlarged, elongated and blade-like with moderate coverage of enamel along the lingual aspect of the incisor. The lophids on the molars (like observed in the above specimens) have a sharp cone, semi-triangular-like shape and are more distinct in the m4 and m3. The metaloph and protoloph also become wider in size in m1 and m2, being less distinct in m4 and m3. The cristid obliqua is straight and shallow and is broader in the first and second molars and is narrower in the third and fourth molars. There is a slight decrease in size from m4 to m1. Any sign of lophid enamel crenulation seems to be absent (or perhaps may have been worn away). The premetacristids and the postentocristids are present, however shallow and trivial in comparison to the specimens described above. Both p3s are significantly worn and the number of ridgelets and the ridgelets morphology are hard to determine. The p3's do align with the molar rows, and have a narrow and elongated shape, with a narrow base.

### Comparison of *Protemnodon anak*'s Cranial, Dentary and Dental Fossil Material

An immediate apparent observation is that the skull and lower jaw elements of *P. anak* appear to be far more elongated than in other wallabies and kangaroos, where the cranium and mandibles are comparatively shorter and broader in the latter. The elongation of the cranium is also observed in other *Protemnodon* species: *Protemnodon hopei* (Irian Jaya, Indonesia) (Flannery 1992), *Protemnodon snewini* (Allighnam Formation, Queensland, Australia) (Bartholomai 1978), and the Pliocene *Protemnodon bandharr* (Wellington Caves, New South Wales, Australia) (Dawson et al. 1999) (See **Paper V** for description of the Fossil Localities). Furthermore, slight variation in the lower mandibles of the *Protemnodon* members is apparent. The ramus in *P. anak* are located beneath the molar rows. In *Protemnodon hopei*

(Flannery, 1992) and in *Protemnodon tumbuna* (Flannery et al. 1982) the rami are also located beneath the molar rows, but are situated considerably lower. The rami in other *Protemnodon* taxa are positioned above the molar rows, these include *Protemnodon otibandus* (Plane 1967) (Otibanda Formation in Papua New Guinea) and *Protemnodon nombe* ((Flannery et al. 1982) (from Papua New Guinea). The symphyseal plate along the dentaries of *P. anak* are of a straighter morphology, similar to *Protemnodon chinchillaensis* (Bartholomai 1973). *Protemnodon snewini*'s (Archer and Wade 1976, Bartholomai, 1978) lower mandibles are more ventrally aligned in comparison to the dentaries of *P. anak*, and the dentaries belonging to *Protemnodon roechus* (Bartholomai 1973) have a slight convex symphyseal plate. Furthermore, *P. brehus* dentaries reveal a curved nature, while in *P. anak* (and in *P. chinchillaensis* and *P. roechus*) the dentaries lack this trait and are of a more non-curved profile. The upper dentition of *P. anak* follows into a semi arch, also seen in *P. hopei* and *P. snewini*. *P. hopei*'s upper dentition differ from *P. anak* in having the molars decrease in size, with M4 being the largest and M1 the smallest, while in *P. anak*, *P. chinchillaensis*, *P. snewini*, there is only a slight successive decrease in size in the upper molars. In *P. devisi* and *P. brehus* the M3 is the largest molar. The P3's in *P. snewini* and *P. chinchillaensis* are significantly larger than the molars, which are not observed in the P3's of *P. anak* or any other *Protemnodon* species, where the P3's are of a relatively equal size to the molars. *P. hopei*'s and *P. brehus*'s P3s are non-caved and similar to *P. anak*'s P3s. A large occlusal area on the P3s of *P. brehus*, *P. snewini*, and *P. buloloensis* are observed, where this feature in *P. anak* is reduced in comparison. The lower molars of *P. anak* resemble the lower molars of *P. roechus*. The p3s in *P. buloloensis*, *P. nombe*, *P. tumbuna*, and *P. roechus* have a more robust morphology and the p3 in *P. chinchillaensis* and *P. devisi* are more gracile to the p3s associated with *P. anak*.

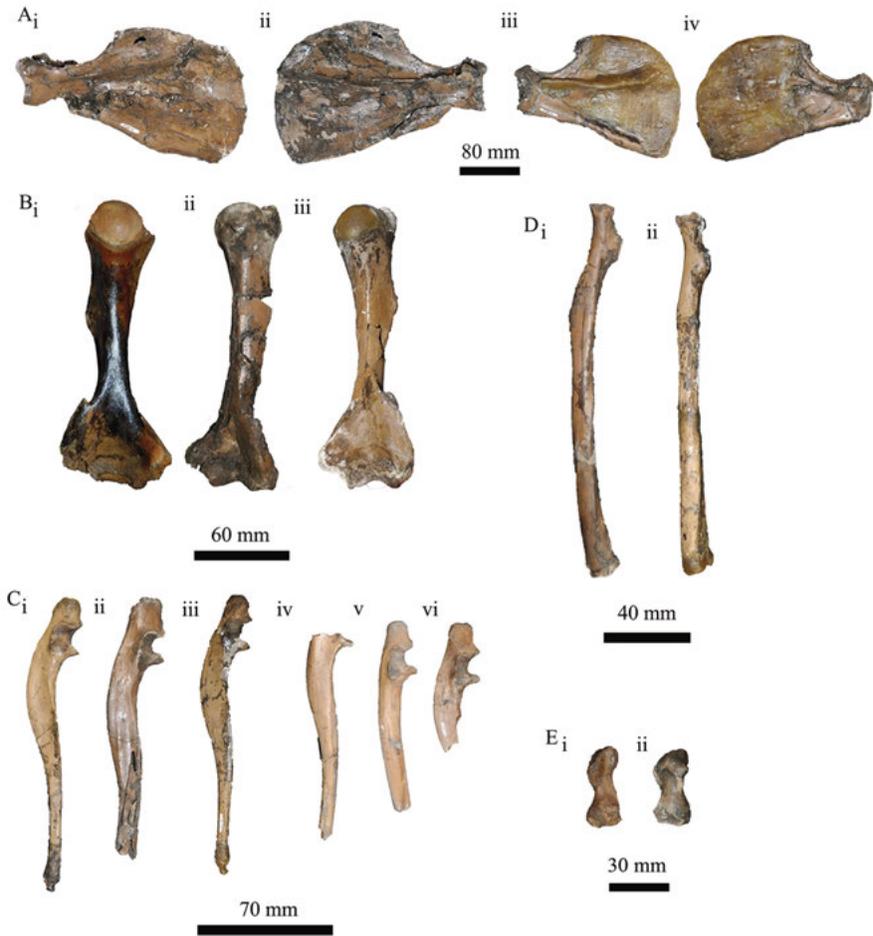
The upper and lower dentitions of *P. anak* are low-crowned bilophodont, similar to other members of the *Protemnodon* genus, *Simosthenurus* and *Sthenurus* spp. (Bishop 1997, Prideaux and Warburton 2010). Traits that are similar to living wallabies are; extension of the post-protocrista into the interloph valley, presence of a metaloph, and a reduced or absent post-paracrista. However, the post-meta-conulecrista, post-metacrist, post-protocrista, pre-protocrista on the upper molars and post-protocristid on the lower molars are poorly developed in *P. anak*, but in extant *Macropus* spp. and wallabies these feature are more developed. *P. anak*'s upper incisors are transversely

broad with slight proximal tapering and the I1 is slightly larger than the I2 and I3. The I1 in *P. roechus* is considerably larger than the I3 and the upper incisors of *P. buloloensis* the I2 is reduced, and the I1 and I3 are of a comparatively equal size. The upper incisors of *P. roechus* are of a more robust nature and the upper incisors belonging to *P. hopei* are more cone-shaped than the upper incisors of *P. anak*. The lower incisors of *P. anak* are blade-like, a condition similar to the lower incisors of *P. roechus* and *P. tumbuna*. The lower incisors associated with *P. snewini* and *P. buloloensis* are distally sharper and far less blade-like than the lower incisors of *P. anak*.

## Description and Functional Interpretations of *Protemnodon anak*'s Post-Cranial Fossil Material

### Forelimb Elements

**Scapulae** – Two complete scapulae (P39101) (Fig. 24Ai - iv), each largely lacking the coracoid processes. A convex inferior angle and a concave lateral angle are depicted on both scapulae. The morphology of the scapulae are sub-rectangular-like, large and relatively broad. The large and sub-rectangular morphology of the scapulae suggests a large attachment area for the M. supraspinatus and infraspinatus muscles, which are muscles that aid an animal during quadrupedal movements, also seen in *N. gillespieae* and the extant *Hypsiprymnodon moschatus* (Kear et al. 2007). The subscapular, supraspinous and infraspinous fossae are strongly developed, also seen in *N. gillespieae* (Kear et al. 2007) and in species that commonly climb, which is suggestive of a large region for attachment of the M. subscapularis muscle. The fragmented coracoid fossae suggest an elongated and aligned condition, which is a similar nature to the coracoid processes in *H. moschatus*, the Miocene short-faced kangaroo *Hadronomus puckeridgei*, *N. gillespieae*, *Sthenurus* spp. and extant potoroids, whereby this feature permits a larger inclusion area for the M. biceps brachii muscles. These muscles increase the level of flexibility in the shoulder region, and may suggest the ability to pull, grasp and hold onto branches (Wells and Tedford 1995, Murray 1995, Kear et al. 2007).



**Figure 24.** Scapulae and fore-limb elements of *Protegnodon anak*. **A.** Scapulae: **Ai.** Scapula (P39101) in medial view, **Aii.** Scapula (P39101) in lateral view, **Aiii.** Scapula (P39101) in medial view, **Aiv.** Scapula (P39101) in Lateral View, **B.** Humerii: **Bi.** Humerus (P39105) in dorsal view, **Bii.** Humerus (P39105) in dorsal view, **Biii.** Humerus (P39101) in dorsal view, **C.** Ulnae: **Ci.** Ulna (P39101) in medial view, **Cii.** Ulna fragment (P39105) in medial view, **Ciii.** Ulna (P39105) in medial view, **Civ - vi.** Ulnae fragments (P2229316), **Di.** Radii: Radius (P39101) in medial view, **Dii.** Radius (P39105) in medial view, **C.** Metacarpals: **Ci.** Metacarpal (P39101) in dorsal view, **Cii.** Metacarpal (P39101) in dorsal view.

**Humeri** - Two humeri (P39105) (Fig. 24Bi) whereby clay was utilized to reconstruct the missing parts of the bones. Enlarged heads and dorso-ventrally broad surgical necks. Deltoid tuberosity large and protruding anteriorly. Medial supracondylar ridge significantly large, bulging upwards shaping into a thick rectangular-like shape. A robust shaft with a well-developed pectoral crest and enlarged deltoid ridge. Deep and hollow, U-shaped trochlea and a capitulum of equal height. Lateral epicondyle elevates into a triangular-like shape laterally and the bicipital groove has a shallow and wide morphology.

One complete humerus (P229318) (Fig. 24ii) with lateral supracondylar ridge markedly elevated, extending into a strongly developed lateral epicondyle. Medial epicondyles are medially and upwardly projected with an almost rectangular form. Deltoid tuberosity is significantly enlarged and laterally oriented. Shaft is robust and reveals the presence of a shallow and elongated inter-tubercular sulcus. Radial and coronoid fossae are represented by deep grooves. The surgical and anatomical necks are dorso-ventrally wide with a large rounded head. Trochlea groove is enlarged, deep and v-shaped.

A broad and completely intact humerus (P39101) (Fig. 24iii), with a large head, attached to a broad anatomical and surgical neck, large protruding deltoid tuberosity and a lateral supracondylar ridge. The trochlea is shallow and straight, as is the olecranon fossa with a smooth medial and lateral epicondyle. Bicipital groove is relatively wide and shallow. The medial epicondyle extends out antero-posteriorly, the pectoral crest is well developed and the deltoid ridge is enlarged. The medial supracondylar ridge is semi-stepped, the radial fossa is large, deep, and rectangular, and the capitulum is slightly protruding upwardly.

A robust humeral shaft, a dorso-ventrally wide and shallow bicipital groove, large pectoral crest and deltoid ridge are features also commonly seen in tree-kangaroos (*Dendrolagus, Bohra*) (Warburton et al. 2011). The presence of these traits may advocate flexibility in *P. anak's* forelimbs as well as the regular use of the forelimbs (Kear et al. 2007). Moreover, the transversely wide trochlea accompanied with a shallow and reduced furrow, might suggest increased flexibility within the elbow. Furthermore, the enlarged medial epicondyle, the well-developed capitulum, the strongly developed and laterally oriented supracondylar ridge on *P. anak's* humeri, suggest a large insertion area for the pectoral muscles (pectoralis minor, pectoralis quartus, pectoralis superficialis), which may further imply a frequent need for the utilization of the upper arms.

**Ulnae** – One almost complete ulna (P39101) (Fig. 24Ci) with a curved shaft, with a relatively short and stout form. Semilunar notch is reduced and coronoid process is enlarged. A thin, yet prominent olecranon process and a deep radial notch are present on the ulna. One almost complete ulna and one largely complete ulna (P39105) (Fig. 24Cii - iii). The ulna bears the presence of a shallow trochlear notch and an enlarged and protruding upwards olecranon. The radial notch is shallow but distinctly large and antero-posteriorly wide. Olecranon and anconeal processes (olecranon tip) are of relatively equal length. Ulna's shaft is curved and medially-laterally compressed.

Three ulna fragments (P2229316) (Fig. 24Civ - vi). One lacking the distal part of the ulna with only the coronoid process present and lacks the styloid process and head. One ulna only has the distal region present and the shaft is completely lacking. One ulna lacks the ulna's head. All three ulna fragments depict a shallow but enlarged semilunar (trochlear) notch, and a large and extensive olecranon. The shafts (where present) are of a curvature nature, and the trochlear notch and anconeal (olecranon tip) are of almost equal height with the coronoid process slightly more extended dorsally. The trochlear notch is slightly deeper than in the other ulnae described here, although, are of a similar level of broadness.

Only one other ulna belonging to *Protemnodon otibandus* (Plane 1967) from the Otibanda Formation in Papua New Guinea (Fig. 1) (See **Paper V** for description of the Otibanda Formation) is available for comparison. *P. otibandus*'s ulna appears to have a more reduced, but deeper radial notch in comparison to *P. anak*. Furthermore, *P. otibandus*'s ulna bears the presence of a tall and strongly developed olecranon process, similar to *P. anak*. Although, this feature is slightly shorter in comparison. The sinuous and relatively robust nature of the ulnar shafts, the reduced trochlea and radial notch concedes the possibility for high mobility in *P. anak*'s elbow. Additionally, the tall condition of the coronoid process indicates an enlarged insertion area for the M. anconeus and M. triceps brachii muscles, which are muscles that assist in flexibility of the elbow region (Kear et al. 2007). The combination of these characteristics, may infer the constant employment of the forelimbs, aiding *P. anak* in quadrupedal strategies or in grasping of branches and twigs during feeding.

**Radii** - One largely complete radius and one distal radial fragment (P39101) (Fig. 24Di). Shaft has a sinuous and robust nature, whereby it curves laterally towards the neck and the head of the radius and then

curves medially towards the distal portion of the radius. The tubercle is enlarged and ovally shaped, enabling a large insertion area for the M. biceps brachii muscles. The styloid process is rectangular, significantly stepped, and protruding outwardly. The radial head is tall and slender, and the neck of the radius is slightly thicker than the head. The radial tuberosity is large with a flat surface. The interosseous border of the radius extends for 2/3 of the radius shaft. The ulnar notch weakly protrudes antero-posteriorly.

One almost complete radius (P39105) (Fig. 24Dii) with an enlarged tubercle that serves as an attachment area for the M. biceps brachii muscle is present on the radius. The head of the radius has an oval profile. The neck region of the radial shaft projects a deep curve that bends into a relatively straight shaft that continuous of equal width towards the distal region of the ulna. Styloid process (although represented here by clay) is markedly stepped and enlarged. The interosseous border along the radial shaft extends for approximately 2/3 of the entire radius. The distal radio-ulnar notch is shallow and relatively broad.

The strongly developed tuberculae are evocative of a large attachment region for the M. biceps brachii muscles, commonly seen in extant tree-kangaroos (Prideaux and Warburton 2010), suggestive of a high degree of plasticity and constant usage of the lower forelimbs. Furthermore, *P. anak*'s radii depict a robust and sinuous-like morphology, a poorly developed obliquely displaced styloid process, and a wide interosseous membrane. These features too are common amongst modern tree-kangaroos. The potentially quadrupedal *P. otibandus* also has a robust and curved radius, although the interosseous membrane is not as wide as in *P. anak*. Nonetheless, these traits on *P. anak*'s radii may signify the everyday employment of the forelimbs for a quadrupedal-like posture.

**Metacarpals** – Two non-fragmented robust metacarpals (P39101) (Fig. 24Ei - ii). Shafts of the metacarpals bear a slight bend with a relatively wide base and an elongated scar for the attachment of the interosseous muscles. The carpo-metacarpal joint is significantly stepped. Strongly developed tuberculae are present suggesting an enlarged attachment region for the extensor musculature. The robust profile and the enlarged tuberculae are indicative of a large insertion area for the extensor muscles, which may signify that *P. anak* may have had a high capability for grasping and manipulation of various food items.

## Ribs, Pelves, and Vertebrae Elements

**Ribs** – Fifteen fragmented rib elements (P39101) (Fig. 25A). The shafts of each rib reveals a curved profile, with curvature gradually increasing successively from the false ribs (costae spuriae) to the last vertebral ribs (costae fluctuantes). The necks and tubercles are slender and reduced. The articular facets are enlarged and well developed.

**Sacrum** – One almost intact rectangular-like broad and compressed sacral element (P3101) (Fig. 25Bi - ii). The superior articular processes and the coccyx are absent. The transverse processes have a relatively wide morphology and are semi-enlarged. The sacral foramina are large and have a semi-circular profile. The sacral canal is laterally and medially broad. The short and broad anatomy of *P. anak*'s sacrum is of a similar condition to *Sthenurus* spp. (Janis et al. 2014), where it is of a narrow and elongated nature, providing increased rigidity. The sacral in largely bipedal saltating kangaroos (such as *Macropus*) has an elongated profile.

**Pelves** – One partially complete right pelvis fragment (P39105) (Fig. 25Ci - ii). The obturator foramen appears to be relatively large and may have had an oval shape. Pubis is broken off towards the inferior end, however is rectangular, large, and broad with a well developed and almost spiral like proximally oriented acetabulum. Ilium is partially broken off superiorly, and the anterior-superior iliac spine and sacroiliac joint on the ilium is missing completely. Despite the ilium being fragmented distally, it still gives away a hint of a relatively lengthy morphology. The acetabulum is significantly enlarged and the obturator foramen depicts a rectangular shape. The ilium bears large surface areas for the attachment of the *M. gluteus profundus*, *M. iliacus* and *M. gluteus medius* muscles.

Two pelvis fragments (P391114, P39114) (Fig. Ciii - viii) of the ischial bones, depicting the presence of partial residuals of the ilium and pubis and proximal distal ilium fragments. The acetabulum is deep, enlarged and ovally (anteriorly-posteriorly wide) shaped. The ischial body holds an enlarged ischial spine. A deep and elongated groove is present on the ilium fragmented region suggesting a large attachment for the iliacus muscle. The enlarged attachment area along



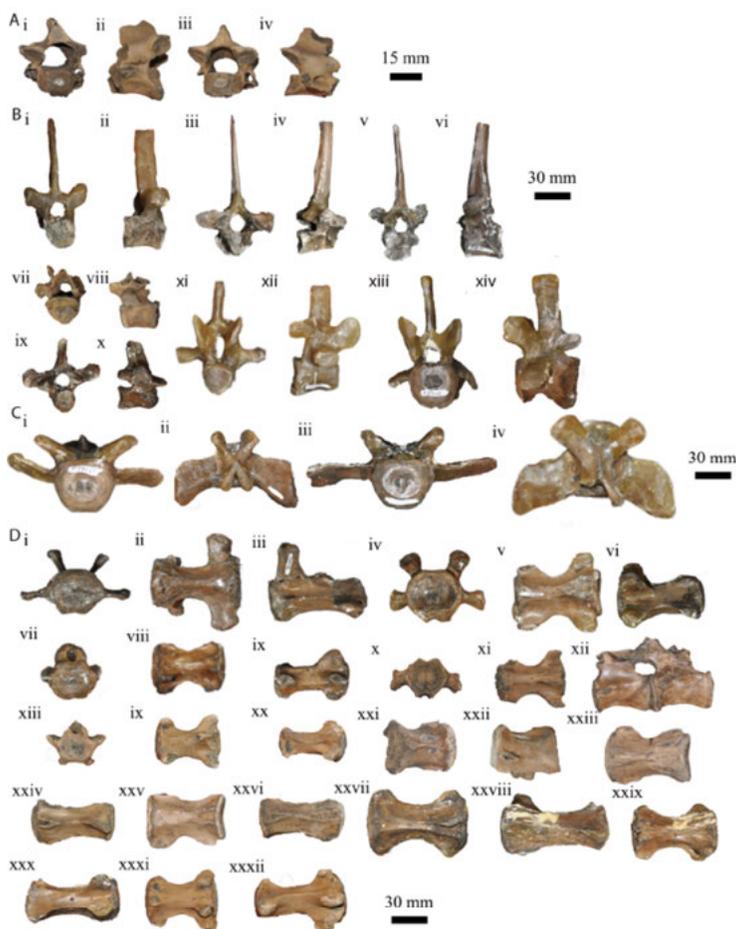
**Figure 25.** Ribs, sacrum and pelvis of *Protamnodon anak*. **A.** Ribs (P39101), **Bi.** Sacrum (P3101) in dorsal view, **Bii.** Sacrum (P3101) in ventral view, **Ci.** Pelvis fragment (P39105) in medial view, **Cii.** Pelvis fragment (P3105) in lateral view, **Ciii.** Pelvis fragment (P391114) in medial view, **Civ.** Pelvis fragment (P391114) in lateral view, **Cv.** Pelvis fragment (P391114) in medial view, **Cvi.** Pelvis fragment (P391114) in lateral view, **Cvii.** Pelvis (P391114) in medial view, **Cviii.** Pelvis (P391114) in lateral view.

*P.anak*'s ilia for the *M. iliacus*, *M. gluteus medius* and *M. gluteus profundus* muscles, is also observed in tree-kangaroos (Warburton et al. 2012), implying a high degree of flexibility in the hip region. Furthermore, a well-developed acetabulum is a feature also observed in *Sthenurus* spp. (Janis et al. 2014), which may suggest a relatively broad demeanour when *P. anak* stood upright, analogous to the sthenurines.

**Cervical Vertebrae** - Two incomplete cervical vertebrae (P39101) (Fig.26Ai-iv), lacking the neural spines and fragmented post-zygapophyses. The neural centrum in each is large and has a semi-circular morphology and the neural arch has a triangular-like profile. The pre and post-zygapophyses have an oval-like shape. The pre-zygapophyses are well-developed and the post-zygapophyses are significantly reduced.

The strongly developed neural centrum is also seen in the balbarids *Balbaroo nalima* (See Paper I) (Black et al. 2014) and *N. gillespieae* (Kear et al. 2007), and *Sthenurus* spp. (Wells and Tedford 1995, Janis et al. 2014), which are characteristic of a large insertion region for the ep-axial and nuchal ligament muscles. These muscles assist the animal in the rotational capacity within the neck region (Finch and Freedman 1988, Kear et al. 2007). Although, the reduction of the post-zygapophyses, similar to frequent bipedal saltating extant kangaroos (such as *Macropus* taxa), suggests reduced flexibility in the vertebral column (Christian and Preuchoft 1996, Kear et al. 2007).

**Thoracic Vertebrae** - Five largely intact thoracic vertebrae, and two incomplete thoracic vertebrae lacking the neural spine (P39101) (Fig. 26Bi - xiv). The centrum is semi-circular and the elliptical neural canal is elongated in each thoracic vertebrae element. The neural spine present in three thoracic vertebrae are long and gracile. The post-zygapophyses are poorly developed, and the pre-zygapophyses are relatively enlarged. Both are horizontally oriented and have a lobated-like shape. The enlargement of the pre-zygapophyses in the thoracic vertebrae are also seen in *Macropus* spp., whereby this feature advocates increased rigidity within the spinal column for increased stability during bipedal locomotion strategies (Christian and Preuchoft 1996, Kear et al. 2007).



**Figure 26.** Vertebrae associated with *Protemnodon anak*. **Ai.** Cervical (P39101) posterior view, **Aii.** Cervical (P39101) lateral view, **Aiii.** Cervical (P39101) posterior view, **Aiv.** Cervical (P39101) lateral view, **Bi.** Thoracic (P39101) posterior view, **Bii.** Thoracic (P39101) medial view, **Biii.** Thoracic (P39101) posterior view, **Biv.** Thoracic (P39101) medial view, **Bv.** Thoracic (P39101) posterior view, **Bvi.** Thoracic (P39101) lateral view, **Bvii.** Thoracic fragment (P39101) posterior view, **Bviii.** Thoracic fragment (P39101) lateral view, **Bix.** Thoracic fragment (P39101) posterior view, **Bx.** Thoracic fragment (P39101) medial view, **Bxi.** Thoracic (P39101) posterior view, **Bxii.** Thoracic (P39101) medial view, **Bxiii.** Thoracic (P39101) posterior view, **Bxiv.** Thoracic (P39101) lateral view, **Bi.** Lumbar (P39101) posterior view, **Cii.** Lumbar (P39101) ventral view, **Ciii.** Lumbar (P39101) posterior view, **Civ.** Lumbar (P39101) ventral view, **Di - xxxii.** Caudal and mid-eris caudal (P29121) (P39101) (P39105) (P39132) (P39134) (P391114).

**Lumbar vertebrae** - Two fragmented lumbar vertebrae, which have been reconstructed with the use of clay (P39101) (Fig. 26Ci-iv). The transverse processes are significantly elongated and dorso-ventrally displaced as are the pre- and post-zygapophyses. The neural canals have an ovoid-like morphology, and the centroms are rounded. The anapophyses are elongated and strongly developed. The elongated and large transverse processes suggest a large attachment area for the M. erector spinae muscle, similar to *N. gillespieae* (Kear et al. 2007). These muscles are suggestive of a high degree of flexibility in the lumbar vertebrae of *P. anak*.

**Caudal Vertebrae** – A number of caudal and mid-series caudal elements (P29121) (P39101) (P39105) (P39132) (P39134) (P391114) (Fig. 26Di - xxxii) Elongated and laterally oriented pre-zygapophyses and large blade-like pre- and post-zygapophyses. The transverse processes are elongated and horizontally oriented. Centrum depicts a large and rounded hexagonal-like form. The centrum is also dorso-ventrally compressed and the mid-section is considerably waisted. Well-developed and medially-laterally oriented oblong shaped transverse processes whereby the proximal transverse processes are markedly larger than the distal transverse processes. The dorso-ventrally compressed profile of *P. anak*'s caudal vertebrae and the presence of elongated transverse processes are similar to the caudal vertebrae of *N. gillespieae* (Kear et al. 2007), *B. nalima* (See **Paper I**) (Black et al. 2014), extant dorcopsids and tree-kangaroos (Flannery and Szalay 1982). This condition is suggestive for an enhanced flexibility in the dorso-ventral aspect of the tail.

## Hind Limb Elements

**Femora** - Two largely complete, left and right femurs (P39115) (Fig. 27Ai - iv) both depicting large and significantly wide greater trochanters and modest in comparison lesser trochanters. Trochanteric neck is relatively wide, and a deep and distinct plantar groove. Femoral shaft is elongated and bears the presence of a distinct mid-line boss and large insertion area for the M. quadratus femoris muscle.

One fragmented femur, whereby the lesser trochanter is lacking and has been replaced by clay to reconstruct the femur (P159918) (Fig. 27Av - vi). The palanter groove is deep and distinct. Large and rounded greater trochanter and the femoral shaft is slender,

elongated and bears an enlarged attachment for the *M. quadratus femoris* muscle and the mid-line boss.

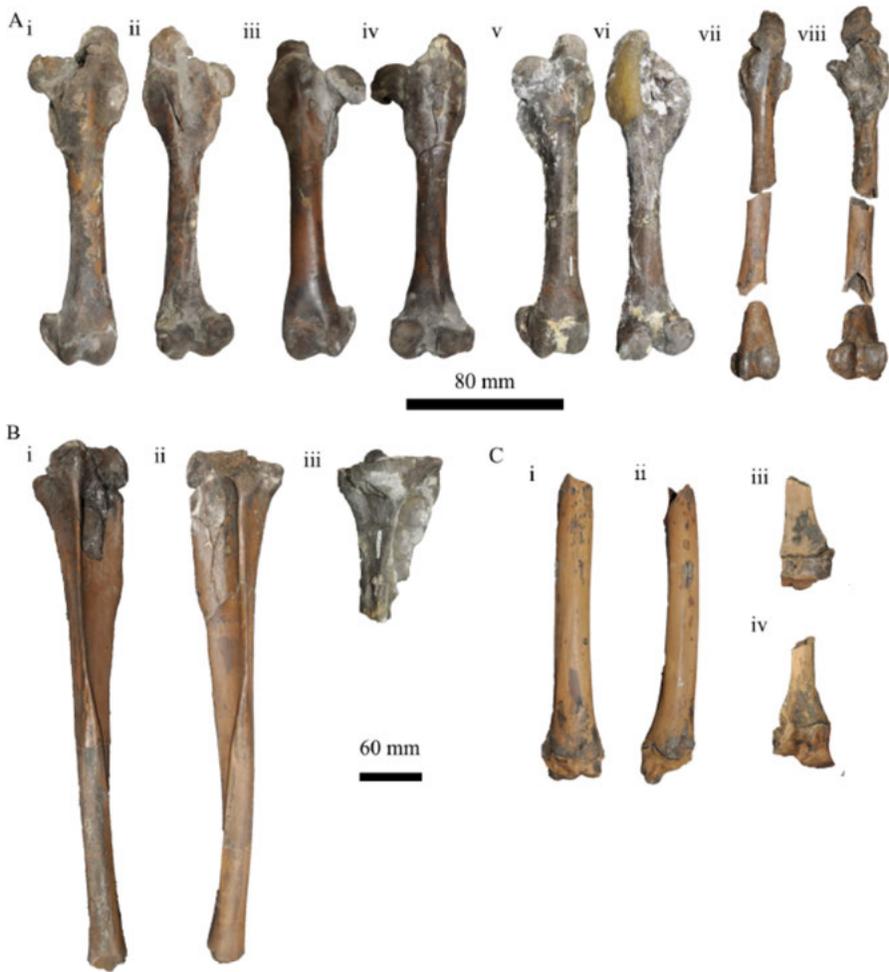
One femur (P39101) (Fig. 27Avii - viii), broken in three regions along the shaft and the proximal aspect of the femur is significantly fragmented. Despite the shaft having fractured in three different regions, the shaft still gives the appearance of a long and slender femur, and the midline boss is extensive. A large insertion area for the *M. quadratus femoris* muscle is present. Palanter groove is distinct and deep. Greater trochanter is large as is the lesser trochanter.

The femoral neck in *P. anak* is wide and robust, similar to members of *Dendrolagus* (Warburton et al. 2011). An enlarged and rounded morphology of the femoral head is also a condition observed in the extant tree-kangaroos. Furthermore, a large attachment area along the femoral shaft for the *M. quadratus femoris* muscle in *P. anak*, is possibly indicative of a preference towards quadrupedal locomotion.

**Tibiae** - Two fragmented and incomplete tibiae (P39105) (Fig. 27Bi - ii), of which only the inferior parts are present, lacking the superior regions of the tibiae. Although, imperceptible, one of the tibial fragments gives away a slight bend. A raised and enlarged anterior border is present and an elongated and wide lateral surface.

One partially complete tibia (P39101) (Fig. 27Biii), lacking the distal region of the bone. The tibia proximal fragment exhibiting large and posteriorly protruding lateral intercondyle tubercle and medial intercondylar tubercle. Both of the medial and lateral tubercles are large and extend antero-posteriorly and dorso-ventrally. The oblique line of the tibia runs deep as does the tuberosity of the tibia. A large region for the attachment of the *M. tibialis cranialis* and *popliteus* muscles is observed along the distal region of the tibia.

The slight curve in *P. anak*'s tibial shafts is also perceived in *Protomnodon snewini* (Bartholomai 1978), which is believed to indicate the insertion region for the *M. flexor digitorum profundus* and *M. gastrocnemius soleus* muscles, indicative of flexibility within the pes and ankle. The reduced tibia-fibula contact in *P. anak* is a feature also observed in *N. gillespieae* (Kear et al. 2007), the potentially quadrupedal Papua New Guinean *Protomnodon tumbuna* (Flannery et al. 1982), in both living and extinct tree-kangaroos (Flannery and Szalay 1982), in the strictly quadruped *H. moschatus*, and in *Protomnodon snewini* (Bartholomai 1978). This trait is suggestive of high mobility within the lower hind limbs and ankle. Furthermore, the



**Figure 27.** Humeri, tibiae and fibulae material of *Protegnodon anak*. **A<sub>i</sub>**. Humerus (P39115) in Dorsal View, **A<sub>ii</sub>**. Humerus (P39115) Ventral View, **A<sub>iii</sub>**. Humerus (P39115) in dorsal view, **A<sub>iv</sub>**. Humerus (P39115) in ventral view, **A<sub>v</sub>**. Humerus (P159918) in dorsal view, **A<sub>vi</sub>**. Humerus (P159918) in ventral view, **A<sub>vii</sub>**. Fragmented humerus (P39101) in dorsal view, **A<sub>viii</sub>**. Fragmented humerus (P39101) in ventral view, **B<sub>i</sub>**. Tibia (P39105) in dorsal view, **B<sub>ii</sub>**. Tibia (P39105) in dorsal view, **B<sub>iii</sub>**. Tibia (P39101) in dorsal view, **C<sub>i</sub>**. Fibula proximal fragment (P39105) in dorsal view, **C<sub>ii</sub>**. Fibula proximal fragment (P39105) in medial view, **C<sub>iii</sub>**. Fibula distal fragment (P39114) in dorsal view, **C<sub>iv</sub>**. Fibula distal fragment (P39114) in medial view.



**Figure 28.** Astragali, calcanea and cuboid material of *Protemnodon anak*. **Ai.** Astragalus (FU400118) in dorsal view, **Aii.** Astragalus (P159917) in dorsal view, **Aiii.** Astragalus (P39113) in dorsal view, Astragalus (P209937) in dorsal view, **Bi.** Calcaneum (P159917) in posterior view, **Bii.** Calcaneum (P39101) in posterior view, **Biii.** Left calcaneum (P39132) in posterior view, **Biv.** Right calcaneum (P39132) in posterior view, **Bv.** Left calcaneum (P39113) in posterior view, **Bvi.** Right calcaneum (P39113) in posterior view, **Bvii.** Left calcaneum (P3105) in posterior view, **Bviii.** Right calcaneum (P3105) in posterior view, **Bix.** Calcaneum (P209937) with cuboid still attached, **Ci.** Cuboid (P159917), **Cii.** Cuboid (P39132), **Ciii.** Cuboid (P39101/P39105), **Civ.** Cuboid (P39101/P39105), **Cv.** Cuboid (P39113).

tibiliae of *P. anak* appear to be relatively shorter than its femora. Which is a condition seen in other members of the *Protemnodon* genus (Kear et al. 2008), *H. moschatus*, *Dendrolagus* (Warburton et al. 2011) and Dorcopsids (Janis et al. 2014) and is a characteristic commonly associated with preference towards quadrupedal and pentapedal locomotion. Also, the enlarged insertion area for the M. tibialis cranialis and popliteus muscles along the distal tibia is indicative towards an increase in the ankle-joints flexibility, which further infers possibility of the utilization of a combination of quadrupedal and slow bipedal movements.

**Fibulae** - Fibula fragment (P39105) (Fig. 27Ci - ii) of which only the superior and inferior parts are available, with the shaft and head lacking. The lateral malleolus is large and significantly stepped. The medial malleolus is much smaller than the lateral malleolus and is quite minuscule. The neck of the fibula is dorso-ventrally wide and has a triangular-like shape.

One fragmented fibula (P39114) (Fig. 27Ciii - iv) with only the distal and proximal portions of the bone available and shaft largely absent. Some depiction of the fibula shaft is provided from the proximal fragment suggesting a semi-lengthened attachment area for the M. fibularis longus et brevis muscle. Medial malleolus is reduced in comparison to the lateral malleolus, which is enlarged and markedly stepped. Fibula head is comparatively enlarged and is wider than the fibular neck. Both the distal and the proximal tibiofibular joint are deep and wide. Distally a relatively large tibia-fibula contact area is present.

The well-developed fibular sulcus and the broad proximal tibio-fibular joint on *P. anak*'s fibulae are characteristics also observed in *Dendrolagus* spp. (Bishop 1997) and in *N. gillespieae* (Kear et al. 2007), which are reminiscent of plasticity within the lower hind limbs. The lengthening of the M. fibularis longus et brevis muscle insertion area along the fibulae's shafts of *P. anak* is another trait suggestive of increased mobility (particularly towards dorsal flexion) in the lower hind limb region. The attachment area for the M. fibularis longus et brevis muscles in the fibulae associated with *Dendrolagus* is of a comparable nature (Warburton et al. 2012).

**Astragali** – One complete isolated astragalus (FU400118) (Fig. 28Ai), with a reduced lateral trochlear crest and a heightened and extensive medial trochlear crest. Compressed trochlear sulcus with a deep groove and a large and posteriorly protruding navicular facet. Lateral

and medial trochlear crest are unequal in height and antero-posteriorly oriented, with the medial trochlear crest extending significantly higher than the lateral trochlear crest. Slightly extended and shallow medial malleolar fossa.

One isolated, largely intact right astragalus (P159917) (Fig. 28Aii). Enlarged and anteriorly protruding navicular facet. Medial trochlear crest larger and lateral trochlear crest are unequal in height. Lateral trochlear crest marginally reduced. Trochlear sulcus compressed bearing the presence of a deep groove.

One complete right astragalus (P39113) (Fig. 28Aiii). Medial trochlear ridge is considerably elevated and is significantly larger than the lateral trochlear ridge. Lateral trochlear crest is compressed and reduced. Trochlear sulcus is transversely wide and the astragalus morphology is dorsally wide. Navicular facet extends out laterally, is enlarged and has a square-like morphology.

One semi-worn left astragalus (P209937) (Fig. 28Aiv) with a reduced lateral trochlear crest and a raised and extensive medial trochlear crest. Navicular facet is significantly worn but is enlarged, square-like in outline and distally displaced. Trochlear sulcus is semi-deep and medially-laterally wide.

The strongly developed, obliquely oriented navicular facet, the reduction of the lateral trochlear crest, the enlargement of the medial trochlear crest, and the semi-deep trochlea groove on the astragali associated with *P. anak* are all features common to extant (Bishop 1997) and extinct tree-kangaroos (Warburton and Prideaux 2010). These astragali characteristics are similar to *N. gillespieae* (Kear et al. 2007) and suggest increased mobility within the ankle, and could potentially indicate a more quadrupedal-like lifestyle for *P. anak*.

**Calcanea** - One largely intact calcaneum (P159917) (Fig. 28Bi) with an elongated yet dorso-ventrally wide tuber calcanei. A significantly stepped calcaneum-cuboid articulation. A broad tuber calcanei which cuts off straight horizontally towards the lateral end of the calcaneum. Astragalus-calcaneum facet large and distinct. The talar facet protrudes dorsally with distinct contours, and extends anteriorly. Sustentaculum tali protrudes out anteriorly but extends down ventrally. Presence of a distinct and markedly tapered lateral talar facet. Plantar rugosity angulates ventrally and the ventral-medial facets are separated and well developed.

One, isolated, largely complete calcaneum (P39101) (Fig. 28ii), with a slender and elongated tuber calcanei, with a ventrally angulated plantar rugosity. Stepped calcaneum-cuboid articulation and a large and antero-ventrally protruding sustentaculum tali. Enlarged talar facet and the astragalus-calcaneum facet is large and divided.

Two, left and right, largely non-fragmented calcanea (P39132) (Fig. 28iii - iv). Gracile tuber calcanei, and a dorso-ventrally broad and ventrally oriented plantar rugosity. Sustentaculum talus enlarged and is antero-ventrally directed. The calcaneum-cuboid articulation is significantly stepped, and the talar facet and astragalus-calcaneum facet are distinct and deep.

A left and a right calcaneum (P39113) (Fig. 28v - vi). Tuber calcanei is elongated and widens posteriorly along the plantar rugosity. Calcaneum-cuboid articulations are significantly stepped. Sustentacula talorum are anteriorly displaced and have a reduced semi-rectangular-like shape. Lateral talar facets are tapered and have a circular contour. Talar facets are distinctly separated. The astragalus-calcaneum facets on both calcaneums are broad and enlarged.

Two calcaneums, both relatively complete (P39105) (Fig. 28vii - viii). Both calcaneums bear an elongated tuber calcanei and a large, ventrally and semi-anteriorly oriented sustentaculum tali. The calcaneum-cuboid articulation in both calcaneums is significantly stepped, the plantar rugosity is semi-rounded, and the astragalus-calcaneum and talar facet are significantly elevated.

Almost complete calcaneum (P209937) (Fig. 28ix) with cuboid still attached. Calcaneum's sustentaculum tali has a rectangular-like outline and is horizontally and medially oriented. Talar facet is antero-laterally oriented and the astragalus-calcaneum facet appears to be enlarged (although is difficult to interpret due to the condition of the calcaneum). Tuber calcanei is semi-elongated and extends into an ovally-shaped and broad plantar rugosity.

An elongated tuber calcanei and a significantly stepped calcaneum-cuboid facet are often associated with the employment of fast bipedal saltation as this would provide the animal with restriction in the heel region and hence increased stability during hopping (Bishop 1997). The elongated tuber calcanei in *P. anak*'s calcanea is also seen in the calcaneum belonging to *P. snewini* (Bartholomaii 1978), and is suggestive of restricted mobility. However, the smooth-edged and posteriorly oriented sustentaculum tali on *P. anak*'s calcanea is different to bipedal saltating kangaroos (such as *Macropus* spp.)

(Prideaux and Warburton 2010) and in *Sthenurus* spp. (Janis et al. 2014), and may suggest some partial rotational ability.

**Cuboids** - One complete cuboid (P159917) (Fig. 28Ci), with a robust, large and relatively square-like shape. The calcaneal facet on the proximal end of the cuboid is large, with a centralized protruding bump. The external cuneiform facet is represented by a large and shallow convex surface and is laterally displaced. The fourth metatarsal attachment feature is strongly developed, has a rounded end, and is anteriorly displaced. The lateral plantar tuberosity is broad and is significantly stepped anteriorly, and extends out and flattens out laterally. The navicular contact facet is enlarged and has an ovoid shape. A semi-deep groove is present for the attachment of the *M. peroneus longus* muscle.

One complete square-shaped cuboid (P39132) (Fig. 28Cii). A shallow and wide calcaneum contact area, and a laterally enlarged navicular facet. The cuneiform contact area is laterally oriented and is well developed. The lateral plantar tuberosity is strongly developed and flattens out in a lateral direction. Two complete (but relatively worn) squared cuboids (P39101/P39105) (Fig. 28Ciii - iv), one slightly larger than the other. An enlarged proximal calcaneum attachment area is observed in both cuboids. A deep and elongated groove is present on each cuboid representing a large attachment area for the *M. peroneus longus* muscles. An ovoid contact area for the navicular and a laterally oriented robust and enlarged lateral plantar tuberosity are present on the cuboids. A laterally facing and strongly developed convex external cuneiform contact region is also observed in each cuboid.

One completely intact cuboid (P39113) (Fig. 28Cv) with a squared outline. A strongly developed and wide calcaneum and navicular facet, and a laterally displaced enlarged cuneiform contact area are depicted on the cuboids. A well developed and profound groove for the *M. peroneus longus* muscle and a large laterally oriented plantar tuberosity is also present on the cuboid.

*P. anak*'s cuboids are comparatively large in comparison to the other available pedal material, which is equivalent to the cuboid associated with the Miocene *Hadronomus puckeridgei* (Murray 1995) and in *Simosthenurus* spp. (Pledge 1980). A strongly developed lateral plantar rugosity on the cuboid in *P. anak* is a feature also observed in the Late Miocene *Dorcopsoides fossilis* (Woodburne 1967), which may imply some degree of flexibility was present within *P.*

*anak*'s pes. Other notable characteristic on *P. anak*'s cuboids that are indicative of flexibility within the foot, are the presence of the deep and elongated groove which serves as an attachment are for the M. peroneus longus muscle, and the laterally displaced cuneiform contact, which is also a trait seen in *H. mochatus*, *Dendrolagus* spp., and *N. gillespieae* (Kear et al. 2007). All these features are suggestive of plasticity in the foot of *P. anak* and could possibly indicate the preference towards a probable quadrupedal-like gait.

**Metatarsals** - Two relatively broad fifth metatarsals (metatarsals V) (P39101, P39132) (Fig. 29Ai - iii) showing slightly ventrally curved shafts. Two largely intact fifth metatarsals, one fifth metatarsal fragmented proximally. The sesamoid grooves are distinctly divided. The base and head of the metatarsals are slightly wider than the shaft. The tuberosity is significantly enlarged.

A metatarsal IV, non-fragmented (P159917) (Fig. 29Bi). Metatarsal head intact, antero-posteriorly broad shaft, yet dorso-ventrally intermediate elongated. The grooves for the sesamoid bones run deep and are distinctly separated by a protruding ridge. The base of the metatarsal where the cuboid attaches is deep and distinct. A deep groove is present along the anterior region of the metatarsal's base for the attachment of the second toe. Along the posterior section of the metatarsal's base, a deep and distinct crest is present for the attachment of the third toe.

Two fourth metatarsals (IV) (P39105) (Fig. 29Bii - iii), of which one is complete and the other is moderately fragmented, however is still largely intact. On both metatarsals the head is absent, and both have an elongated (distal-proximally) and relatively broad dorso-ventrally shaft. The necks of the base and neck become dorso-ventrally wide and have a rectangular-like outline.

One fourth metatarsal (P39101) (Fig. 29Biv) lacking the head. Gracile shaft, neck and base become dorso-ventrally wide. Metatarsal I attachment enlarged, Internal cuneiform is distinctly developed, and the middle cuneiform is wide and extensive. The tuberosity is enlarged, as is the tibialis anticus. Grooves for sesamoid bones moderately developed.

One almost complete metatarsal IV (P39134) (Fig. 29Bv), with proximal region of the metatarsal damaged and missing. Shaft is longated with slight widening at the proximal and distal ends of the metatarsal. Grooves for the sesamoid bones are enlarged and distinct.

One isolated fourth metatarsal (P159917) (Fig. 29Bvi) with base present, although hard to observe due to the presence of rock material still attached, making the metatarsal-cuboid attachment hard to interpret. Shaft is slender and elongated, and the metatarsal bears points of attachment on both the dorso-ventral and antero-posterior sides for the second and third toe's first metatarsals. The attachment to the second metatarsal along the metatarsal distal head bears a remnant of a ridge to separate the posterior and anterior parts however, appears to be far less distinct than the ridge in the P159917 metatarsal.

Two relatively complete metatarsals IV (P39113) (Fig. 29Bvii - viii) belonging to the fourth toe. Noticeably, the shafts are elongated with proximal widening (along the necks of the metatarsals) and gradual distal tapering of both metatarsals. External cuneiforms are enlarged. A large and elongated attachment area for the M. flexor digitorum profundus muscles is present along the metatarsal's shafts.

One distal metatarsal fragment (P159917) (Fig. 29Bix), bearing an elongated, medially-ventrally broad and dorso-ventrally compressed shaft. The sesamoid grooves are shallow but relatively large.

**Phalanges** - A number of proximal phalanges (P159917) (P39105) (P39132) (P39134) (Fig. 29Ci - xvi). Anteriorly, the shafts tends to curve, giving the metatarsal a downwards curved appearance. The shafts also give a slightly waisted form and the second metatarsal attachments are anteriorly-posteriorly smooth with a slight increase posteriorly. Along the head of the third metatarsals, the pedal phalange attachments protrude out into an ovoid shape bearing a semi-ridge between the posterior and the anterior regions.

An assortment of middle phalanges (P39101) (P39132) (P39105) (Fig. 29Di - x). In dorsal and ventral view, the shafts of the phalanges are semi-waisted. Additionally, the shafts are dorso-ventrally broad along distal (base) and proximal (head) metaphysis and gradually curve inwards into the diaphysis regions giving away the waisted appearance.

A number of isolated distal pedal phalanges (P39105) (P39134) (P39101) (P159917) (P39132) (P39105) (P39134) (Fig. 29Ei - xxv), all depicting a relatively short, broad and D-shaped-like profile. Anteriorly the shafts are significantly curved, and both necks



**Figure 29.** Metatarsals V, IV, proximal phalanx, distal phalanx, and pedal unguis components of *Protepnodon anak*. **Ai.** Metatarsals V (P39101) in dorsal view, **Aii.** Metatarsals V distal fragment (P39132) in dorsal view, **Aiii.** Metatarsals V proximal fragment (P39132) in dorsal view, **Bi.** Metatarsal IV (P159917) in dorsal view, **Bii - Biii.** Metatarsals IV (P39105) in dorsal view, **Biv.** Metatarsal IV (P39101) in dorsal view, **Bv.** Metatarsal IV (P39134) in dorsal view, **Bvi.** Metatarsal IV (P159917) in dorsal view, **Bvii - Bviii.** Metatarsals IV (P39113) in dorsal view, **Bix.** Metatarsal IV (P159917) in dorsal view. **Ci - xvi.** Proximal phalanx (P159917) (P39105) (P39132) (P39134) in dorsal view, **Di - x.** Distal phalanx (P39101) (P39132) (P39105) in dorsal view, **Ei. - xxv.** Distal pedal phalanx (P39105) (P39134) (P39101) (P159917) (P39132) (P39105) (P39134) in dorsal and ventral view.

of the head and base regions are dorso-ventrally wide and have a rectangular outline with a convex-shaped head and base. Sesamoid bone groove's and tuberosities are of a compact nature.

The relatively short and dorso-ventrally wide state of the metatarsals belonging to *P. anak*, are of a similar condition to the metatarsals in *P. snewini* (Bartholomai 1978), in the likely quadrupedal *P. otibandus* (Plane 1967), in *H. moschatus*, in *Dendrolagus* and *Bohra* spp. (Warburton and Prideaux 2010). This may propose a relatively broad and short foot for *P. anak*, which would have probably aided in maintaining balance when moving at a slow bipedal, or quadrupedal, or even pentapedal (tail powered) stride. Equally, the broad, large, and highly curved pedal phalanges associated with *P. anak* are another indication for the need to maintain balance, as these conditions on the unguals would increase the ability to grip and hold onto irregular substrates and branches (Kear et al. 2001a).

## Conclusion

### Cranial Material

The cranial rostral regions and the dentaries of *P. anak* appear to be of a notably gracile nature, which may have facilitated in obtaining an increased reach to feed on leaves attached to branches that were located higher-up in the canopy, perhaps suggesting a similar ecological role and morphological adaptations to the modern-day giraffe (*Giraffa camelopardalis*) (Mitchell and Skinner 2003, Badlangana et al. 2011). This level of dentary and rostral elongation is absent in *Wallabia*. Furthermore, *P. anak*'s cranial anatomy (aside from dental analogies) is also different to *Wallabia* by being proximally wider (Bartholomai 1973). Furthermore, the dentaries belonging to *Wallabia* are far less robust in comparison to *P. anak*'s lower mandibles. Even though, there is a considerable likeness in dental components between *P. anak* and *Wallabia*, this may suggest a likely comparable diet and perhaps an analogous ecological purpose.

### Post-Cranial Material

The scapulae belonging to *P. anak* are broad, relatively large, sub-rectangular in shape (for the insertion of the M. supraspinatus and infraspinatus muscles), the supraspinous and infraspinous fos-

sae are significantly enlarged (large area for the inclusion of the M. subscapularis muscle), which point towards a high possibility for quadrupedal strategies (Kear et al. 2007). The robustness of *P. anak*'s humeri combined with the reduced bicipital groove, the significantly developed pectoral crest, the enlarged deltoid ridge, the transversely wide trochleae, an amplified capitulum, the strongly developed supracondylar ridge (for attachment of the M. pectoralis minor, M. pectoralis quartus, M. pectoralis superficialis muscles), are all indications for flexibility of the upper arms, and may further propose consistent disposition towards quadrupedalism. The ulnae have a tall coronoid process (indicating a large region for insertion of the M. anconeus and M. triceps brachii muscles), a reduced trochlea, and a weakly developed radial notch. The presence of these characteristics may demonstrate the likelihood of an increase in lower forelimb mobility (Kear et al. 2007), and the probable constant utilization of quadrupedal movements. The radii associated with *P. anak* reveal strongly developed tubercles (for attachment of the M. biceps brachii muscles), have a reduced styloid process, a broad interosseous membrane, and the shaft is robust and sinuous. These traits are suggestive of the persistent use of the forelimbs, likely during a quadrupedal stance (Prideaux and Warburton 2010) and possibly during grasping and holding onto various vegetation types for consumption. Furthermore, the enlargement of the tubercles (suggesting developed of the extensor ligaments) and the robust anatomy of *P. anak*'s metacarpals would imply the possibility for improved grasping abilities.

The cervical vertebrae of *P. anak* have an enlarged neural canal, suggesting a large insertion region for the ep-axial and nuchal ligaments. The lumbar vertebrae bear large and elongated transverse processes, suggestive of an increased inclusion area for the M. erector spinae muscle. The caudal vertebrae are dorso-ventrally compressed and have strongly developed and elongated transverse processes. The combination of these traits would imply some mobility within the spinal column. However, the enlarged pre-zygapophyses on the thoracic vertebrae and the reduction of the post-zygapophyses on the cervical vertebrae of *P. anak* may suggest some restriction in mobility of the upper spinal region (Christian and Preuchoft 1996, Wells and Tedford 1995, Kear et al. 2007, Finch and Freedman 1988). The pelves of *P. anak*, reveal an augmented and broad acetabulum, an extensive and large attachment area for the M. gluteus medius and M. gluteus profundus muscles along the ilia. These features coupled with a relatively broad sacrum, would suggest ample flexibility within the pelvic area.

The extensive inclusion area for the M. quadratus femoris muscle, the amplified and spherical shape of the femoral head, and

the broad and robust morphology of *P. anak*'s femora would suggest a higher probability of quadrupedal strategies as opposed to a fast bipedal hopping gait. The fibulae of *P. anak* bear strong development of the fibular sulcus, a significantly wide proximal tibio-fibular joint, and a deep and elongated insertion scar for the attachment of the M. fibularis longus et brevis muscle. These characteristics are similar to extant tree kangaroos (Bishop 1997, Warburton et al. 2012) suggestive of enhanced flexion within the ankle of *P. anak*, which may indicate a preference towards a more quadrupedal and/or slow bipedal-like walk. The tibiae, exhibit a semi-curved shaft (for the insertion of the M. flexor digitorum profundus and M. gastrocnemius soleus muscles), a reduced tibia-fibula contact area, a well developed, distally located, deep scar suggestive of a large area of attachment for the M. tibialis cranialis and popliteus ligaments. These features are clear indications for an increase in lower limb, ankle, and pes mobility, which would be advantageous for quadrupedal-like strides. *P. anak*'s calcanea bear the presence of a rounded and posteriorly oriented sustentaculum tali, which is suggestive of some flexibility despite the features being similar to extant frequently bipedal hopping macropodoids (such as the significantly stepped calcaneum-cuboid articulation and the relatively elongated tuber calcanei). The large cuboids bear an enlarged lateral plantar rugosity, the laterally oriented cuneiform, and a large attachment area for the peroneus longus muscle. These features are indicative of relatively high degree of flexibility within the pes of *P. anak*. In addition, the strong development of the medial trochlear crest and the navicular facet on the astragali provides another clear indication of increased rotational mobility within the tibia, fibula, and astragalus in *P. anak*. Furthermore, the stout and dorso-ventrally broad metatarsals, and the large unguis claws are characteristics that would suggest a short and broad pes, which would further suggest the need to maintain balance on uneven grounds and a probable inclination towards slower locomotion types. Conjointly, the curved contour of the pedal phalange would indicate gripping of substrates during movement, similar to extant tree kangaroos.

## PAPER V

### Systematic Revision of the Fossil Macropodiformes

The systematics of the fossil macropodiforms is capricious (See **Paper V**). The crown group radiation of Macropodiformes constitutes of the modern groups of macropodiformes: the Macropoididae (consisting of the kangaroos (*Macropus* (with subgenera: *Macropus*, *Notamacropus* and *Osphranter*)), wallabies (*Wallabia*), tree-kangaroos (*Dendrolagus*, *Bohra*), quokkas (*Setonix*), pademelons (*Thylogale*), rock-wallabies (*Petrogale*), hare-wallabies (*Lagorchestes*), nail-tail-wallabies (*Onychogalea*) and the greater and lesser Dorcopsids. The Potoroinae (*Potorous*), bettongs (*Bettoniga*), rufous bettong (or rufous rat-kangaroo) (*Aepyprymnus rufescens*) and the desert rat-kangaroo (*Caloprymnus* (recently extinct)), and the Hypsiprymnodontidae: represented by only one living species - the musky rat-kangaroo (*Hypsiprymnodon moschatus*). - the only extant macropodiform that lacks the anatomical adaptations for bipedal hopping, and can only quadrupedal bound. Within the crown radiation the following extinct genera currently exist: *Borongaboodie*: (Late - Early Pleistocene Potoroid (*Borongaboodie hatcheri*), the macropodids: *Cookeroo* (Late Oligocene - Early Miocene), *Kurrabi* (Early Pliocene - Late Pleistocene), *Galanarla* (Mid Miocene), *Watutia* (Pliocene), *Silvaroo* (Pliocene), and *Baringa* (Early Pleistocene). Various genera have been placed into the tribe *Incertae sedis*, due to uncertainty of their systematic placements and these include; *Congruus* (Late Pleistocene), *Prionotemnus* (Pleistocene), extinct tree-kangaroos (*Bohra*) (Early - Pleistocene), modern tree-kangaroos (Dendrolagini), Dorcopsis (Late Miocene - recent), and the Lagostrophini (Late Pliocene - recent).

The fossil macropodiform clades currently consist of: the Balbaridae (Late Oligocene - Middle Miocene), small to medium sized quadruped and possibly arboreal (See **Paper I** and **III**) kangaroos; the large and extremely diverse ice-age browsing kangaroos, the Sthenurinae (Early Miocene - Late Pleistocene); the omnivorous (and possibly carnivorous) giant extinct rat-kangaroos, the Propleopinae

(Early Miocene – Early Pleistocene); Palaeopotoroinae (Late Oligocene), represented by one species, *Palaeopotorous priscus*, which may (at present) represent the most basally stem macropodiform (See **Paper II**); the Potoroidae, consisting of the extinct genera belonging to the Potoroidae family; and the basal grade of paraphyletic bulungamayines (Late Oligocene - Early Miocene), which are recognised as stem macropodids and potoroids (Cooke, 1999, Cook 1997, Kear et al. 2001b)

Over the years, the placements of the macropodiform key-clades have alternated considerably (Fig. 30, also see **Paper V** Fig. 3). This is likely due to the absence of adequate post-cranial material (with a significant bias in cranial and dental fossil components) and due to various gaps within the macropodiform fossil record (Cooke 1999). Nevertheless, the first hypothesized placement of the key macropodiform fossil clades (Fig. 30A) suggested that the Potoroidae included Propleopinae, Palaeopotoroinae, Bulungamayinae (which was at the time was recognized as a clade) and Hypsiprymnodontinae formed a monophyletic group. The Balbaridae are believed to be a sister-taxon to the Macropodidae (Sthenurinae and Macropodinae) (Archer 1984, Flannery 1989, Flannery and Archer 1985, Archer and Flannery 1987). The placement of Hypsiprymnodontinae changed dramatically when later studies revealed that the modern potoroids are more closely related to modern macropodines than to the the only living representative of the Hypsiprymnodontinae, *Hypsiprymnodon moschatus* (Fig. 2) (Flannery 1989, Flannery and Archer 1987, Archer and Flannery 1985, Burke et al. 1998, Burk and Springer 2000). Henceforth, the Hypsiprymnodontidae no longer was placed within the Potoroidae.

In the second hypothesized relationship of the key fossil macropodiform clades, the Propleopinae are believed to have been closest related to the Hypsiprymnodontinae and are placed into the Hypsiprymnodontidae (Fig. 30B). The Balbaridae are now believed to be the most basally branching macropodiform fossil clade and the Hypsiprymnodontidae, Potoroidae (including the Potorinae and the bulungamayines, Macropodidae (Sthenurinae and Macropodinae) are praphyletic to the Balbaridae (Fig. 30B) (Burk et al. 1998, Burk and Springer 2000, Kear and Cooke 2001, Bates et al. 2014, Meridith et al. 2009, Kear et al. 2001a, Kear et al. 2001b).

The third hypothesis suggested that the propleopines should no longer be placed into the Hypsiprymnodontidae and that they are more closely related to the Balbaridae (Fig. 30C). Bulungamayinae is no longer placed into the Potoroidae, and is no longer recognised as a clade, and the bulungamyines taxa are now regarded as a basal-stock Oligo-Miocene stem macropodids and potoroids (Cooke

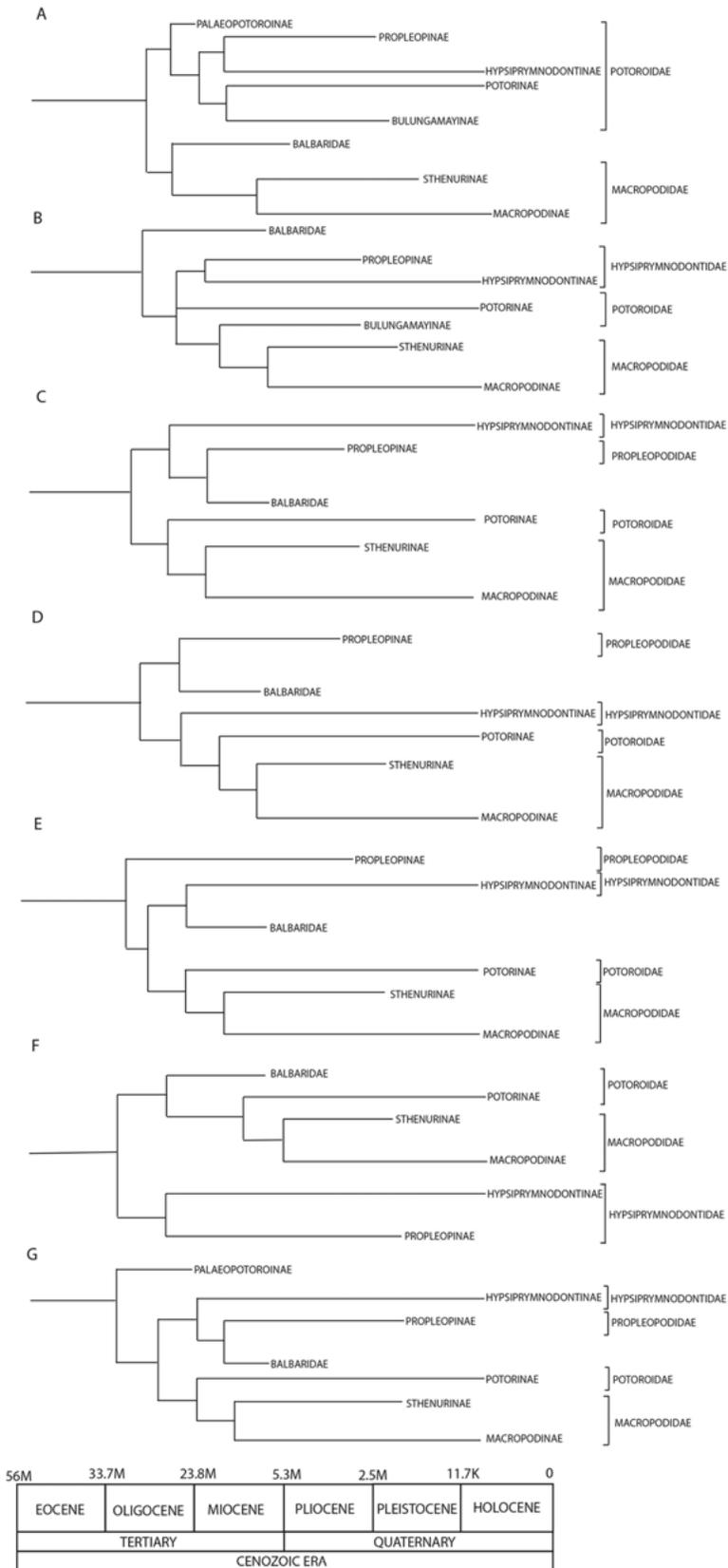
1997, Cooke 1999, Black et al. 2014, Cooke et al. 2015, Butler et al. 2016, Kear and Cooke 2001, Kear and Pledge 2008).

The fourth placement of the key clades suggested that the Propleopodidae and Balbaridae are monophyletic and are the most basal stem lineages (Fig. 30D). The Hypsiprymnodontidae is now believed to have been more closely related to the Potoroidae and the Macropodidae (Oligo-Miocene bulungamayines, Sthenurinae and Macropodinae) (Fig. 30D) (Wroe et al. 1998, Black et al. 2014, Kear et al. 2007).

The fifth hypothesis proposed that the Propleopodidae are the basal sister-taxon clade, and Hypsiprymnodontidae and Balbaridae are monophyletic (Fig. 30E) The Potoroidae and the Macropodidae (Macropodinae, Sthenurinae and bulungamayines) forming the other monophyletic grouping, being paraphyletic with the Propleopodidae, Hypsiprymnodontidae and the Balbaridae (Fig. 30E) (Butler et al. 2016, Bates et al. 2014).

The sixth hypothesized relationship of the main macropodiform clades advocated that Balbaridae was more closely related to the Potoroidae (Fig. 30F). Furthermore, the Propleopinae were placed within the Hypsiprymnodontinae again, and the Hypsiprymnodontidae are now paraphyletic with the Macropodidae (Macropodinae, Stheuninae), Potoroidae and the Balbaridae (Fig. 30F) (Travouillion et al. 2016). The seventh hypothesized placement of the key macropodiform clades suggests Palaeopotoroinae (See **Paper II**) as the most basal macropodiform clade. The Hypsiprymnodontidae are placed in a sister relationship with the now again monophyletic Propleopodidae and Balbaridae (Fig. 30G).

It is clear that the systematics of the main key fossil clades within the macropodiforms are relatively inconclusive and subject to impulsive alterations. The constant changes in the placements of the different macropodiform fossil lineages, has been mainly due to the often complete lack or sparse amounts of post-cranial material associated with many fossil species. This is partially due to past collections taking priority over cranial, jaws and dental fossils than post-cranial material. This has caused the available macropodiform fossil material to largely consist of fossil crania and fossil elements associated with the crania. Furthermore, in most phylogenies including fossil macropodiforms, the characters within matrices are significantly biased towards dental, cranium and dentary features (e.g. see Prideaux and Warburton 2010), with often only a select few characters for the post-cranial material.



**Figure 30.** Different systematic placements over the years of the various macropodiform fossil clades. **A.** The Balbaridae are placed as a sister-taxon to the Macropodidae (Sthenurinae and Macropodinae). Potoroidae consists of the Hypsiprymndontinae, Bulungamayinae, Palaeopotoroinae, and Potoroinae (Flannery 1989, Flannery and Archer 1987, Archer and Flannery 1985). **B.** The Propleopinae are placed within the Hypsiprymndontinae and Palaeopotoroinae is placed within the Bulungamayinae. Bulungamayines are placed as a sister-relationship with the Macropodidae and the Balbaridae are monophyletic (Burk and Springer 2000, Burk et al. 1998, Merideth et al. 2009, Cooke 1997, Cooke and Kear 1999, Kear et al. 2001a, Kear et al. 2001b). **C.** Propleopinae no longer within the Hypsiprymndontidae and is now monophyletic with Balbaridae. Hypsiprymndontidae, Propleopodidae and Potoroidae, Macropodidae are polyphyletic. Bulungamayinae no longer a clade, and are now believed to be basal stem macropodids and potoroids (Black *et al.* 2014, Cooke et al. 2015, Butler et al. 2016, Kear and Cooke 2001, Kear and Pledge 2008). **D.** Propleopodidae, Balbaridae and Potoroidae, Macropodidae, Hypsiprymndontidae are polyphyletic (Wroe et al. 1998, Black et al. 2014, Kear et al. 2007). **E.** Propleopodidae sister-taxon to all macropodiform clades, and Hypsiprymndontidae most closely related to the Balbaridae (Butler et al. 2016, Bates et al. 2014). **F.** Hypsiprymndontinae and Propleopinae are monophyletic and placed together into the Hypsiprymndontidae. Balbaridae is placed as a sister-taxon to Potoroidae (Travouillion et al. 2016). **G.** Palaeopotoroinae is the most basal macropodiform and the other clades are placed in the same arrangement as in C (See **Paper II**).

## Future Objectives

It is overtly clear that additional skeletal fossil bones need to be examined and not merely dentile, dentary and cranial components. Since, the post-cranial remains are just as imperative as the cranial elements, as they too provide key information of the fossil animal's lifestyle. This would allow for a better understanding of fossil macropodiform ecology and evolutionary patterns.

Additionally, the phylogeny of the *Protemnodon* members is arbitrary and ambiguous. This may likely be partly due to the disproportion in matrices whereby very few character scores are present for post-cranial material, making most phylogenies including *Protemnodon* species to be mainly established on dental, cranial and jaw characteristics (e.g. Prideaux and Warburton 2010). Therefore, expansion of character scores within matrices for phylogenetic studies is essential to resolve the proper placement of not only *Protemnodon* species but also for all extinct species within the main macropodiform clades.

## Svensk Sammanfattning

Kängurur, råttkängurur och deras fossila släktingar tillhör en grupp som kallas för Macropodiformes, vilka representerar en av de mest mångformade förgreningarna av pungdjur på jorden. Genom sin evolutionära historia har de anpassat sig till många olika ekologiska roller i Australien, Papua Nya Guinea, Indonesien och på vissa omkringliggande öar. Det fossila fyndmaterialet av macropodiformerna såsom hittills känt, sträcker sig tillbaka till sen Oligocen (ca 25 miljoner år sedan), men baserat på molekylär data, så tros gruppen ha uppstått under Eocen. De kan ha utvecklats ur en förfader som var lik klätterspungdjuren (familjen Phalangeridae) och avknoppades från en utvecklingsgren som var nära släkt med dagens pungrävar kring denna tid. Råttkänguruerna (familjen Potoroidae) som levde under sen Oligocen till tidig Miocen anses ofta vara övergångsformer mellan klätterspungdjurslika former till former som var mer lika makropodiformerna.

De nulevande macropodiformerna är välkända för sin tvåbenta hoppning. Bland moderna känguruer, vallabyer och trädkänguruer (familjen Macropodidae), så existerar flera olika ekomorfologiska anpassningar, som till exempel de till största delen trädlevande trädkänguruerna (släktet *Dendrolagus*) från norra Queensland i Australien och Papua Nya Guinea, de medelstora vallabyerna, av vilka här kan nämnas svartsvansvallabyen (släktet *Wallabia*) vilken lever i tätt bevuxna sumpområden, eller klippkänguruerna (släktet *Petrogale*) som har anpassat sig till att leva i bergiga områden, bara för att nämna några få. Vidare bland macropodiformerna så har vi de mångformiga, små till medelstora råttkänguruerna (familjen *Potoroidae*) som inkluderar opossumråttorna (släktet *Bettongia*) och potouriederna (släktet *Potorous*), vilka har utvecklat många olika ekologiska anpassningar, och lever i flera olika naturtyper på det australiensiska fastlandet, Tasmanien, närliggande öar, samt Papua Nya Guinea. Vidare, så har vi bland de moderna macropodiformerna, myskkängurun (*Hypsiprymnodon moschatus*), den enda nulevande macropodiform som saknar de anatomiska anpassningarna för tvåbent hoppning och är den enda levande arten i familjen Hypsiprymnodontidae.

De utdöda macropodiformerna inkluderar för närvarande följande grupper: Palaeopotoroinae från sen Oligocen, utgörades av endast en art, *Palaeopotorous priscus*, vilken kan för närvarande rep-

resentera den allra basalaste stammacropodiform (se **Studie II**), familjen Balbaridae från sen Oligocen till mellersta Miocen, som utgjorde fyrbenta och möjligen trädlevande kängurur (se **Studie I** respektive **Studie III**), de mångformiga sen Oligocena till sen Miocena bulungamayina känguruerna och råttkänguruerna vilka tros vara förfäder till moderna kängurudjur och råttkängurur, de medelstora till stora, möjligen köttätande Miocen-Pleistocena jätteråttkänguruerna av underfamiljen Propleopinae, och de extremt mångformiga istidskänguruerna av underfamiljen Sthenurinae. De fylogenetiska affiniteterna hos de utdöda macropodiformerna har varit föremål för flera olika hypotetiserade fylogener genom åren (se **Studie V** för en sammanfattning), vilka till stora delar har utgjorts av luckor inom de fossila macropodiformerna, på grund av antingen en total avsaknad av eller endast litet känt postkraniellt skelett hos många fossila macropodiformer. Som en konsekvens av detta, så ha fylogenierna ifråga till största delen testats på enbart kraniellt och tandmaterial. Detta har lett till att placeringen av nästan samtliga macropodiforma grupper förblir förhållandevis osäkra. En stor del av denna avhandling utgörs av studiet av postkraniellt material av flera olika macropodiformer för att klargöra deras ekologiska affiniteter, rörelsesätt och fylogenetisk tillhörighet hos de studerade arterna. Vidare, för att få en bättre förståelse för hela gruppens ursprung, så studerades de äldsta macropodiforma fossilen på nytt inkluderandes opublicerat material. Därför, så studerades fossila tänder från sen Oligocen associerade med den fossila råttkängurur *Palaeopotorous priscus* (Nambaformationen, South Australia) (**Studie II**). Arten *P. priscus* är evolutionärt en nyckelart, då den delar kännetecknen som observeras i både macropodiformerna och klätterpungdjuren, det vill säga den påstådda ursprungsgrenen från vilken macropodiformerna kan ha avknoppats. Resultaten som fås från en fylogenetisk analys och jämförande geometrisk morfometri hos oxeltänderna hos *P. priscus* antyder att *P. priscus* är den för närvarande basalaste kända macropodiformen.

Den funktionella ekomorfologiska tolkningen hos olika fossila macropodiformer har än så länge till största delen baserats på drag i kraniet och i tänderna. Detta kan delvis förklaras med bristen på adekvat macropodiformt postkraniellt material, men även på grund av att insamlingar i det förflutna har fokuserat på fossila kranier och tänder. För att fylla i informationsluckan, så har postkraniellt material från olika fossila grupper studerats. Därför så undersöks i **Studie I och III** postkraniellt material från miocena balbarida känguruer, inkluderandes *Balbaroo nalima* och en obestämbalbarid från Riversleighs världsarvsområde i nordvästra Queensland (Australien). Den detaljerade anatomiska undersökningen av de påträffade benen och jämförelsen med andra arter antyder att en trädlevande och fyrbent natur för

balbariderna. . Vidare, så undersökte postkraniellt material från den pleistocena arten *Protemnodon anak* för första gången (**Studie IV**). Det rika fossila materialet som inkluderar bland annat lårben, skenben och mellanfotsben, mättes och jämfördes med ett urval av fossila och utdöda arter, användandes multivariata statistiska metoder. Erhållna resultat föreslår en långsamt gående gångart för *Protemnodon anak* i jämförelse med det påtagliga tvåfota hoppandet som ses hos nulevande macropodiformerna.

I **Studie V** så försöks en revision av de fossila macropodiformerna på, inkluderandes den godtyckliga systematiska historien hos nyckelgrenar bland macropodiformerna

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