MORPHOLOGICAL CORRELATES OF PENTAPEDAL LOCOMOTION IN KANGAROOS AND WALLABIES (FAMILY: MACROPODIDAE)

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BSc (Hons)

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THE UNIVERSITY OF WESTERN AUSTRALIA
THESIS ABSTRACT

Across the animal kingdom, many animals engage the tail as part of the locomotor repertoire. However, nothing compares to the use of the tail as a fifth leg while moving at slow speeds, known as pentapedal locomotion. During pentapedal locomotion, the tail is used to support the body weight while the hindlimbs are drawn forward, and to provide power to propel the body weight forward in kangaroos and wallabies. The central aim of this project is to identify behavioural and morphological correlates of pentapedal locomotion within the Macropodidae.

The adoption of pentapedal locomotion is often attributed to all members of the subfamily Macropodinae. Study 1 of this project tested this assumption using a landmark-based approach to classify locomotion of 16 macropodine species as either pentapedal locomotion or quadrupedal bounding (no use of tail support) at slow speeds. *Macropus agilis, M. fuliginosus, M. irma, M. robustus, M. rufogriseus, Onychogalea unguifera* and *Wallabia bicolor* species used pentapedal locomotion, while *Petrogale xanthopus, M. eugenii, P. lateralis, M. parma, Thylogale thetis, T. stigmatic, T. billardierii,* and *Setonix brachyurus* engaged in quadrupedal bounding at slow speed. The utilization of pentapedal locomotion was linked with the lengthening of the tibia (relative to the femur) and the preference for open habitat.

Study 2 investigated the caudal musculature of the pentapedal western grey kangaroo, *M. fuliginosus*. This was carried out to establish a detailed account of the muscular anatomy prior to subsequent studies of bony morphology. The remarkable features of this species include the large ventral flexors along the entire tail, the heavy development of
the lateral flexors that connect the proximal tail to the pelvis, and the fleshy sacrocaudal musculature that span from the end of the thoracic region to the eighth caudal vertebra. These features reflect the repositioning of the tail under the pelvis prior to the hindlimb swing phase of pentapedal locomotion, and the extension of the tail which occurs during the bipedal hopping cycle.

In Study 3, a comparative approach was undertaken to elucidate how the first fifteen caudal vertebrae (Ca) are specialised for the use of the tail during pentapedal locomotion. Seven functional measurements, based on caudal vertebral dimensions, were used to construct caudal vertebral profiles for 14 species of macropodines categorized into one of four groups with functionally different uses of the tail - pentapedal macropodines, quadrupedal bounding macropodines, rock-wallabies and tree-kangaroos. Pentapedal macropodines demonstrated adaptations of the centrum to resist sagittal plane bending and to bear load in Ca5-13. Additionally, it was evident that large terrestrial kangaroos have adaptations of caudal vertebrae that give stability during bipedal hopping, while smaller wallabies, rock-wallabies and tree-kangaroos have caudal vertebrae that are adapted for lateral mobility as part of their locomotor repertoire.

Study 4 used a geometric morphometric approach on three key caudal vertebrae (Ca1, Ca5 and Ca10) in sthenurines and macropodines. This methodology was used to test differences between the four groups of extant Macropodidae identified in Study 3, and to test the hypothesis that sthenurines (the extinct sister clade to Macropodines) did not engage in pentapedal locomotion. Pentapedal macropodines differ in morphology from all other macropodines in Ca1 and Ca5, but to a lesser extent in Ca10. Sthenurine caudal vertebral morphology was found to be significantly different to pentapedal macropodines in Ca1 and Ca5, and there were also significant differences between sthenurines and non-pentapedal macropodines. The outcomes from this study were two-fold. First, it
corroborated the functional analyses of Ca1-15 in extant macropodines in Study 3. Second, sthenurines were found to lack adaptations associated for the use of the tail in pentapedal locomotion and bipedal hopping. These findings support the hypothesis that sthenurines were unlikely to have adopted a locomotor repertoire similar to extant macropodines. Moreover, sthenurine caudal vertebral morphology is indicative of the adoption of an upright bipedal posture and a striding gait.

These four studies found distinctive morphologies of the caudal vertebral and muscular anatomy that are associated with pentapedal locomotion. This thesis further highlights that the adoption of pentapedal locomotion is associated with extreme specialisation of the body plan for bipedal hopping within the Macropodinae. Importantly, the diversity in tail use as part of the locomotor repertoire reflects the adaptive radiation that has characterised the evolution of the Macropodidae.
STATEMENT OF CANDIDATE CONTRIBUTION

The work presented in this thesis was undertaken from March 2011 to August 2015 at the University of Western Australia in the School of Anatomy, Physiology and Human Biology. Funding for this research was provided by the School of Anatomy, Physiology and Human Biology.

This work is original and was carried out by myself, except where the contributions by other persons are acknowledged.

Chapter 2 (Study 1) was co-authored by my PhD supervisors Natalie M. Warburton and Nick Milne, and data collected by Hazel L. Richards was included in this study. Chapter 3 (Study 2) was also co-authored with Natalie M. Warburton and Nick Milne, and the line drawing in Fig. 3-2 in this study was done by Natalie M. Warburton. The majority of the work in these publications is my own.

Rebekah Shanti Dawson

August 28th 2015
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<td>2D</td>
<td>Two-dimensional</td>
</tr>
<tr>
<td>3D</td>
<td>Three-dimensional</td>
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<tr>
<td>ANCOVA</td>
<td>Analysis of co-variance</td>
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<td>C</td>
<td>Centrum</td>
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<td>Ca</td>
<td>Caudal vertebrae number</td>
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<td>Centrum length</td>
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<td>CoM</td>
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<td>Cy</td>
<td>Coccygeus</td>
</tr>
<tr>
<td>DEP</td>
<td>Distal endplate</td>
</tr>
<tr>
<td>D. ramus</td>
<td>Dorsal ramus</td>
</tr>
<tr>
<td>DTP</td>
<td>Distal transverse process</td>
</tr>
<tr>
<td>DTPB</td>
<td>Distal transverse process breadth</td>
</tr>
<tr>
<td>DVPE</td>
<td>Dorsoventral height of the proximal endplate</td>
</tr>
<tr>
<td>DZ</td>
<td>Distal zygapophyses</td>
</tr>
<tr>
<td>F</td>
<td>Female</td>
</tr>
<tr>
<td>FL</td>
<td>Femur length</td>
</tr>
<tr>
<td>GPA</td>
<td>Generalised Procrustes analysis</td>
</tr>
<tr>
<td>GPA/PCA</td>
<td>Combined generalised Procrustes and principal components analyses</td>
</tr>
<tr>
<td>HP</td>
<td>Haemal process</td>
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<td>HL</td>
<td>Haemal lip</td>
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<tr>
<td>ICH</td>
<td>Interchevronii</td>
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<tr>
<td>IDC</td>
<td>Intertransversarii dorsalis caudalis</td>
</tr>
<tr>
<td>ILC</td>
<td>Intertransversarius lateralis caudalis</td>
</tr>
<tr>
<td>IMC</td>
<td>Intertransversarius medialis caudalis</td>
</tr>
<tr>
<td>IMI</td>
<td>Intermembral index</td>
</tr>
<tr>
<td>IVC</td>
<td>Intertransversarii ventralis caudalis</td>
</tr>
<tr>
<td>kg</td>
<td>Kilogram(s)</td>
</tr>
<tr>
<td>Abbreviation</td>
<td>Description</td>
</tr>
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<td>--------------</td>
<td>-------------</td>
</tr>
<tr>
<td>km/h</td>
<td>Kilometers per hour</td>
</tr>
<tr>
<td>L</td>
<td>Left</td>
</tr>
<tr>
<td>LCV</td>
<td>Longest caudal vertebra</td>
</tr>
<tr>
<td>LM</td>
<td>Landmarks(s)</td>
</tr>
<tr>
<td>M</td>
<td>Male</td>
</tr>
<tr>
<td>MANCOVA</td>
<td>Multivariate analysis of co-variance</td>
</tr>
<tr>
<td>Meta.</td>
<td>Metatarsal</td>
</tr>
<tr>
<td>MLPE</td>
<td>Mediolateral width of the proximal endplate</td>
</tr>
<tr>
<td>mm</td>
<td>Millimetre</td>
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<tr>
<td>movt</td>
<td>Movement</td>
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<tr>
<td>MP</td>
<td>Mammillary process</td>
</tr>
<tr>
<td>MPL</td>
<td>Mammillary process length</td>
</tr>
<tr>
<td>MVR</td>
<td>Multivariate regression</td>
</tr>
<tr>
<td>n</td>
<td>Number of samples</td>
</tr>
<tr>
<td>NA</td>
<td>Neural arch</td>
</tr>
<tr>
<td>p</td>
<td>Probability</td>
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<td>Page number</td>
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<td>PC</td>
<td>Pubococcygeus</td>
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<tr>
<td>PC</td>
<td>Principal component(s)</td>
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<td>PCA</td>
<td>Principal components analysis</td>
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<tr>
<td>PEA</td>
<td>Proximal endplate area</td>
</tr>
<tr>
<td>PrEP</td>
<td>Proximal endplate</td>
</tr>
<tr>
<td>PrZ</td>
<td>Proximal zygapophyses</td>
</tr>
<tr>
<td>PTP</td>
<td>The caudal vertebra where the proximal transverse process first appears</td>
</tr>
<tr>
<td>R</td>
<td>Robusticity</td>
</tr>
<tr>
<td>R</td>
<td>Right</td>
</tr>
<tr>
<td>RCL</td>
<td>Relative centrum length</td>
</tr>
<tr>
<td>RDTTPL</td>
<td>Relative distal transverse process length</td>
</tr>
<tr>
<td>SB</td>
<td>Sagittal bending</td>
</tr>
<tr>
<td>s.d.</td>
<td>Standard deviation</td>
</tr>
<tr>
<td>SDL</td>
<td>Sacrocaudalis dorsalis lateralis</td>
</tr>
<tr>
<td>SDL-L</td>
<td>Lateral belly of sacrocaudalis dorsalis lateralis</td>
</tr>
<tr>
<td>SDL-M</td>
<td>Medial belly of sacrocaudalis dorsalis lateralis</td>
</tr>
<tr>
<td>SDM</td>
<td>Sacrocaudalis dorsalis medialis</td>
</tr>
<tr>
<td>s.e.</td>
<td>Standard error</td>
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<tr>
<td>sec</td>
<td>Second(s)</td>
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<tr>
<td>SP</td>
<td>Spinous pro</td>
</tr>
<tr>
<td>sp.</td>
<td>One species</td>
</tr>
<tr>
<td>spp.</td>
<td>Multiple species</td>
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<tr>
<td>SVL</td>
<td>Sacrocaudalis ventralis lateralis</td>
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<td>xxiv</td>
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<tr>
<td>SVM</td>
<td>Sacrocaudalis ventralis medialis</td>
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<tr>
<td>TEM</td>
<td>Technical error of measurement</td>
</tr>
<tr>
<td>TrCV</td>
<td>Transitional caudal vertebra</td>
</tr>
<tr>
<td>V. ramus</td>
<td>Ventral ramus</td>
</tr>
<tr>
<td>W</td>
<td>Centrum width</td>
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</table>
Kangaroos are well known for being the largest mammals to engage in bipedal hopping. Remarkably, bipedal hopping in kangaroos is very energetically efficient at speeds above 18km/h, particularly in comparison with quadrupedal locomotion in animals of similar size (Dawson & Taylor 1973). To achieve this efficiency, the kangaroo musculoskeletal system has been modified to enable powerful and economical strides as part of the bipedal hopping gait cycle. While these modifications are a key to the success of these enigmatic creatures, the long, heavy hindlimbs of kangaroos complicate efficacy of gait at slow speeds (Dawson 1977). Consequently, kangaroos have evolved a distinctive gait at slow speeds: pentapedal locomotion. During this gait the tail supports and propels the body weight forward (Dawson & Taylor 1973; O'Connor et al. 2014). Despite this unique use of the tail in kangaroos, we understand little about the adoption of this gait more broadly among the Macropodidae, and how the utilization of pentapedal locomotion translates to morphological attributes of the tail within this group.

**The Macropodidae**
The Macropodidae are the family of marsupials more commonly referred to as kangaroos and wallabies. Within the Macropodidae, generally four subfamilies are recognised; the Macropodinae, the Sthenurinae, the Bulungamayinae and the Lagostrophinae (Flannery 1989; Cooke & Kear 1999; Kear & Cooke 2001; Westerman et al. 2002; Prideaux & Warburton 2010). Of these subfamilies, the Macropodinae and the Sthenurinae comprise
majority of the taxa belonging to the Macropodidae. The Macropodinae includes all modern kangaroos and wallabies in Australia and New Guinea (Flannery 1990; Strahan 1995; Menzies 2011). Macropodines first emerged in the fossil record in the late Miocene alongside its sister clade, the Sthenurinae (Prideaux & Warburton 2010). The sthenurines, commonly known as short-faced kangaroos, were principally browsers of sclerophyll vegetation and were diverse during the mid to late Pleistocene (Prideaux 2004). A continent-wide extinction of 90% of Australia’s large herbivores about 40,000 years ago also saw the demise of the sthenurines (Roberts et al. 2001). The bulungamayines, small Miocene macropodids, are also extinct, but are evident in the fossil record between the late Oligocene to the early Miocene (Flannery 1983, 1984 cited in Kear & Cooke 2001). The lagostrophines are represented by two known genera, *Tropsodon* and *Lagostrophus*, of which only the latter is extant (Westerman et al. 2002; Prideaux & Warburton 2010).

In contrast to these lineages, the macropodines radiated into various niches that emerged due to the ongoing aridification of Australia that began in the Miocene, resulting in a rich diversification within this clade still present today (Raven & Gregory 1946; Flannery 1982; Dawson 2006; Martin 2006; Prideaux & Warburton 2010).

The expansion of semi-arid grasslands across the interior of Australia saw the diversification of the most recognisable of the macropodines, the kangaroos (Raven & Gregory 1946; Dawson 1977; Dawson 2012). Kangaroos and ‘typical’ wallabies belong to the genus *Macropus*, which includes fourteen extant species (Nowak, 1991, Strahan, 1995). This genus can be subdivided into three subgenera (Dawson & Flannery 1985); *Macropus Macropus* (the grey kangaroos: *M. fuliginosus* and *M. giganteus*), *M. Osphranter* (the red kangaroo: *M. rufus*; and the euro-wallaroo group: *M. antilopinus, M. robustus*, and *M. bernardus*) and *M. Notamacropus*, which includes the smaller wallabies (Dawson & Flannery 1985). Kangaroos and wallaroos are separated from wallabies within the genus *Macropus* on the basis that they are highly specialised for
grazing, compared to mixed-feeding (grazer/browsers) and browsing taxa (Dawson 2006; Dawson 2012).

The Macropodinae comprises an additional ten extant genera, six of which occur only in Australia, while the four others are native to both Australia and New Guinea. Of these genera, the New Guinean forest-wallabies (*Dorcopsis* spp. and *Dorcopsulus* spp.) are the most plesiomorphic of the macropodines, and are found only in New Guinea (Flannery 1990). Ongoing changes to forest understory and the expansion of woodlands during the Miocene saw the radiation of small-to-medium sized wallabies into a variety of mixed-feeding niches. Tree-kangaroos (*Dendrolagus*) and rock-wallabies (*Petrogale*) became adapted and increasingly isolated to the trees and rocky outcrops, respectively. Of the other small-to-medium sized macropodines, nail-tail wallabies (*Onychogalea*) and hare-wallabies (*Lagorchestes*) moved into mixed-feeding niches, while pademelons (*Thylogale*), the swamp wallaby (*Wallabia*), and the quokka (*Setonix*) occupy browsing niches. Among these species, pademelons and tree-kangaroos are found in both New Guinea and Australia (Raven & Gregory 1946; Groves 1982; Groves & Flannery 1989; Flannery 1990; Strahan 1995; Prideaux & Warburton 2010). This radiation within the Macropodinae has resulted in the evolution of, arguably, the most diverse and successful group of marsupials to ever have existed.

**LOCOMOTOR REPERTOIRE IN THE MACROPODINAe**

Across the macropodines, all members utilize bipedal hopping during fast locomotion (Windsor & Dagg 1971; Hume et al. 1989; Strahan 1995). In this gait, the hindlimbs are moved in unison to transport the body forward (Windsor & Dagg 1971; Dawson & Taylor 1973; Alexander & Vernon 1975; Baudinette 1977; Bennett 1987; Baudinette, Snyder & Frappell 1992). The adoption of this hindlimb dominated gait has led to enlargement and elongation of the hindlimb, and reduction of forelimb length and size. The resultant
forelimb-hindlimb asymmetry is shared by most macropodines (Flannery 1982; Bennett 1987; Grand 1990; Lodder 1991; Kear et al. 2008; McGowan, Skinner & Biewener 2008; Richards, Grueter & Milne 2015).

Kangaroos demonstrate even further refinement of the body plan to increase the efficiency of bipedal hopping. Importantly, metabolic costs are reduced by lengthening the hindlimb (achieved by the lengthening of the tibia relative to the femur), which enables increased stride length. This, in turn, allows kangaroos to increase speed without increasing stride rate above 12 km/h, and contributes to the uncoupling of speed from oxygen consumption within this range (Dawson & Taylor 1973; Alexander & Vernon 1975; Bennett 1987; Dawson 2012). Additionally, with 40% of the body weight positioned around the hips (Dawson et al. 2004), the centre of mass is shifted posteriorly in kangaroos (Alexander & Vernon 1975), which likely reduces the tendency of the body to pitch/rotate during take-off and landing (Grand 1990).

While these modifications are key to the efficiency of bipedal hopping at speeds above 12 km/h, bipedal hopping is very energetically costly at speeds below 6 km/h, and the long and muscular hindlimbs that contribute to achievement of efficient fast locomotion prevent adoption of a typical quadrupedal gait at slow speeds (Dawson & Taylor 1973; Dawson 1977; Dawson et al. 2004; Webster & Dawson 2004; O'Connor et al. 2014). As such, at speeds below 6 km/h kangaroos have co-opted the tail as a fifth leg, for pentapedal locomotion (Dawson & Taylor 1973). During pentapedal locomotion the tail is used to support the body while the hindlimbs are drawn forward, in addition to propelling the body weight forward (Dawson & Taylor 1973; O'Connor et al. 2014). Because adaptations of the body plan that are thought to preclude quadrupedal gait at slow speeds are not universal across the Macropodinae, some authors have proposed that pentapedal locomotion is unique to kangaroos (Dawson 1977; O'Connor et al. 2014).
Despite these postulations, the generalisation that pentapedal locomotion is universal in this group is commonplace in the literature. Hitherto, there has been no establishment of the prevalence of pentapedal locomotion among members of the Macropodinae, or investigations of how body plan specialisations for bipedal hopping may influence the adoption of pentapedal locomotion more broadly across the Macropodidae. Moreover, despite pentapedal locomotion being a highly unusual gait, we know little about the anatomical correlates of this mode of locomotion, either in kangaroos or other macropodines that may engage in this gait. Not understanding the form-function relationship of pentapedal locomotion in extant macropodines makes it impossible to determine whether members of the extinct sister clade, Sthenurinae, utilized this gait. The focus of this thesis is to clarify these areas regarding macropodid locomotor repertoire, which are pivotal to understanding the evolution of gait within this group.

**OVERVIEW OF THIS THESIS**

The general aim of this research is to identify and evaluate the morphological correlates of pentapedal locomotion in kangaroos and wallabies. This is achieved through firstly; identifying which members of the group adopt pentapedal locomotion, and then; investigating the functional morphology of the tail across the Macropodidae, to determine how pentapedal caudal morphology differs from non-pentapedal caudal morphology.

**RESEARCH OBJECTIVES**

To this end, the specific objectives of this project are to:

- Formally identify which taxa among the Macropodinae engage in pentapedal locomotion, and which do not (Study 1)
- Test whether lengthening of the tibia relative to the femur is related to the adoption of pentapedal gait in the Macropodinae (Study 1)
- Provide a detailed description of the muscular anatomy of the tail in a kangaroo (Study 2)
- Investigate how caudal vertebral morphology correlates with the use of the tail during pentapedal locomotion (Studies 3 and 4)

- Investigate caudal vertebral morphology in sthenurines to ascertain whether pentapedal locomotion was a part of their locomotor repertoire in (Study 4)

**THESIS STRUCTURE**

Four experimental studies were designed to address the five research objectives of this thesis. As such, each study is presented as a separate chapter (2, 3, 4 and 5), with a relevant introduction, methods, results and discussion. Studies 1 and 2 are published.

**STUDY 1 - WALKING ON FIVE LEGS: INVESTIGATING TAIL USE DURING SLOW GAIT IN KANGAROOS AND WALLABIES**

Within the literature, the generalisation that pentapedal locomotion is ubiquitous in Macropodidae is commonplace (Blumstein, Daniel & McLean 2001; Prideaux & Warburton 2010). This generalisation is made in spite of previous authors informally noting that pentapedal locomotion is absent, or unlikely, in some species (Baudinette 1977; Strahan 1983; Baudinette, Snyder & Frappell 1992); and, more importantly, that pentapedal locomotion is hypothesised to be associated with specialisations of the body plan (Dawson 1977; Dawson et al. 2004; O'Connor et al. 2014) that are not shared by all members of the Macropodidae (Grand 1990; Kear et al. 2008). To meaningfully compare the morphology between pentapedal and non-pentapedal macropodines, this distinction needed to be resolved. To do so, this study classified slow gait as either pentapedal or non-pentapedal in 16 members of the Macropodinae, from the following genera: *Macropus, Onychogalea, Petrogale, Setonix, Thylogale*, and *Wallabia*. Using raw femur and tibia lengths provided by Hazel. L. Richards (personal data), this study also investigated if hindlimb morphology, measured as crural index (lengthening of the tibia relative to the femur), was associated with the adoption of pentapedal locomotion, as
previously proposed (Dawson 1977; O'Connor et al. 2014). The results from this study informed subsequent studies of pentapedal functional morphology.

**STUDY 2 - MUSCULAR ANATOMY OF THE TAIL OF THE WESTERN GREY KANGAROO, *Macropus fuliginosus***

Interpretation of bony morphology is greatly facilitated by detailed knowledge of the musculature. In the absence of a description of the caudal musculature within the Macropodidae, this study sought to provide a comprehensive account of the musculature in one member of this family, the western grey kangaroo, *M. fuliginosus*. This species was chosen as it is one of the largest extant kangaroos (Strahan 1995), which corresponds to extreme specialisations of the bauplan for bipedal hopping (Dawson 2012), and the use of pentapedal locomotion (Dawson et al. 2015). The detailed description of the caudal musculature of *M. fuliginosus* revealed particular adaptations for the role of the tail in both pentapedal locomotion and bipedal hopping. These findings informed the investigations of caudal vertebral anatomy in Studies 3 and 4.

**STUDY 3 - FUNCTIONAL ANALYSIS OF THE FIRST FIFTEEN CAUDAL VERTEBRAE IN KANGAROOS AND WALLABIES***

To elucidate the morphological patterns in the bony skeleton of the tail that may characterise the use of the tail during pentapedal locomotion, an investigation of the first fifteen caudal vertebrae was undertaken in this study. To achieve this, seven functional measurements based on the caudal vertebral dimensions of these vertebrae were calculated and used to construct caudal vertebral profiles for seven pentapedal macropodines. These caudal vertebral profiles were compared with seven non-pentapedal taxa. As the aim in this study was to describe how the first fifteen caudal vertebrae (together), reflect the role for the tail in locomotion, this chapter provides a description of the caudal vertebral profiles and how they vary between and within groups. Thus,
statistical analyses were not undertaken here, rather, the findings from this study provided a descriptive baseline that informed more fine-grained analysis undertaken in Study 4.

**Study 4 - Did sthenurines use pentapedal locomotion? A geometric morphometric analysis of three caudal vertebrae in the Macropodidae**

While previous authors have proposed that sthenurines did not engage in pentapedal locomotion (Wells & Tedford 1995; Janis, Buttrill & Figueirido 2014), no study has tested if the sthenurine caudal vertebral morphology is different to that of the pentapedal macropodines. Using geometric morphometric methods, this study established how the morphology of the first, fifth and tenth caudal vertebrae of pentapedal macropodines differs from non-pentapedal macropodines, in order to investigate whether it is likely that sthenurines engaged in pentapedal locomotion. Elucidating whether sthenurines engaged in pentapedal locomotion will shed more light on aspects of gait selection in this clade, and in turn, evolution of gait more broadly within the Macropodidae.

**Significance of this research**

Three major contributions to the field of macropodid evolutionary biology have been made as a result of these four studies. Firstly, this research provides the first detailed description of the anatomical correlates of pentapedal locomotion. Secondly, investigations of locomotor repertoire in living and extinct macropodids further elucidates selective pressures that may be associated with the evolution of pentapedal locomotion across the family. Thirdly, the comparative nature of this project enabled the provision of the first family-wide description of caudal functional morphology across the Macropodidae, highlighting the association between tail use, ecology and locomotor repertoire within this group. These contributions are discussed in detail in the final chapter (general discussion and conclusions) of this thesis.
CHAPTER TWO

WALKING ON FIVE LEGS: INVESTIGATING TAIL USE DURING SLOW GAIT IN KANGAROOS AND WALLabies

The first study in this thesis, chapter two is published as Dawson, RS, Warburton, NM, Richards, HL & Milne, N 2015, ‘Walking on five legs: investigating tail use during slow gait in kangaroos and wallabies’, Australian Journal of Zoology, available online from 28the July 2015, DOI: 10.1071/ZO13085. In this thesis, a supplementary figure has also been provided.

ABSTRACT

Pentapedal locomotion is the use of the tail as a fifth leg during the slow gait of kangaroos. Although previous studies have informally noted that some smaller species of macropodines do not engage in pentapedal locomotion, a systematic comparative analysis of tail use during slow gait across a wide range of species in this family has not been done. Analysis of relative movement of the pelvis, tail, and joint angles of the lower limbs during slow gait, using 2D landmark techniques on video recordings, was carried out on 16 species of macropodines. We also compared the relative lengthening of the tibia using crural index (CI) to test whether hindlimb morphology was associated with pentapedal locomotion. Pentapedal locomotion was characterised by three features: the presence of the ‘tail repositioning phase’, the constant height of the pelvis and the stationary placement of the distal tail on the ground during the hindlimb swing phase. The mean CI of pentapedal species was significantly greater than non-pentapedal species (1.71 versus 1.36; \( p < 0.001 \)). This lends support to the hypothesis that the use of pentapedal
locomotion is associated with the relative lengthening of the hindlimb, which in turn is associated with body size and habitat preference within Macropodinae.
INTRODUCTION
Kangaroos are characterised by large hindlimbs, reduced forelimbs and heavy tails. The heavy tail of a kangaroo works as a dynamic cantilever which opposes the torque generated about the hips by the downward pitching of the torso, head and arms during bipedal hopping (Alexander & Vernon 1975; Bennett 1987; Usherwood & Hubel 2012) and as a fifth limb during the slow (walking) gait, known as pentapedal locomotion (Dawson & Taylor 1973; O'Connor et al. 2014). The term ‘pentapedal locomotion’ was coined by Dawson and Taylor (1973) to describe the use of the tail as a fifth leg to support the body weight while the hindlimbs are swung forward in the red kangaroo (Macropus rufus). Windsor and Dagg (1971) first described the slow gait in a range of macropodines as ‘slow progression’ characterised by a “triangle of support at the beginning and end of each stride…” (p. 170). ‘Slow progression’ is often misinterpreted as ‘pentapedal locomotion’ in the literature despite the fact that pentapedal locomotion has only been formally described in red kangaroos. Herein, the role of the tail is investigated during slow gait in a range of macropodine species to resolve which species do and do not engage the tail in pentapedal locomotion.

The evolution of pentapedal locomotion in kangaroos likely results from physiological and morphological constraints such as the inefficiency of hopping at slow speeds (Dawson & Taylor 1973) and long hindlimbs in large macropodines (Dawson 1977; O'Connor et al. 2014). The long hindlimbs of kangaroos are thought to preclude efficacy of quadrupedal locomotion at slow speeds (Dawson 1977; O'Connor et al. 2014). However, the disproportionate development of the hindlimbs is not uniform within the Macropodinae. The relative size of the hindlimb increases with body size due to positive allometry of the tibia (McGowan, Skinner & Biewener 2008) contributing to the contrasting bauplans of the smaller ‘wallabies’ and larger ‘kangaroos’. As such, it has been previously hypothesised that true pentapedal gait is unique to the largest members
of the Macropodinae (Dawson 1977; Baudinette, Snyder & Frappell 1992; O'Connor et al. 2014). Indeed, previous studies of locomotor repertoire in smaller macropodines suggest that pentapedal locomotion is not universal within this group. Quokkas (*Setonix brachyurus*) and tammar wallabies (*M. eugenii*) reportedly lack tail support and employ a quadrupedal bounding gait at slow speeds (Baudinette 1977; Baudinette, Snyder & Frappell 1992), and the red-necked pademelon (*Thylogale thetis*) has also been described to “[travel] on all fours when moving slowly but the tail drags behind and is never supportive” (Strahan 1983).

In this study, non-invasive methods were used to identify the engagement of the tail during slow gait in a range of macropodine species of various sizes, in order to ascertain which species employ true pentapedal locomotion. It was predicted that (1) during pentapedal locomotion, the pelvis will remain at a consistent height during the hindlimb swing phase, when being supported by the tail (e.g. *M. rufus*; O'Connor et al. 2014). In contrast, it is expected that the pelvis will dip towards the ground during this phase in non-pentapedal species, reflecting a lack of tail support. It is also hypothesised that (2) in non-pentapedal species there will be evidence of quadrupedal bounding in the joint angles of the hip, knee and ankle. Given that the tail is weight-bearing during pentapedal locomotion, it is hypothesised that (3) the distal portion of the tail will be placed and remain stationary during the hindlimb swing phase in pentapedal species. Conversely, non-pentapedal species are expected to move their tails during the hindlimb swing phase as it does not have a weight-bearing role during slow gait. If movement of the tail is apparent in non-pentapedal species, it should be possible to identify species as non-pentapedal through simple observation of the movement of the distal tail during the hindlimb swing phase. Using these criteria, the aim was to categorise a broad range of species as either pentapedal or non-pentapedal macropodines during slow gait. Secondarily, it was sought to test whether (4) the relative lengthening of the tibia (crural
index, CI) is significantly greater in pentapedal macropodines compared to non-pentapedal macropodines.

**MATERIALS AND METHODS**

**SAMPLE AND VIDEO COLLECTION**

In order to test these hypotheses, videorecordings of seventeen individuals from seven species of Macropodinae was analysed. Animals were filmed at Caversham Wildlife Park (CW, Caversham, Western Australia, Australia) and Perth Zoo (PZ, Perth, Western Australia, Australia) between March and September of 2013. The sample for the kinematic analysis included *M. rufus* (Male = 5, Female = 1, PZ & CW), *M. irma* (M=2, F=1, PZ), *M. eugenii* (M=1, F=1), *Onychogalea unguifera* (M=1, CW), *S. brachyurus* (M=3, PZ), *Petrogale lateralis* (M=1, PZ), *Wallabia bicolor* (M=1, CW). Animals were videorecorded with an Olympus OM-D camera, at a shutter speed of 1/1000 secs in order to reduce blurring. Videorecording of the animals at Caversham Wildlife Park was done from outside the enclosure, for *O. unguifera*, and the male *M. eugenii*. Videorecording of all animals at the Perth Zoo was done inside the enclosures/exhibits. Individuals filmed at Perth Zoo were enticed with food during the morning feeding time by zoo-keepers, in order to get the animals to move in a straight line perpendicular to the camera during videorecording. The distance between the camera and the animal was no more than three meters and no closer than one meter. Individuals of the species *M. eugenii* could not be approached, and videorecording had to be done from approximately five meters away from the individual. 6 – 21 cycles were collected for each individual and analysed for foot and tail movement and calculation of joint angles. Representative cycles for kinematic analysis were selected based on their position in the middle of a string of cycles, rather than an isolated cycle. This research was approved by the Animal Ethics Committees at Perth Zoo and The University of Western Australia (Appendix A).
CHAPTER TWO

KINEMATIC ANALYSIS OF FRAMES

Frames were exported from the video recordings in VLC media player (http://www.videolan.org/vlc/index.html) at a rate of 25 frames per second. The frames were imported into digitising software tpsDIG2 (Rohlf 2009, http://life.bio.sunysb.edu/morph/) where 18 homologous landmarks (LMs) were digitised and the 2D (x, y) coordinates were taken from these landmarks (Fig. 2-1, Table 2-1). Raw 2D coordinates were adjusted according to an arbitrary reference landmark. The reference landmark was a stationary object in the field of view that was visible throughout the videorecording (see Fig. 2-6 in supplementary material). To calculate the joint angles of the ankle, knee and hip (A, K, H) we used the Law of cosines (Fig. 2-2), using lengths a-f which were calculated using Pythagoras theorem (Fig. 2-2). To investigate the changing height of the pelvis, the distance between the y-coordinates of LM 2 (where the tail touches the ground) and LM3, LM4 and LM5 (pelvis) were calculated and plotted over time. To investigate movement of the foot and the tail, the distance moved by the x-coordinate of LM11 (foot) and LM1 (distal tail), from the first frame of the cycle was calculated and plotted over time. Distances were first standardised with respect to the reference landmark, and then were size-adjusted by applying the femur length of the individual (calculated from the first frame). To smooth the data for graphical representation we used three-point moving averages.
Table 2-1. Landmarks (LMs) used for digitising the frames.

<table>
<thead>
<tr>
<th>Number</th>
<th>Definition of landmark</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Distal tip of the tail</td>
</tr>
<tr>
<td>2</td>
<td>Cranial-most point of the tail where ground contact occurs</td>
</tr>
<tr>
<td>3</td>
<td>Base of the tail (ventral)</td>
</tr>
<tr>
<td>4</td>
<td>Base of the tail (dorsal)</td>
</tr>
<tr>
<td>5</td>
<td>Ischial tuberosity</td>
</tr>
<tr>
<td>6</td>
<td>Greater trochanter of the femur</td>
</tr>
<tr>
<td>7</td>
<td>Iliac crest</td>
</tr>
<tr>
<td>8</td>
<td>Above the tibial plateau of the knee</td>
</tr>
<tr>
<td>9</td>
<td>Lateral malleolus of the fibula</td>
</tr>
<tr>
<td>10</td>
<td>Posterior-most point of the calcaneal tuberosity of the pes</td>
</tr>
<tr>
<td>11</td>
<td>Anterior-most point of the terminus of claw IV</td>
</tr>
<tr>
<td>12</td>
<td>Metatarsophalangeal joint of digit V</td>
</tr>
<tr>
<td>13</td>
<td>Anterior-most point of the terminus of digit III</td>
</tr>
<tr>
<td>14</td>
<td>Carpus of the hand</td>
</tr>
<tr>
<td>15</td>
<td>Olecranon process of the ulna</td>
</tr>
<tr>
<td>16</td>
<td>Frontal prominence of the nose</td>
</tr>
<tr>
<td>17</td>
<td>Rostral tip of the nose</td>
</tr>
<tr>
<td>18</td>
<td>Reference landmark</td>
</tr>
</tbody>
</table>

**Figure 2-1.** Landmarks used for digitising the frames illustrated on a video frame of *M. rufus.*
Based on the descriptions of the ‘slow progression’ and pentapedal locomotion by Windsor and Dagg (1971) and Dawson and Taylor (1973), we defined the beginning of the slow gait cycle as when the animal places its hands on the ground, and the end of the cycle where the animal places the hands on the ground again to engage in the next cycle. The slow gait cycle is broken into three phases: pre-hindlimb swing, hindlimb swing (where the hindlimbs are swung forward) and post-hindlimb swing. The duration of the slow gait cycle was calculated from the movement of the hand (LM13), and the duration of the hindlimb swing phase was calculated from the movement of the toe (LM11).

In preliminary analyses of the landmark data it was confirmed that during pentapedal locomotion the distal tip of the tail did not move relative to the ground during hindlimb swing phase. So to expand the sample, movement of the distal end of the tail was observed in footage of *M. parma* (n=2), *M. agilis* (n=3), *M. rufogriseus* (n=2), *M. fuliginosus* (n=2), *M. eugenii* (n=1) *Thylagale thetis* (n=2), *T. stigmatica* (n=2), *T. billardierii* (n=4)

**Figure 2-2.** A schematic diagram of the lower limb of a macropodid indicating the landmarks used to derive lengths.

Lengths were used to calculate joint angles of the ankle (A), the knee (K) and the hip (H). Angles A, K and H were calculated using lengths of solid black lines (represent the long axis of the ilium, femur, tibia and metatarsal III) and dashed lines (representing hypothetical lines between landmarks; are labelled a-g). The numbers indicate the landmarks used to calculate these lengths: 6 (greater trochanter of femur), 7 (iliac crest), 8 (above the tibial plateau of the knee), 9 (lateral malleolus of the fibula) and 12 (metatarsophalangeal joint of digit V).
and *Petrogale xanthopus* (n=4) from YouTube; and in poorer quality video footage of *M. robustus* (n=1) and *M. fuliginosus* (n=2) from Caversham Wildlife Park, WA. The number of cycles observed for each individual ranged from one to seven. For this part of the study it was simply recorded whether or not the distal end of the tail moved during the hindlimb swing phase. Publishers of YouTube footage were contacted via the YouTube messenger application and they agreed to the use of the footage for this research (Appendix B).

**Duty Factor, Hindlimb Swing Phase Duration and Total Phase Duration**

For species used in the kinematic analysis (*M. eugenii, M. irma, M. rufus, P. lateralis, O. unguifera, S. brachyurus* and *W. bicolor*), duty factor, hindlimb swing phase duration and total phase duration were calculated. Duty factor was calculated to ensure that the observed gait was in fact a slow gait; duty factor was calculated for the hindlimb closest to view as the proportion of time the foot was off the ground in the total slow gait cycle, 

\[
\text{Duty Factor} = \frac{\text{total time} - \text{hindlimb swing time}}{\text{total time}}
\]

(Alexander 1982). Duty factors greater than 0.5 are considered walking gaits in quadrupeds (Alexander 1982) and kangaroos (Hayes & Alexander 1983). Duty factors greater than 0.5 define the gait as slow due to the fact that the foot is on the ground for more than half of the duration of the stride. Previous studies have shown that duty factor increases as speed decreases (Alexander 2003).

Hindlimb swing phase duration and total cycle duration was calculated according to the definitions of these phases as described earlier in text.

**Crural Index**

Crural index (CI; the ratio of tibia length to femur length) has been reported to correlate with locomotor adaptation of the hindlimb in many mammals (Davenport 1933; Howell 1944; Strasser 1992; Anyonge 1993; Polk 2004; Samuels, Meachen & Sakai 2013), and was used the current study to quantify the lengthening of the hindlimb. CI was calculated
from measurements of dry skeletal specimens housed in the mammal collections at the Western Australian Museum, South Australian Museum, Queensland Museum, Australian Museum, Australian National Wildlife Collection, and Museum Victoria. Femur and tibia lengths were calculated for a total of 193 individuals of *M. fuliginosus*, *M. rufus*, *M. robustus*, *M. rufogriseus*, *M. irma*, *M. agilis*, *O. unguifera*, *W. bicolor*, *P. xanthopus*, *M. eugenii*, *M. parma*, *P. lateralis*, *T. thetis*, *T. stigmatica*, *T. billardierii*, and *S. brachyurus*. Femur length was defined as the longest distance between the femoral head and the articular surface of the medial condyle. Tibia length was defined as the distance between the intercondyloid eminence to the distal articular surface (not including the medial malleolus). Femur and tibia lengths were measured using steel tape if larger than 150mm or with digital calipers if smaller than 150 mm. Measurements represent the functional length of the bone, i.e. the measurement between terminal articular surfaces (Howell 1944). A t-test was used to test whether CI was significantly different between the species which did engage in pentapedal locomotion at slow speeds with those that did not. The data used for this test were the 16 mean values, one for each species.

**RESULTS**

**MOVEMENT OF THE PELVIS AND TAIL DURING SLOW GAIT**

Duty factor was above 0.5 for all individuals investigated in the kinematic analysis (Table 2-2). A consistent height of the pelvis during the hindlimb swing phase was maintained by *M. rufus*, *M. irma* and *O. unguifera* (Fig. 2-3). In *M. irma*, the height of the dorsal surface of the tail base remained consistent throughout the cycle, but the ischium and the ventral surface lowered slightly during the hindlimb swing phase, corresponding to gradual tilting of the pelvis as the hindlimbs swing forward. *O. unguifera* had a small decrease in the height of the pelvis during the hindlimb swing phase (Fig. 2-3). During the pre-hindlimb swing phase *M. rufus*, *M. irma*, *O. unguifera* and *W. bicolor* were observed to straighten the proximal and mid-sections of the tail as it was drawn under
their pelvis, between the hindlegs, in preparation for the supporting role during the hindlimb swing phase (hereafter referred to as the ‘tail repositioning’ phase) (Figs. 2-3 and 2-4). In these species the tail remains stationary and in contact with the ground during hindlimb swing phase and the distal tip of the tail did not move cranially until after the hindlimbs made contact with the ground (Figs. 2-3 and 2-4).

In contrast, there were substantial changes in the height of the pelvis from the ground during the hindlimb swing phase in *S. brachyurus, P. lateralis, W. bicolor* and *M. eugenii* (Fig. 2-3). In these species the pelvis lowers a little, then, distinctly rises before the commencement of the hindlimb swing phase and then lowers again in height after the foot is taken off the ground (Fig. 2-3). The tail was not noticeably repositioned under the pelvis before the hindlimb swing phase and the distal tail tip moved in a cranial direction throughout the hindlimb swing phase. In some cases the tail was not even touching the ground when the hindlimb swing phase was initiated.
Table 2-2. Descriptive statistics of total cycle duration, hindlimb swing phase duration and duty factor in species videorecorded in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th># strides analysed</th>
<th>Total cycle duration (secs)</th>
<th>Hindlimb swing phase duration (secs)</th>
<th>Duty factor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Range</td>
<td>Mean</td>
<td>s.e.</td>
</tr>
<tr>
<td>M. eugenii</td>
<td>2</td>
<td>39</td>
<td>1.15-1.35</td>
<td>1.25</td>
<td>0.07</td>
</tr>
<tr>
<td>M. irma</td>
<td>3</td>
<td>62</td>
<td>1.7-2.55</td>
<td>1.92</td>
<td>0.14</td>
</tr>
<tr>
<td>M. rufus</td>
<td>6</td>
<td>84</td>
<td>2.3-4.55</td>
<td>3</td>
<td>0.37</td>
</tr>
<tr>
<td>P. lateralis</td>
<td>1</td>
<td>19</td>
<td>1.9</td>
<td>1.9</td>
<td>-</td>
</tr>
<tr>
<td>O. unguifera</td>
<td>1</td>
<td>21</td>
<td>2.55</td>
<td>2.55</td>
<td>-</td>
</tr>
<tr>
<td>S. brachyurus</td>
<td>3</td>
<td>59</td>
<td>0.8-2.55</td>
<td>1.92</td>
<td>0.57</td>
</tr>
<tr>
<td>W. bicolor</td>
<td>1</td>
<td>18</td>
<td>1.8</td>
<td>1.8</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 2-3. Movement of the tail, pelvis and foot during the slow gait cycles of some macropodids, relative to the reference landmark.

Traces at the top of each graph indicate the changing joint angles of the ankle, knee and the hip across the cycle. The trace in the middle indicates the forward movement of the tip of the tail (tail movt) relative to the reference landmark. The grey traces at the bottom indicate relative forward movement of the base of the tail and the vertical movement of the pelvis (pelvis movt – LM4, LM3, LM5); relative to the reference landmark. The black trace at the bottom indicates forward movement of the foot (foot movt); relative to the reference landmark. The shaded area indicates the hindlimb swing phase during the slow gait cycle (as indicated by the forward movement of the foot). The area to the left of the shaded area is the pre-swing phase and the area to the right is the post-swing phase. FL = femur length.
Figure 2-3. Movement of the tail, pelvis and foot during the slow gait cycles of some macropodids, relative to the reference landmark.
From the range of video recordings available, where it was not possible to digitise the landmarks (either due to low resolution or oblique view), the distal tail remained steady in *M. agilis*, *M. rufogriseus*, *M. fuliginosus* and *M. robustus*, but moved during the hindlimb swing phase in *M. parma*, *T. thetis*, *T. billardieri* and *T. stigmatica*. Indeed, in some individuals of *S. brachyurus* and *M. eugenii* the tail had no contact with the ground during this period.

**Crural Index**
Mean crural index was significantly (*p < 0.001*) greater in pentapedal species (CI = 1.71 ± s.d. 0.106) than non-pentapedal species (CI = 1.36 ± s.d. 0.218) (Table 2-3).
Table 2-3. Tail use during the slow gait of macropodines observed in this study with associated crural index, body mass and habitat data.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Gait at slow speed</th>
<th>Crural index (CI)</th>
<th>Body mass (kg)</th>
<th>Preferred habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Macropus rufus</em></td>
<td>Pentapedal</td>
<td>2.02</td>
<td>0.06</td>
<td>M=85, F=35</td>
</tr>
<tr>
<td><em>Macropus fuliginosus</em></td>
<td>Pentapedal</td>
<td>1.90</td>
<td>0.10</td>
<td>Grasslands</td>
</tr>
<tr>
<td><em>Macropus robustus</em></td>
<td>Pentapedal</td>
<td>1.88</td>
<td>0.05</td>
<td>M=53.5, F=27.5</td>
</tr>
<tr>
<td><em>Macropus agilis</em></td>
<td>Pentapedal</td>
<td>1.63</td>
<td>0.06</td>
<td>Open forests/woodlands</td>
</tr>
<tr>
<td><em>Macropus riogrigorsa</em></td>
<td>Pentapedal</td>
<td>1.56</td>
<td>0.07</td>
<td>Open forests/woodlands</td>
</tr>
<tr>
<td><em>Onychogalea unguifera</em></td>
<td>Pentapedal</td>
<td>1.54</td>
<td>0.07</td>
<td>Open forests/woodlands</td>
</tr>
<tr>
<td><em>Wallabia bicolor</em></td>
<td>Pentapedal</td>
<td>1.52</td>
<td>0.03</td>
<td>Grasslands</td>
</tr>
<tr>
<td><em>Petrogale xanthopus</em></td>
<td>Quadrupedal bounding</td>
<td>1.45</td>
<td>0.04</td>
<td>M=11, F=6</td>
</tr>
<tr>
<td><em>Petrogale lateralis</em></td>
<td>Quadrupedal bounding</td>
<td>1.35</td>
<td>0.04</td>
<td>M=10, F=6</td>
</tr>
<tr>
<td><em>Thylogale thetis</em></td>
<td>Quadrupedal bounding</td>
<td>1.31</td>
<td>0.02</td>
<td>M=6, F=4</td>
</tr>
<tr>
<td><em>Thylogale billardierii</em></td>
<td>Quadrupedal bounding</td>
<td>1.25</td>
<td>0.02</td>
<td>M=12, F=10</td>
</tr>
<tr>
<td><em>Setonix brachyurus</em></td>
<td>Quadrupedal bounding</td>
<td>1.14</td>
<td>0.02</td>
<td>M=9, F=15</td>
</tr>
</tbody>
</table>

Body mass data from (Strahan 1995) and Perth Zoo (indicated by †), values are maximum weights known for each species. Habitat classifications are modified from and habitat data from Warburton and Prideaux (2010) after Strahan (1995),
JOINT ANGLES DURING THE SLOW GAIT CYCLE

In all species, the ankle dorsiflexes, and the knee extends and then the ankle plantarflexes during the hindlimb swing phase (Fig. 2-3). In species so far determined to be pentapedal (M. rufus, M. irma, and O. unguifera) there are no large changes to the angle of the hip during the slow gait cycle. However, in S. brachyurus, P. lateralis, M. eugenii and W. bicolor just prior to the hindlimb swing phase, the ankle plantarflexes and the hip extends resulting in the elevation of the pelvis as described above (Fig. 2-3).

VARIATION IN THE SLOW GAIT CYCLE

Table 2-2 shows that there is a large range in total cycle duration, hindlimb swing phase and duty factor within M. rufus, M. irma, P. lateralis, S. brachyurus and M. eugenii. It should be noted that the cycle is often broken in all species after the hindlimb swing phase; animals may lift their forelimbs off the ground, and pause before engaging in the next cycle of slow gait.
**DISCUSSION**

Gait selection requires optimization of mechanical and physiological properties such as economy of energy, stability, endurance, manoeuvrability, speed or acceleration (Alexander 1989; 2003). Previous studies have identified variation in gait selection at slow speeds among macropodines (Kawata 1971; Windsor & Dagg 1971; Dawson & Taylor 1973; Baudinette 1977; Baudinette, Snyder & Frappell 1992). This study has provided a formal framework for categorising slow gait within the Macropodinae, using a landmark based approach. Using these methods, this study classified sixteen species of macropodines as engaging in either pentapedal locomotion or quadrupedal bounding during slow gait, as determined by the relative movement of the pelvis, hindlimbs and tail (Fig. 2-5, Table 2-3). The results confirm previous descriptions for the adoption of pentapedal locomotion during slow gait in *M. rufus* (Dawson & Taylor 1973; O'Connor et al. 2014) and *M. agilis* (Kawata 1971), and the absence of the use of the tail in *S. brachyurus* (Baudinette 1977), *M. eugenii* (Baudinette, Snyder & Frappell 1992) and *T. thetis* (Strahan 1983). In addition, this study has added descriptions of the role of the tail in a further eleven species (Table 2-3).

Pentapedal locomotion was characterised by three features during the slow gait cycle. First, pentapedal macropodines have a distinctive repositioning and an apparent stiffening of the tail prior to the hindlimb swing phase; the ‘tail repositioning phase’ (Fig. 2-4), preceding the ‘tail support phase’; as described in *M. rufus* by Dawson and Taylor (1973) (Fig. 2-4). Second, these species maintain a consistent pelvic height during the hindlimb swing phase of the locomotor cycle. This stability demonstrates that the caudal muscles act through the skeleton of the tail to exert vertical force on the ground during the hindlimb swing phase of pentapedal locomotion (O'Connor et al. 2014). Third, pentapedal macropodines fix their distal tail during the hindlimb swing phase/tail support phase (Fig. 2-3). The fixed tail would provide greater friction between the ventral surface of the tail
and the ground, necessary for the propulsive role of the tail during pentapedal locomotion (Alexander 2003; O'Connor et al. 2014).

In contrast, species that employ quadrupedal bounding gait at slow speeds non-pentapedal macropodines (Table 2-3), did not display any of the ‘pentapedal’ features during their slow gait cycle. As such, it is unlikely that the quadrupedal bounders engaged the tail in supporting the body weight, or to provide power and propel the body mass forward, as seen in *M. rufus* (O'Connor et al. 2014). Quadrupedal bounding was also characterised by extension and flexion of the hip prior to the hindlimb swing phase (resulting in the rise of

**Figure 2-5.** Phylogeny of the Macropodoidea adapted from Cardillo et al. (2004) highlighting species that this study categorised as engaging in pentapedal locomotion (black circles) or quadrupedal bounding (grey circles) at slow speed.
the pelvis just before hindlimb swing) as observed in *S. brachyurus, P. lateralis,* and *M. eugenii.* Although *W. bicolor* did not maintain a consistent pelvis height during the hindlimb swing phase, this species did display a fixed distal tail during the hindlimb swing phase, and also demonstrated a tail repositioning phase prior to the hindlimb swing phase.

That *W. bicolor* displayed two of the three characteristic features associated with pentapedal locomotion, has led us to interpret the slow gait cycle of this species as pentapedal locomotion.

Pentapedal locomotion within the Macropodinae appears to be associated with the relative lengthening of the hindlimb. The relative elongation of the tibia (CI), enables increased stride length, and thus faster attainable speeds in larger kangaroos and wallabies (Davenport 1933; Howell 1944; Hildebrand 1974; Hayes & Alexander 1983; Bennett 1987). The relative lengthening of the tibia is part of a suite of morphological specialisations for bipedal hopping in kangaroos and large wallabies, which also includes other modifications to the bauplan such as a long and heavy tail, muscular hindlimbs and long feet (Dawson & Taylor 1973; Alexander & Vernon 1975; Dawson 1977; Baudinette 1989; Grand 1990; Baudinette 1994; McGowan, Skinner & Biewener 2008; Dawson 2012; Usherwood & Hubel 2012; O’Connor et al. 2014). The preclusion of a quadrupedal bounding or walking gait caused by long hindlimbs in kangaroos and large wallabies, has led previous authors to propose that the adoption of pentapedal gait is associated with the relative lengthening of the hindlimb, which is driven relative lengthening of the tibia (high crural index) in macropodines (Dawson 1977; Dawson, Milne & Warburton 2014; O’Connor et al. 2014). That all species that adopt pentapedal locomotion at slow speed also have a high CI, supports this hypothesis (Table 2-3).

The lengthening of the hindlimbs in larger macropodines is driven by the positive allometry of the tibia, such that larger macropodines have a relatively longer tibia
compared to smaller macropodines (McGowan, Skinner & Biewener 2008). This
correlation between body plan and body size corresponds to the observation that
pentapedal locomotion is mostly used by larger wallabies and kangaroos, but not in
smaller wallabies (Table 2-3) (Kawata 1971; Dawson 1977). Despite there being an
apparent relationship between body size and pentapedal locomotion, CI would appear to
be a stronger selective pressure in the evolution of pentapedal locomotion. We propose
this in light of the observation that pentapedal locomotion is used by *M. irma* and
*O. unguifera*, both of which are smaller than *T. billardierii*, which engages in quadrupedal
bounding. *M. irma* and *O. unguifera*, do however have a higher CI than *T. billardierii*.

The use of pentapedal locomotion also corresponds to habitat preference. All species that
engage in pentapedal locomotion inhabit open forests and woodlands, or grasslands
(Table 2-3). The association between the high CI (as a specialisation for bipedal hopping)
and the adaptive radiation of the Macropodinae into open forest and plains has been
previously recognised (Raven & Gregory 1946; Windsor & Dagg 1971; Flannery 1982;
Groves & Flannery 1989; Kear et al. 2008; Prideaux & Warburton 2010). Thus, it is
intuitive given the relationship between CI and pentapedal locomotion described above,
that pentapedal locomotion is likely to be most common in those species with high CI
that inhabit open areas. However, while the relatively long hindlimbs in large kangaroos
and wallabies apparently precludes the use of quadrupedal bounding at slow gait, species
that have relatively ‘medium’ length tibia/medium CI appear to be less constrained to use
pentapedal locomotion. Rather, in these species, gait selection appears to reflect their
environment. For instance, *W. bicolor*, *P. xanthopus* and *M. eugenii* all have a CI of 1.45,
but only *W. bicolor* engages in pentapedal locomotion. Of these three species, *W. bicolor*
is the only one associated with relatively more open habitats (Table 2-3). In contrast,
*P. xanthopus*, adapted to rocky outcrops, and *M. eugenii*, mostly found in dense
understorey and thickets, engage in quadrupedal bounding at slow speeds. The absence
of pentapedal locomotion from the *Petrogale* spp. locomotor repertoire reflects the broader suite of adaptations this genus have evolved for life in three-dimensional environments. Most of these adaptations provide for increased stability and agility in unpredictable environments, and it is not surprising that pentapedal gait would be ill-suited to such environments (Flannery 1982; Sharman & Maynes 1983; McGowan 2006; McGowan, Baudinette & Biewener 2006; Prideaux & Warburton 2010; Warburton & Prideaux 2010). The selection of quadrupedal bounding gait in *M. eugenii* is a point of interest, in that it belongs to the genus *Macropus* for which pentapedal locomotion is most characteristic. That the small wallaby *M. eugenii* does not engage in pentapedal locomotion, further highlights that gait selection at slow speeds in the Macropodinae is associated with both CI and habitat preference (Table 2-3).

The varied locomotor patterns within the Macropodoidea superfamily reflect convergent evolution within this group, as exemplified by the independent evolution of bipedal hopping within the potoroine and macropodine lineages (Flannery 1989). In light of this, it is reasonable to ask whether pentapedal locomotion arose more than once within the Macropodinae. While our data provides some interesting clues, lack of consensus between phylogenetic trees, unfortunately, make it difficult to propose a hypothesis regarding this. In particular, it is the inconsistent placement of *Setonix, Wallabia* and *Onychogalea* as either sister taxa to remaining Macropodinae, or as closely allied with the *Macropus* genus that is problematic (Baverstock et al. 1989; Kirsch, Lapointe & Foeste 1995; Cardillo et al. 2004; Meredith, Westerman & Springer 2009). If *Macropus, Onychogalea* and *Wallabia* represent a single lineage (as depicted in Fig. 2-5), then it could be inferred that that pentapedal locomotion may have only arisen once; in the lineage that gave rise to these genera. However, a more distant relationship between *Onychogalea* and *Macropus* (e.g. Meredith, Westerman & Springer 2009) would lead to a hypothesis that pentapedal locomotion has been converged upon independently in these
two groups. Functional analysis of fossil taxa and greater consensus between phylogenetic trees will shed more light on this.

CONCLUSIONS
This study contributes to the understanding of evolution of locomotor repertoire within the Macropodinae, and highlights the link between hindlimb specialisation, habitat and locomotor repertoire within this group. Importantly, we have reported that not all Macropodines utilise pentapedal locomotion, in contrast to the generalisation that is often made in the literature. The association between hindlimb specialisation and habitat use has been linked to bipedal hopping, but our results are the first to support the hypothesis that pentapedal locomotion is also associated with the relative lengthening of the hindlimb and open country. These findings, in addition to the establishment of features that characterise pentapedal locomotion within the Macropodinae; provide a more informative framework for interpreting locomotor repertoires in both living and extinct macropodines.
Figure 2-S1. Video frames taken from videorecording (from top to bottom) of a male *M. rufus*, a female *M. irma* and a female *P. lateralis* in (A) pre-hindlimb swing (B) hindlimb swing and (C) post-hindlimb swing phases. The small orange circle is the reference landmark.
CHAPTER THREE

MUSCULAR ANATOMY OF THE TAIL OF THE WESTERN GREY KANGAROO, *MACROPUS FULIGINOSUS*


ABSTRACT

The western grey kangaroo is a large bodied kangaroo which engages in pentapedal locomotion at low speeds and bipedal hopping at high speeds. The tail is thought to have functional roles in both of these modes of locomotion. In pentapedal locomotion the tail acts as a ‘fifth limb’ to support the body weight along with the forelimbs while the hindlimbs are drawn forward. The tail has also been suggested to have a role as a counterbalance during bipedal hopping. Based on these functional roles for the tail in locomotion, the caudal musculature of the western grey kangaroo (*Macropus fuliginosus*) was dissected and described in this study. The arrangement of the caudal musculature showed particular adaptations for the role of the tail in both pentapedal locomotion and bipedal hopping.
INTRODUCTION
The heavy tail of a kangaroo is often referred to as the fifth limb, and appears to have important roles during both slow and fast gaits. The most striking use of the tail in locomotion in the kangaroo is during slow progression, where the tail is employed together with the forelimbs to form a tripod, to support the body weight while the two hindlimbs are drawn forward simultaneously (Frith & Calaby 1969; Windsor & Dagg 1971; Dawson & Taylor 1973). The term pentapedal locomotion was coined by Dawson and Taylor (1973) when they described the large bodied red kangaroo, *Macropus rufus*, engaging in this form of slow progression and noting that the animal was ‘supporting itself on front limbs and tail …while swinging its [hind]limbs forward’ (p. 313). The weight-bearing role of the tail has been associated with the development of chevron bones, which provide attachment sites for flexor musculature in the kangaroo (Owen 1848; 1876; Flower 1885; Parsons 1896). The relationship between chevron bone development and ventral flexor musculature has been reported in other mammal groups such as aardvarks (Endo et al. 2012), prehensile-tailed new world monkeys (Chang & Ruch 1947; Organ 2010), cetaceans (Murie 1870; Howell 1971) and ground sloths (Flower 1885).

During bipedal hopping the role of the tail is less well-defined in the kangaroo. Hopwood and Butterfield (1990) described the changing role of the tail during the different parts of the hopping cycle, in an eastern grey kangaroo (*M. giganteus*). While the kangaroo is hopping, the tail was noted to be curved upwards and being actively moved up and down. The tail is at its lowest point in the take-off stage of the hop, when it is positioned just caudal to the extended hindlimb. The tail is at its highest point towards the end of the floating stage of the hop, as the kangaroo is about to land. This description highlights the role of the kangaroo tail in fast locomotion as an active and engaged organ, rather than as a passive appendage (Hopwood & Butterfield 1976). Baudinette (1994) also highlights
that; the large, heavy tail, along with the enlarged hindlimbs and the conical shape of the body, serves to place the centre of mass in a more posterior position in macropodids, in order to facilitate balance in a bipedal posture. Further, that downward rotation of the tail whilst the limbs move backward provides a counteractive force during bipedal hopping. In Baudinette’s (1994) study it was also postulated that the heavy tail in the kangaroo prevents forward pitching upon landing during the bipedal hopping cycle. Alexander and Vernon (1975) and Baudinette (1994) have both suggested that the action of the tail moving up and down works as a counterbalance during locomotion. The movement of the tail, which is counter to the movement of the hindlimbs, is suggested to counteract the tendency of the body to pitch forward while hopping at high speeds. Grand (1990) also suggested that the heaviness of the tail may minimize the tendency of the body to pitch upon landing and take-off. More recently, Usherwood and Hubel (2012) report that energetic savings during bipedal hopping are also achieved through the long tail and head of kangaroos.

Despite its potentially multifaceted role, the detailed muscular anatomy of the tail has not yet been documented. Hopwood and Butterfield (1990) emphasise the active role of the tail in both pentapedal locomotion and bipedal hopping in eastern grey kangaroos (*M. giganteus*) and report that these actions are caused by the contraction of the sacrocaudal musculature rather than by a passive dragging of the tail. Comparative studies of the body composition of macropodines show the tail to be highly muscular and comprise a relatively large proportion of the total body weight, especially in large bodied macropods, suggesting specialisation of the caudal muscles for locomotion (Tribe & Peel 1963; Alexander & Vernon 1975; Grand 1990).

Here we report the detailed muscular anatomy of the western grey kangaroo (*M. fuliginosus*). This species is one of the largest extant kangaroos, males stand up to 2
metres tall. Adults show high sexual dimorphism in body mass and males usually weigh up to 54 kg, and occasionally up to 80 kg, while females, usually weigh up to 28 kg (Hume et al. 1989; Nowak 1991; Strahan 1995). Western grey kangaroos are strong bipedal hoppers and inhabit grasslands, woodlands, open forests, shrubland and heathland (Coulson 1990; 1993). It is expected that the caudal musculature of the western grey kangaroo will show functional specialisations, which may reflect the unique role of the tail in pentapedal locomotion and bipedal hopping.

**MATERIALS AND METHODS**

Six female western grey kangaroos (*M. fuliginosus*) were dissected for this study. The specimens were thawed and skinned. The most ventral part of the pubis was cut through in five of the specimens. This allowed a clear view of the ventral surface of the proximal tail and sacrum, to observe the sacrocaudal musculature of the ventral compartment. The other specimen was cut transversely into 2 cm slices for muscle identification. Specimens were then fixed in 10% formalin for six weeks prior to dissection. Muscles were identified and reflected to confirm points of origin, from the cranial end to the insertion at the caudal end. Radiographs of two of the specimens were used to complement the dissection and confirm bony structures, particularly of the first caudal vertebrae. Additional loose and articulated lumbar, sacral and caudal vertebrae and os coxae were used to confirm landmarks and structures. Published descriptions of the proximal hindlimb Hopwood and Butterfield’s (Hopwood & Butterfield 1976) and an illustration of epaxial muscles (Dawson et al. 2004) were consulted during dissection. Illustrations of the musculature were produced by tracing or sketching high quality photos of the dissected specimens and the cross-sectioned tail. The muscles were named based on the guidelines set out in the Nomina Anatomica Veterinaria (2012) and where necessary, functional synonyms are given, based on caudal muscle descriptions in the literature (Barbour 1963; Lemelin
1995). A table that summarises synonyms of muscle names from previous descriptions of the caudal musculature is provided as supplementary material.

RESULTS

TENDON TRACKS, FUNCTIONAL GROUPS AND BASIC OSTEOLOGY IN THE TAIL OF THE WESTERN GREY KANGAROO

The tail is covered in deep caudal fascia which is a continuation of the thick and fibrous thoracolumbar fascia. Across the dorsum the fascia provides an area for attachment of fibres from the large caudal extensor groups (see below). The deep caudal fascia along with bony processes divides the tail into six osteofascial compartments in the tail; two dorsal, two lateral and two ventral compartments. The dorsal compartments lie between the mammillary processes and the midline, the lateral compartments between the mammillary processes and the transverse processes and the ventral compartments between the transverse processes and the chevron bones, which attach to the haemal processes (Fig. 3-1). These six compartments are enclosed in deep caudal fascia. Embedded in the deep caudal fascia are six tracks of tendons which run along the length of the tail; the dorsal, lateral and ventral tracks. The dorsal tracks are comprised of tendons which insert on the mammillary processes (Fig. 3-1), and the muscles which send these tendons comprise the extensor group. These muscles lie in the dorsal and lateral compartments of the tail and are supplied by dorsal rami only. The lateral tracks are comprised of tendons which insert on the transverse processes and the muscles which send these tendons comprise the lateral flexor group (Fig. 3-1). These muscles lie in the lateral and ventral compartments of the tail and are supplied by both dorsal and ventral rami (the precise supply is indicated later in the text). The ventral tracks are comprised of tendons which insert on the chevron bones, which attach to haemal processes ‘B’ in figure 3-1, and the muscles which send these tendons comprise the ventral flexor group. The
flexors are only located in the ventral compartment of the tail and are supplied by exclusively ventral rami.

The tail is divided into two regions, the proximal region, which includes the first four caudal vertebrae (Ca), and the distal region, which contains the last twenty or so caudal vertebrae. The transitional caudal vertebra (Ca5 in *M. fuliginosus*) divides these two regions and is characterised by the presence of cranial zygapophyses but not caudal zygapophyses (beyond the transitional vertebrae). The distal caudal vertebrae have no zygapophyses, though they retain mammillary processes and transverse processes (German 1982). Observations of articulated skeletons of *M. fuliginosus* suggest that caudal vertebrae 11 to 13 are likely to contact the ground during pentapedal locomotion.

The proximal and transitional caudal vertebrae possess only a distal transverse process,

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**Figure 3-1.** Major osteological landmarks on the fifth caudal vertebra and the tenth caudal vertebra. The caudal vertebrae are show from the dorsal view (left) and proximal view (right). A, the mammillary process; B, the haemal process; C, the distal transverse process; D, the proximal transverse processes.
which is quite large. Through the distal caudal series, a proximal transverse process (Fig. 3-1) appears and gradually increases in size while the distal transverse process diminishes towards the end of the tail.

**EXTENSOR GROUP**

**MM. SACROCAUDALIS DORSALIS LATERALIS (EXTENSOR CAUDAЕ LATERALIS)**

Most of mm. sacrocaudalis dorsalis lateralis (SDL) is restricted to the lumbar and sacral regions where it occupies the space between the ilia, and is divided into medial and lateral bellies. Although the bellies are restricted to the base of the tail, their tendons extend further into the tail where they are embedded in deep caudal fascia. This muscle lies deep to the thoracolumbar fascia, which is continuous with the deep caudal fascia that insheathes the tail. Each belly is comprised of multi-segmental fascicles, which form a strong rounded muscle. The long tendons from the lateral belly and the short tendons from the medial belly insert on mammillary processes and form the proximal portion of the dorsal track of tendons (Figs. 3-2A,B & 3-4).

**LATERAL BELLY**

The lateral belly of SDL appears to be a continuation of the m. longissimus thoracis. Fibres of the lateral belly run between the mammillary processes in the lumbar region to those in the base of tail (Figs. 3-2A & 3-3). The lateral belly shares the mammillary processes with mm. longissimus and mm. multifidus in the lumbar region. Long thin tendons from each segment of the muscle stretch into the tail and attach to the mammillary processes of the fourth to the ninth caudal vertebra (Fig. 3-2A). The twelve tendons (six on each side) of the lateral belly insert laterally on their respective mammillary process (Figs. 3-2A & 3-3). Each of these long tendons arise from inter-muscular tendons within the belly itself. Figure 3-4 shows the long tendons of the lateral belly inserting on mammillary processes.
Figure 3-2. Superficial musculature of the (A) dorsal, (B) lateral and (C) ventral aspects of the caudal musculature in the western grey kangaroo.

Abbreviations: SDL-M, medial belly of sacrocaudalis dorsalis lateralis; SDL-L, lateral belly of sacrocaudalis dorsalis lateralis; SDM, sacrocaudalis dorsalis medialis; ILC, intertransversarius lateralis caudalis; Cy, coccygeus; SVL, sacrocaudalis ventralis lateralis; SVM, sacrocaudalis ventralis medialis; ICH, interchevronii; PC, pubococcygeus; CFM, caudofemoralis. Drawing By NMW.
MEDIAL BELLY

The medial belly is much larger and extends farther caudally than the lateral belly, and appears to be homologous with the m. semispinalis thoracis. The thoracolumbar fascia over the medial belly of SDL remains attached to the dorsal surface of the belly, even when freed from the surrounding muscle. The thoracolumbar fascia gives rise to an intermuscular septa, which divides the left and right sides of the medial belly and attaches to the spinous processes of the lower thoracic and lumbar vertebrae. The deep fascia covering this gives rise to the cranial head of m. caudofemoralis. M. caudofemoralis is a thick muscle with two heads, which extends laterally from its origin from this fascia, the ilium and the transverse processes of the first two caudal vertebrae, over the medial belly of SDL, to insert its tendon on the patelloid (Hopwood & Butterfield 1976). At its medial edge, m. caudofemoralis and the medial belly of SDL share some muscular fibres (Hopwood & Butterfield 1976). The segments of the medial belly run from the spinous processes of the lumbar and sacral vertebrae to the mammillary processes of the caudal vertebrae, crossing five or six segments. In the lumbar region, the fibres arise from the lateral surface of the spinous processes. In this region the medial belly occupies the space between the mammillary processes and the spinous processes (Fig. 3-3). At the caudal end, short tendons of the medial belly, attach to the lateral sides of the first seven mammillary processes. The medial belly is the most superficial muscle on the dorsal surface before it terminates on the mammillary processes of the seventh caudal vertebra. Figure 3-2 shows the dorsal and lateral aspects of SDL in the proximal region of the tail. In figure 3-3 and 3-4 the relative reduction of SDL can be seen along the tail.
Figure 3-3. Cross-section of the tail at the level of the first caudal vertebra.

Abbreviations: A, mammillary process; SDL-M, medial belly of sacrocaudalis dorsalis lateralis; SDL-L, lateral belly of sacrocaudalis dorsalis lateralis; SDM, sacrocaudalis dorsalis medialis; IMC, intertransversarius medialis caudalis; IDC, intertransversarii dorsalis caudalis; ILC, intertransversarius lateralis caudalis; IVC, intertransversarii ventralis caudalis; Cy, coccygeus; SVL, sacrocaudalis ventralis lateralis; SVM, sacrocaudalis ventralis medialis; ICH, interchevronii; PC, pubococcygeus. The stipple indicates the dorsal extensor group, the black indicates the lateral flexor group and the grey indicates the ventral flexor group.
Figure 3-4. Cross-section of the tail at the level of the 4th, 9th and 14th caudal vertebrae.

Where there is more than one segment belonging to the muscle, segments are given an asterisk to identify which muscle segments belong to the same group. Abbreviations: A, mammillary process; B, haemal process; C, transverse process; SDL-M, medial belly of sacrocaudalis dorsalis lateralis; SDL-L, lateral belly of sacrocaudalis dorsalis lateralis; SDM, sacrocaudalis dorsalis medialis; IMC, intertransversarii medialis caudalis; IDC, intertransversarii dorsalis caudalis; ILC, intertransversarius lateralis caudalis; IVC, intertransversarius ventralis caudalis; Cy, coccygeus; SVL, sacrocaudalis ventralis lateralis; SVM, sacrocaudalis ventralis medialis; PC, pubococcygeus; ICH, the interchevronii; D. ramus, dorsal ramus; and V. ramus, ventral ramus. The stipple indicates the dorsal extensor group, the black indicates the lateral flexor group and the grey indicates the ventral flexor group.
M. SACROCAUDALIS DORSALIS MEDIALIS (EXTENSOR CAUDAЕ MEDIALIS)

M. sacrocaudalis dorsalis medialis (SDM) is a small multi-segmental muscle which is the caudal continuation of the m. multifidus lumborum. The fibres of SDM run from spinous processes of the sacrum to the medial side of the mammillary processes, spanning two or three segments. The three segments at the cranial part of the muscle are quite fleshy and distinct from each other, whilst those more caudal are less distinct. At the cranial end of the tail, this muscle lies deep to SDL (Figs. 3-2A, 3-3 & 3-4). The deeper parts of SDM have shorter fibres that only span one or two segments, (Fig. 3-2) similar to the mm. rotatores in the pre-sacral vertebral column (Evans and Christensen 1979; Jüschke 1972).

M. INTERTRANSVERSARIUS MEDIALIS CAUDALIS (IMC)

M. intertransversarius medialis caudalis (IMC) lies in the medial part of the space between the mammillary process and the transverse process (Figs. 3-3 & 3-4) and is supplied by dorsal rami. At the cranial end, IMC arises from a tendinous arch which is continuous with the m. longissimus lumborum. The tendinous arch extends caudally, attaching to the transverse processes of the sacrum and the first three caudal vertebrae. At the cranial border of the fourth caudal vertebra the tendinous arch gives rise to muscle fibres. These fibres form a small belly that generally spans three vertebrae, with a long tendon that inserts on the medial surface of the mammillary process of the thirteenth caudal vertebra. In the remainder of the tail this muscle forms nine more bellies. Each of these bellies arise from the cranial border of the transverse process, span three vertebrae and send a long tendon that inserts on the medial surface of the mammillary process of the caudal vertebra, which is ten segments caudal from the transverse process of origin. Each tendon runs more laterally than the preceding tendon, and they are embedded in deep caudal fascia. These tendons form the distal part of the dorsal track of tendons.
M. INTERMAMMILLARY

Deep in the extensor group, lies the uni-segmental m. intermammillary which is comprised of fascicles which run from mammillary process to mammillary process, similar to the m. inter-mammillary (intermammilares in Slijper 1946) described in the lumbar region of the kangaroo (Lickley 1904). Due to the arrangement of these fibres, and the nature of the sections being in line with the mammillary processes, this muscle is not depicted in figures 3-3 and 3-4.

LATERAL FLEXOR GROUP

M. COCCYGEUS

M. coccygeus is a multi-segmental muscle which fans out medially from the coccygeal fossa of the ischium toward the distal transverse processes of the proximal eight caudal vertebrae (Fig. 3-2B). At the base of the tail the belly of m. coccygeus lies on the lateral aspect of the tail until the level of the seventh/eighth caudal vertebra where it forms a broad aponeurotic attachment to the deep caudal fascia; note its absence from the distal segments of the tail (Figs. 3-2B [towards the caudal end] & 3-4). M. coccygeus is a triangular shaped muscle, with an elongated base and a short, stout apex. Although it is a relatively thin muscle in the sacrocaudal region, as the muscle passes the tuber ischia on the caudal end of the pelvis it becomes very thick, but becomes thinner upon its caudal attachment. At the caudal end of its belly m. coccygeus is crossed cranially by m. piriformis, and both of these muscles lie deep to m. caudofemoralis, as it passes the pelvis laterally. M. coccygeus is supplied by ventral rami.

M. INTERTRANSVERSARIUS LATERALIS CAUDALIS

M. intertransversarius lateralis caudalis (ILC) is multi-segmental and lies laterally. Typically, fibres pass from distal transverse process to distal transverse process and span five segments. At the base of the tail, the cranial attachment is formed by two thin
tendinous slips, which arise close to the attachment of m. longissimus thoracis on the iliac crest. ILC also receives fibres from IMC and the lateral part of the dorsal surface of the distal transverse process (note its relations in Figs. 3-3 & 3-4). The belly of ILC tapers from its cranial attachment until it is eventually represented by a thin aponeurosis (Fig. 3-2B) note its absence in at the cross section at the level of the fourteenth caudal vertebra in figure 3-4. This aponeurosis lies ventral to the dorsal track of tendons and becomes continuous with the deep caudal fascia (9th caudal vertebral level, Fig. 3-4). ILC lies laterally to the lateral belly of SDM over the sacrum, and is deep to the cranial head of m. caudofemoralis, and is supplied by ventral rami.

M. INTERTRANSVERSARII DORSALIS CAUDALIS (IDC)

This muscle is uni-segmental and fascicles run from the mammillary processes to the root of the distal transverse processes of the first six caudal vertebrae and the proximal transverse process of the remainder of the caudal vertebrae. Its close relation to the mammillary process can be seen in figures 3-3 and 3-4. The bundles of fibres are relatively small in the proximal part of the tail. The IDC becomes larger toward its caudal end, as the proximal transverse processes become more pronounced (14th caudal vertebral level, Fig. 3-4). The IDC is supplied by dorsal rami.

M. INTERTRANSVERSARII VENTRALIS CAUDALIS

M. intertransversarii ventralis caudalis (IVC) is a uni-segmental muscle supplied by ventral rami. This muscle is comprised of short fibres that run between consecutive distal transverse processes throughout the tail and in the distal portion of the tail is also comprised of fibres which run from proximal transverse process to proximal transverse process (Figs. 3-3 & 3-4).
M. SACROCAUDALIS VENTRALIS LATERALIS (FLEXOR CAUDAE LONGUS/LATERALIS)

M. sacrocaudalis ventralis lateralis (SVL) is the most dorsal bundle of fibres in the ventral compartment (Figs. 3-2B,C, 3-3 & 3-4). The fibres of SVL arise from the ventral surfaces of the transverse processes and the lateral part of the ventral side of the sacrum. A few fibres also blend with the ILC. The most cranial segment of SVL inserts on the tip of the transverse process of the fifth caudal vertebra, and subsequent tendons continue to the end of the tail. This muscle group forms the lateral tendon track which merges into the ventral tendon track in the distal tail.

VENTRAL FLEXOR GROUP

M. PUBOCOCCYGEUS

M. pubococcygeus (PC) is the most superficial of the ventral musculature in the tail (Fig. 3-2). M. pubococcygeus arises from the cranial end of the sacrum, the ventral surfaces of the pubis and the ischium. The belly of m. pubococcygeus does not extend farther into the tail than the fourth caudal vertebra; note its belly is present at level 4, but not at 9 or 14 in figure 3-4. The tendon of the most cranial segment of m. pubococcygeus attaches to the chevron bone of the intervertebral joint between the 12th and 13th caudal vertebrae. Nine more consecutive tendons are inserted; the tendons lie laterally to the preceding tendon. The medial tendons of the ventral track are initially comprised of tendons from the m. pubococcygeus. The adjacent tendons extend from muscle bellies which arise from the segments of m. sacrocaudalis ventralis medialis.

M. SACROCAUDALIS VENTRALIS MEDIALIS (FLEXOR CAUDAE BREVIS/MEDIALIS)

M. sacrocaudalis ventralis medialis (SVM) is a multi-segmental muscle which arises from along the ventral midline of the sacral and caudal vertebrae, deep to m. pubococcygeus, and lateral to the m. interchevronii muscle groups (Figs. 3-2C, 3-3 & 3-4). The most cranial segment of SVM attaches to the tip of the chevron bone between the 13th and 14th
caudal vertebrae, the next segment attaches on the same place at the consecutive intervertebral joint, this continues throughout the tail (Fig. 3-4). The first three segments of SVM, those which lie under the sacrum and the proximal caudal vertebrae are distinct segments, are relatively uniform in size and shape. Beyond this point the segments of SVM become less distinct, but retain approximately the same size. These tendons span up to ten caudal vertebrae before inserting. Nervous supply from the ventral rami is visible to SVM. Deeply, fibres of SVM blend with the m. interchevronii muscles.

**M. interchevronii**

The m. interchevronii (ICH) muscle group is comprised of superficial and deep fibres. The superficial fibres arise from the ventral aspect of the sacrocaudal joint and continue between bony segments to the tip of the tail. The superficial fibres of m. interchevronii span two segments and attach on the tip of the chevron bone of the next intervertebral joint. The deep fibres of m. interchevronii are short, uni-segmental fibres, which run between adjacent chevron bones (Figs. 3-2C, 3-3 & 3-4).

**DISCUSSION**

The role of the tail in kangaroo locomotion is one of an active organ, which provides support as a fifth limb during pentapedal locomotion, and contributes to the efficiency in bipedal hopping. In this study, we have revealed the anatomy of the caudal musculature, which has shed new light about the potential role of the caudal musculature in both bipedal hopping and pentapedal locomotion.

During the floating phase of bipedal hopping, the tail is thought to be actively raised (Hopwood & Butterfield 1990). Such action would require powerful extension of the tail and lumbar spine. It is likely that the relatively large mm. sacrocaudalis dorsalis lateralis, which passes from the lower lumbar region and the sacrum, and attaches to mammillary processes in the proximal tail would be responsible for this action. The large mm.
sacrocaudalis dorsalis lateralis are also likely to be responsible for the action of the tail moving counter to the hindlimbs, which may act to prevent pitching of the body (Baudinette 1994). The caudal extensors (mm. sacrocaudalis dorsalis lateralis and medialis) run continuously with the extensors of the back (mm. longissimus and mm. multifidus systems). The connection forms a functional chain of muscles from the presacral spine to the tail, and may act to maintain posture and stability of the body axis during the floating phase of hopping. This function is analogous to that seen in quadrupedal mammals during running (Schilling 2011). The extensive thoracolumbar fasciae of the lumbar and caudal regions are also likely to contribute to support the body axis during the hopping cycle.

Upon landing, the tail is at its highest (most extended) point of the bipedal hopping cycle (Hopwood and Butterfield 1990). The large proximal extensor mass, mainly the mm. sacrocaudalis dorsalis lateralis and medialis, may act to extend the tail and the trunk prior to landing. On landing, active extension of the tail and trunk may prevent the tail from hitting the ground in reaction to vertical reaction ground forces (Usherwood & Hubel 2012), which would tend to flex both the trunk and tail; the mm. sacrocaudalis dorsalis lateralis and medialis may act eccentrically to resist such flexion of the tail, and to prevent forward pitching of the body (Dawson & Taylor 1973; Bennett 1987; Baudinette 1994).

As such, the tail may function as a dynamic cantilever in conjunction with the pre-sacral spine to prevent forward pitching during the contact and floating phases of bipedal hopping.

The function of the tail as a counterbalance may be emphasised by the sharing of fibres between the medial belly of the mm. sacrocaudalis dorsalis lateralis with the cranial head of m. caudofemoralis, together with the extensive dense thoracolumbar fascia over the
lumbar region (Hopwood & Butterfield 1990). This appears to create a second functional chain between the extensors of the tail and an extensor of the hip and knee joints.

During pentapedal locomotion the kangaroo alternates between using the hindlimbs, forelimb and tail to support it’s body weight (Windsor & Dagg 1971; Dawson & Taylor 1973). Before the body weight can be supported by the tail, the proximal tail is flexed and drawn under the pelvis (close to the centre of mass), while the mid-distal tail (Ca8-13) is extended, creating the characteristic ‘S-shape’ of the tail (Frith & Calaby 1969; Windsor & Dagg 1971; Dawson & Taylor 1973; Alexander & Vernon 1975; Dawson 1977; Bennett 1999) (Fig. 5B). The relatively large ventral flexors, the m. pubococcygeus and the m. sacrocaudalis ventralis lateralis which extend from the sacrum to the chevron bones and transverse processes of the mid-distal region, would appear to be largely responsible for the repositioning of the distal tail. The lateral flexors, the m. coccygeus from the ischium to the proximal caudal vertebrae, and the intertransversarius lateralis caudalis and the m. sacrocaudalis ventralis lateralis which connect the ilium to the caudal vertebrae, are also likely to be involved in the repositioning of the proximal tail under the kangaroo’s centre of mass (Fig. 3-5A,B).

The strong action of m. coccygeus is demonstrated by a marked fossa where it takes origin on the ischium in *M. fuliginosus*. Beyond the sacral region, the flexor musculature is relatively larger than the other functional groups in the tail of the *M. fuliginosus*, in comparison to other terrestrial mammals that have relatively equal dorsal and ventral caudal musculature, highlighting the functional importance of these muscles (Lemelin 1995; Endo et al. 2012). The role of the flexor caudal musculature for weight-bearing in large kangaroos is further evidenced by the large ‘hatchet-shaped’ chevron bones which provide large areas for insertion of caudal flexors (Owen 1876; Flower 1885).
After the tail has been repositioned under the pelvis, it then provides a rigid column of support for the body weight in conjunction with the forelimbs, while the hindlimbs are swung forward (Dawson & Taylor 1973) (Fig. 3-5B,C). During this movement, it is likely that the proximal extensor mass (m. sacrocaudalis dorsalis lateralis and m. sacrocaudalis dorsalis medialis), acts eccentrically to prevent the proximal tail from flexing further under load bearing. Similarly, the flexors, which send long tendons to the mid-distal tail (m. pubococcygeus and m. sacrocaudalis dorsalis ventralis) may also act eccentrically to prevent further extension of the mid-distal tail under load.

The maintenance of the relatively stable pelvis by the tail during this weight-bearing phase of pentapedal locomotion, is likely to be the action of lateral flexors that provide a muscular link between the pelvis and the proximal caudal vertebrae. Inter-segmental
muscles (m. interchevronii, m. intermamillary, m. intertransversarius medialis caudalis, m. intertransversarius lateralis caudalis, and m. intertransversarius dorsalis caudalis) are all likely to provide additional support, in a similar manner to the short postural muscles of the lumbar spine in humans (Lickley 1904; Basmajian & Slonecker 1989). Not considered here are the caudal intervertebral discs, which could contribute to the weight bearing role of the tail during pentapedal locomotion.

While the tail is supporting the body weight, the centre of mass moves forwards as the hindlimbs are swung forward, and the tail straightens from the characteristic ‘S-shape’ (Fig. 3-5B,C). The extensors may act concentrically to straighten (or ‘un-flex’) the proximal tail, while the flexors may act to ‘un-extend’ the mid-distal tail. The action of these muscles likely contribute to the propulsive force that causes the forward movement of the centre of mass while the tail is supporting the body weight during pentapedal locomotion (Fig. 3-5) (Dawson & Taylor 1973).

The inclusion of only female specimens is a potential limitation of this study, and certainly this will need to be considered in future studies. *M. fuliginosus* display significant sexual dimorphism in body size; mature males may attain double the body mass of breeding females (Jarman 1991). Warburton, Bateman and Fleming (2013) demonstrated in *M. fuliginosus* that the extreme forelimb development of males; with significant positive allometry of muscle mass and the disproportionate development of muscles, specifically involved in male-male fighting, are under sexual selection. That study highlighted the potential infraspecific implications on muscle development where there are differences in behaviour by males and females. In terms of tail use, male kangaroos utilise their tails as a supporting limb during male-male fighting, and thus sexual dimorphism in the muscular anatomy of the tail is likely (Jarman 1991). As the focus of the current study was the functional morphology of the tail for locomotion, the
study was restricted to females in order to remove the possibly confounding effects of male-specific fighting behaviour and growth traits.

CONCLUSIONS
This study has shown that the extensor muscles dominate in the sacral and most proximal parts of the tail and that the flexors dominate in the proximal half of the tail, and how this relates to the tail’s role in pentapedal locomotion and bipedal hopping. However, the arrangement of the long tendons and short muscles appear to continue in a uniform, segmented pattern along the entire length of the tail, emphasising its unitary structure in continuity with the pre-sacral spinal musculature.
## SUPPLEMENTARY MATERIAL

Table 3S-1. Homologous names for caudal muscle groups used in different species.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Veterinary based names</th>
<th>Functional based names</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lateral extensor</td>
<td>Sacrocaudalis dorsalis lateralis(^1,4)</td>
<td>Levator caudae lateralis (extensor caudae lateralis and externus)(^5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Extensor caudae lateralis(^6)</td>
</tr>
<tr>
<td>Medial extensor</td>
<td>Sacrocaudalis dorsalis medialis(^1,4)</td>
<td>Levator caudae medialis (extensor caudae medialis)(^5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Extensor caudae medialis(^6)</td>
</tr>
<tr>
<td>Lateral flexor</td>
<td>Sacrocaudalis ventralis lateralis(^1,4)</td>
<td>Flexor caudae lateralis(^5)</td>
</tr>
<tr>
<td></td>
<td>Sacrococcygeus (ventral lateral insertions)(^2)</td>
<td>Flexor caudae longus(^6)</td>
</tr>
<tr>
<td>Medial ventral flexor</td>
<td>Sacrocaudalis ventralis medialis(^1,4)</td>
<td>Flexor caudae brevis(^3,6)</td>
</tr>
<tr>
<td></td>
<td>Sacrococcygeus (ventral insertion)(^2)</td>
<td>Flexor caudae medialis(^5)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flexor caudae profundus(^5)</td>
</tr>
<tr>
<td>Lateral flexor with ischial origin</td>
<td>Coccygeus(^1)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ischiococcygeus(^2,3,5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coccygeus medialis(^4)</td>
<td></td>
</tr>
<tr>
<td>Lateral flexor with iliac origin and dorsal insertion</td>
<td>Intertransversarius dorsalis(^1,4)</td>
<td>Abductor caudae lateralis (medial portion)(^5)</td>
</tr>
<tr>
<td>Lateral flexor with iliac origin and ventral insertion</td>
<td>Intertransversarius dorsalis(^1)</td>
<td>Abductor caudae medialis(^6)</td>
</tr>
<tr>
<td></td>
<td>Puboiliococcygeus(^2)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Iliococcygeus(^3,5)</td>
<td></td>
</tr>
<tr>
<td>Lateral flexor with pubic origin</td>
<td>Pubococcygeus(^1,3,5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Puboiliococcygeus(^2)</td>
<td></td>
</tr>
<tr>
<td>Unisegmental lateral flexor</td>
<td>Intertransversarius ventralis(^1)</td>
<td>Abductor caudae medialis(^5)</td>
</tr>
<tr>
<td></td>
<td>Intertransversarii ventralis(^6)</td>
<td>Abductor caudae lateralis(^5,6)</td>
</tr>
<tr>
<td>Unisegmental muscle between spinous processes</td>
<td>Interspinales(^6)</td>
<td></td>
</tr>
</tbody>
</table>

CHAPTER FOUR

FUNCTIONAL ANALYSIS OF THE FIRST FIFTEEN CAUDAL VERTEBRAE IN KANGAROOS AND WALLABIES (MACROPODIDAE: MACROPODINAE)

The third study in this thesis, chapter four has not yet been published. In this chapter, Studies 1 and 2 are referred to as Dawson et al. (2015) and Dawson, Milne and Warburton (2014), respectively.

ABSTRACT
The tail plays an integral role in the locomotor repertoire of kangaroos, acting as a dynamic cantilever during bipedal hopping, and as a fifth limb used to support the body weight and propel the body forward during slow pentapedal locomotion. However, pentapedal locomotion is not universal amongst the Macropodinae, and the role of the tail varies within the group. In this study, a comparative approach is taken to investigate how the role of the tail is reflected in the osteology of the first 15 caudal vertebrae of macropodines. The caudal vertebral profiles in 14 species of Macropodinae were examined using seven functional measurements from the first 15 caudal vertebrae.

Caudal vertebral morphology in the Macropodinae appears to reflect two divergent adaptations for the tail. On the one hand, the tails of large terrestrial kangaroos have adaptations for stability, while the tail is stationary during pentapedal locomotion, and while the tail is moving during bipedal hopping. The weight-bearing role of the tail during pentapedal locomotion is reflected in the large proximal endplate area and high resistance to sagittal bending in Ca5-Ca13. Stability of the tail during bipedal hopping is evident in
CHAPTER FOUR

the short distal transverse processes and low robusticity (resistance to coronal plane bending) in kangaroos, which indicates reduced lateral movement for the tail in these species.

On the other hand, smaller wallabies, rock wallabies and tree-kangaroos have tails that are adapted for lateral mobility. The caudal vertebrae are characterised by long distal transverse processes, high relative centrum length and high robusticity of the proximal tail. In the small wallabies this is interpreted as adaptations for strong lateral movements of the tail, which are likely to assist in jinking-and-weaving locomotion. Lateral movements of the tail aid in balance during vertical jumping and leaping in rock-wallabies, and during climbing in tree-kangaroos.

The diversity of tail use within the Macropodinae is more so than any other mammalian clade, suggesting that the functional role for the tail as part of the locomotor repertoire has been key in the adaptive radiation of kangaroos and wallabies.
INTRODUCTION

Many animals have tails that assist in locomotion, either for balancing, changing direction or for grasping. Remarkably, kangaroos use their tail as a fifth limb during slow progression (pentapedal locomotion), and as a dynamic cantilever during bipedal hopping (Dawson & Taylor 1973; Alexander & Vernon 1975; Bennett 1987; Baudinette 1989; 1994; Kram & Dawson 1998; Usherwood & Hubel 2012; O'Connor et al. 2014). During pentapedal locomotion the tail supports the body weight and propels the body forward while the hindlimbs are drawn forward (Dawson & Taylor 1973; O'Connor et al. 2014). Pentapedal locomotion is thought to have evolved in response to the high energetic costs of hopping at low speeds, and a bauplan with relatively elongated tibiae that precludes the use of quadrupedal bounding in large-bodied macropodines (Dawson & Taylor 1973; Dawson 1977; Dawson et al. 2015).

Pentapedal locomotion, however, is not universal among the Macropodinae. ‘Non-pentapedal’ macropodines engage in a quadrupedal bounding gait at slow speeds and include small wallabies (such as *Macropus eugenii*, *Setonix brachyurus* and *Thylogale* spp.), tree-kangaroos (*Dendrolagus* spp.) and rock-wallabies (*Petrogale* spp.) (Windsor & Dagg 1971; Baudinette 1977; Dawson 1977; Strahan 1983; Baudinette, Snyder & Frappell 1992; Dawson et al. 2015). Among ‘non-pentapedal’ taxa there is diversity in the role for the tail in the locomotor repertoire. Tree-kangaroos and rock-wallabies engage the tail as an organ of balance while negotiating the three-dimensional environments of trees and rocky outcrops (Windsor & Dagg 1971; Groves 1982; Sharman & Maynes 1983; Groves & Flannery 1989; Strahan 1995; Martin 2005; Menzies 2011), and these specialisations are not apparent in the more typically terrestrial ‘non-pentapedal’ wallabies (e.g. *Macropus eugenii*, *Setonix brachyurus* and *Thylogale* spp.) (Windsor & Dagg 1971; Baudinette 1977; Strahan 1983; Baudinette, Snyder & Frappell 1992). In this study, how the caudal vertebral morphology reflects pentapedal locomotion within the
Macropodinae, and how this differs from other functional adaptations of the tail is investigated.

Morphological variation between vertebrae within a tail exists due to a combination of genetic (e.g. Hox genes) and environmental cues (load from muscles and tendons) that result in each vertebra having a distinctive shape (Kessel & Gruss 1990; Krumlauf 1994; Carapuco, Novoa & Bobola 2005). Shape variation along any vertebral series reflects the variable biomechanical demands along the series (German 1982; O'Higgins et al. 1997; Kida et al. 1999; Boszczyk, Boszczyk & Putz 2001; Youlatos 2003; Chen, Milne & O'Higgins 2005; Bruner & Bartolino 2008; Pierce, Clack & Hutchinson 2011; Viglino et al. 2014). The caudal (post-sacral) vertebral series demonstrates intersegmental variation in mammals with a generalised morphological pattern of gradual reduction of neural arches and other processes from the base to the tip of the tail, where they become rudimentary projections from the centrum (Owen 1848; 1876; Flower 1885; Ankel 1962; 1972; Hildebrand 1974; German 1982; Youlatos 2003).

Variability in caudal vertebral number (Flower 1885; Rockwell, Evans & Pheasant 1938; Hildebrand 1974; Romer & Parsons 1986; Kardong 2009) prohibits detailed descriptions of caudal vertebrae at specific levels. Rather, studies typically divide the mammalian tail into two distinct regions; proximal and distal. The proximal region usually includes the first four to six caudal vertebrae that are characterised by the presence of cranial and caudal zygapophyses, a feature shared with the lumbar vertebrae (Fig. 4-1) (Ankel 1962; 1972; German 1982; Youlatos 2003; Schmitt et al. 2005; Organ 2010; Russo 2014). The first caudal vertebra has a strongly developed vertebral arch and a distinct vertebral foramen, and is often the broadest of all the caudal vertebrae with flared transverse processes (Flower 1889).
In subsequent caudal vertebrae the centrum (vertebral body) becomes more elongate and the vertebral foramen becomes reduced in size. The ‘transitional’ caudal vertebra, identified by the presence of cranial zygapophyses (articulating processes), but no caudal zygapophyses (Fig. 4-1) demarcates the beginning of the distal region. The distal caudal vertebrae have elongate centra with greatly reduced processes compared to those more proximal (Ankel 1962; 1972; German 1982). Despite having no cranial zygapophyses, distal caudal vertebrae retain mammillary processes for the insertion of caudal extensor

Figure 4-1. Characteristics of representative caudal vertebrae from different regions of the tail in a specimen of *Macropus fuliginosus* shown from the dorsal view. Ca1: proximal region, Ca5: transitional region, Ca10: distal region.
muscles (Lemelin 1995; Organ, Teaford & Taylor 2009; Organ 2010; Dawson, Milne & Warburton 2014). Some studies include a transitional region, distinct from the distal region that includes the transitional vertebra and the successive vertebrae to the longest caudal vertebra (German 1982; Youlatos 2003; Schmitt et al. 2005; Organ, Teaford & Taylor 2009; Organ 2010; Russo & Young 2011; Deane et al. 2014; Russo 2014) (Fig. 4-2).

**Figure 4-2.** Proximal, transitional and distal regions of the *M. fuliginosus* tail. The beginning of the transitional region is demarcated by Ca5 (transitional caudal vertebra) and the end of this region is demarcated by Ca7 (longest caudal vertebra).
The regional definitions of the caudal vertebral series provide anatomically homologous boundaries, which have enabled functionally meaningful comparisons where related taxa exhibit different behavioural roles for the tail (e.g. prehensile versus non-prehensile tails in primates and carnivores; German, 1982, Youlatos 2003, Organ 2010). Importantly, these previous studies have highlighted that the distal region of the tail, which is more often engaged in specialised roles during locomotion, reflect functional specialisations more significantly than the proximal region.

The varied behaviours within the Macropodinae reflects divergent evolution of the tail, which is expected to be evident in the osteology of the tail. In order to make comparisons between functionally different roles for the tail, the macropodine taxa have been categorised into four groups (Table 4-1) based on the role of the tail in their locomotor repertoire:

1. **pentapedal** macropodines are bipedal hopping terrestrial kangaroos and wallabies that engage in pentapedal locomotion at slow speeds

2. **quadrupedal bounding** macropodines are bipedal hopping wallabies that use a quadrupedal bound rather than pentapedal locomotion when moving at low speeds

3. **rock-wallabies**, are adapted for vertical jumping and leaping over uneven habits and do not use pentapedal locomotion

4. **tree-kangaroos**, are adapted for climbing and an arboreal lifestyle, and utilise a range of locomotor patterns, not including pentapedal locomotion.

It is hypothesised that species within functional groups will share similar vertebral profiles along the tail, while differences in vertebral profiles between the four groups will reflect differential tail use.
Table 4-1. Sample size, ecological and locomotory characteristics, and general caudal osteology of the Macropodinae used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Body mass (kg)</th>
<th>Locomotor repertoire</th>
<th>Habitat</th>
<th>General osteology</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n  M   F</td>
<td></td>
<td></td>
<td>TrCV LCV PTP</td>
</tr>
<tr>
<td>Pentapedals</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macropus agilis</td>
<td>4 16-27 9-15</td>
<td>Pentapedal&lt;sup&gt;1,2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;3&lt;/sup&gt;</td>
<td>Woodlands</td>
<td>Ca5 Ca7 Ca7</td>
</tr>
<tr>
<td>Macropus irma</td>
<td>6 7-9 7</td>
<td>Pentapedal&lt;sup&gt;2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;4&lt;/sup&gt;</td>
<td>Woodlands</td>
<td>Ca5 Ca6 Ca7</td>
</tr>
<tr>
<td>Macropus fuliginosus</td>
<td>3 3-53.5 4.5-27.5</td>
<td>Pentapedal&lt;sup&gt;2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;4&lt;/sup&gt;</td>
<td>Woodlands</td>
<td>Ca5 Ca6 Ca6</td>
</tr>
<tr>
<td>Macropus robustus</td>
<td>3 7.3-46.5 6.3-25</td>
<td>Pentapedal&lt;sup&gt;2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;3&lt;/sup&gt;</td>
<td>Woodlands</td>
<td>Ca5 Ca6 Ca6</td>
</tr>
<tr>
<td>Macropus rufus</td>
<td>3 15-23.7 12-15.5</td>
<td>Pentapedal&lt;sup&gt;2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;5&lt;/sup&gt;</td>
<td>Grasslands</td>
<td>Ca5 Ca7 Ca7</td>
</tr>
<tr>
<td>Onychogalea unguifera</td>
<td>4 6-9 4.5-7</td>
<td>Pentapedal&lt;sup&gt;2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;4&lt;/sup&gt;</td>
<td>Grasslands</td>
<td>Ca5 Ca10 Ca7</td>
</tr>
<tr>
<td>Wallabia bicolor</td>
<td>1 12.3-20.5 10.3-15.4</td>
<td>Pentapedal&lt;sup&gt;2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;4&lt;/sup&gt;</td>
<td>Dense woodlands</td>
<td>Ca5 Ca8 Ca6</td>
</tr>
<tr>
<td>Non-pentapedals</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadrupedal bounders</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macropus eugenii</td>
<td>4 6-10 4-6</td>
<td>Quad. bounding&lt;sup&gt;6,2&lt;/sup&gt;; bipedal hopping&lt;sup&gt;6&lt;/sup&gt;</td>
<td>Thickets</td>
<td>Ca5 Ca6 Ca6</td>
</tr>
<tr>
<td>Setonix brachyurus</td>
<td>4 2.7-4.2 2.7-3.5</td>
<td>Quad. bounding&lt;sup&gt;7&lt;/sup&gt;; quad. bounding punctuated with bipedal hopping&lt;sup&gt;7&lt;/sup&gt;</td>
<td>Thickets</td>
<td>Ca5 Ca6 Ca6</td>
</tr>
<tr>
<td>Rock-wallabies</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Petrogale brachyotis</td>
<td>4 4.5</td>
<td>‘3-D’ / ‘vertical’ hopping (jumping/leaping) between rocks&lt;sup&gt;4&lt;/sup&gt;, on flat ground quad. bound and bipedal hopping&lt;sup&gt;3&lt;/sup&gt;</td>
<td>Rocky outcrops</td>
<td>Ca5 Ca6 Ca7</td>
</tr>
<tr>
<td>Petrogale lateralis</td>
<td>3 4.6-5.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Petrogale rothschildi</td>
<td>2 5.3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Tree-kangaroos**

<table>
<thead>
<tr>
<th>Species</th>
<th>Body Mass</th>
<th>Z Score</th>
<th>Locomotor Repertoire</th>
<th>Habitat</th>
<th>TrCV</th>
<th>LCV</th>
<th>PTP</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dendrolagus dorianus</em></td>
<td>1</td>
<td>7.5-14.5</td>
<td>Walking(^3), quad. bounding; rarely bipedal hopping(^3)</td>
<td>Arboreal</td>
<td>Ca6</td>
<td>Ca8</td>
<td>Ca6</td>
</tr>
<tr>
<td><em>Dendrolagus lumholtzi</em></td>
<td>3</td>
<td>3.7-10</td>
<td>5.2-7</td>
<td>Arboreal</td>
<td>Ca5/6</td>
<td>Ca10</td>
<td>Ca6</td>
</tr>
</tbody>
</table>

TrCV: transitional caudal vertebra, LCV: longest caudal vertebra, PTP: the caudal vertebra where the proximal transverse process first appears.
MATERIALS AND METHODS

SAMPLE AND MENSURATION

In this study we measured 46 adult individuals from the Western Australian Museum and the South Australian Museum (Table 4-1). Their status as adults was based on museum records and confirmed by examining dental features and level of fusion of epiphyses. 11 homologous landmarks (Fig. 4-3, Table 4-2) were digitised on the first 15 caudal vertebrae (Ca1–Ca15) of each individual using a hand digitiser (Microscribe 3D-X, Immersion Corporation, San Jose, CA). These 11 landmarks were used to define six lengths from the caudal vertebra (Table 4-3).

If the tail was not articulated, caudal vertebrae were differentiated from lumbar vertebrae based on the lack of a developed neural spine and neural arch (both of which are present in the lumbar region), and seriation was achieved through examining the relative development of the zygapophyses and haemal processes, zygapophyseal intrafacet distances and relative distal transverse process breadth (German 1982; Youlatos 2003; Organ 2010). Where possible, articulated tails were used to confirm seriation. Due to skeletons often missing smaller vertebrae, only the first 15 caudal vertebrae were digitised for each individual, hence the ‘total’ number of caudal vertebrae for each species is not reported. Specimens with pathologies or missing elements were excluded from this study. *Dendrolagus dorianus* and *Petrogale brachyotis* were not included in the analysis of mammillary process length, due to dried soft tissue preventing the access of landmarks via the hand digitiser. To quantify measurement error, technical error of measurement (TEM) and the coefficient of variation (CV) were estimated from five femurs and five Ca10, which were measured once a day on six different days in a randomized order (Table 4-3).
Table 4-2. Landmarks used to digitise caudal vertebrae (labelled on Fig. 4-3).

<table>
<thead>
<tr>
<th>Number</th>
<th>Definition of landmark</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 &amp; 2</td>
<td>Dorsal-most and ventral-most point of the proximal endplate</td>
</tr>
<tr>
<td>3 &amp; 4</td>
<td>Left- and right-most point of the proximal endplate</td>
</tr>
<tr>
<td>5</td>
<td>Dorsal- and distal-most point of the caudal endplate</td>
</tr>
<tr>
<td>6 &amp; 7</td>
<td>Lateral most point of the left and right distal transverse processes</td>
</tr>
<tr>
<td>8 &amp; 9</td>
<td>Left and right side of the narrowest part of the centrum</td>
</tr>
<tr>
<td>10 &amp; 11</td>
<td>Lateral-most tip of the left and right mammillary processes</td>
</tr>
</tbody>
</table>

Figure 4-3. Landmarks (1-11) digitised on caudal vertebrae to generate lengths (Table 4-3) used to derive functional measurements (Table 4-4). Landmarks are shown on a Ca10 from a specimen of *M. fuliginosus*, from the cranial view (top) and dorsal view (bottom).
### Table 4-3. Definitions of lengths measurements on caudal vertebrae and femora.

<table>
<thead>
<tr>
<th>Linear measurement</th>
<th>Definition</th>
<th>LMs</th>
<th>CV</th>
<th>TEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Centrum length</td>
<td>CL Maximum length of the centrum in the sagittal plane</td>
<td>1-5</td>
<td>1.10</td>
<td>0.45</td>
</tr>
<tr>
<td>Centrum width</td>
<td>W Taken from the narrowest point of the centrum from the dorsal view</td>
<td>12-13</td>
<td>1.71</td>
<td>0.21</td>
</tr>
<tr>
<td>Dorsoventral height of the proximal endplate</td>
<td>DVPE Maximum dorsoventral dimensions of the proximal endplate of the centrum</td>
<td>1-2</td>
<td>0.01</td>
<td>0.25</td>
</tr>
<tr>
<td>Mediolateral width of the proximal endplate</td>
<td>MLPE Maximum mediolateral dimensions of the proximal endplate of the centrum</td>
<td>3-4</td>
<td>0.02</td>
<td>0.22</td>
</tr>
<tr>
<td>Mammillary process length</td>
<td>MPL Maximum length of the mammillary process from the centrum</td>
<td>14/15</td>
<td>0.01</td>
<td>0.22</td>
</tr>
<tr>
<td>Distal transverse process breadth</td>
<td>DTPB Maximum lateral dimension of the distal transverse processes</td>
<td>8-9</td>
<td>0.94</td>
<td>0.25</td>
</tr>
<tr>
<td>Mid-shaft anterior-posterior diameter of the femur</td>
<td>-- The anterior-posterior of the femur diameter immediately below the third trochanter</td>
<td>--</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td>Mid-shaft mediolateral diameter of the femur</td>
<td>-- The mediolateral of the femur diameter immediately below the third trochanter</td>
<td>--</td>
<td>0.01</td>
<td>0.02</td>
</tr>
</tbody>
</table>

LMs: the landmarks used to define lengths (Fig. 4-3, Table 4-2)  
CV: coefficient of variation (%)  
TEM: technical error of measurement
SIZE-ADJUSTMENT

Due to large variation in body size within the study sample (Table 4-1), the raw lengths were size-adjusted prior to comparative analyses. Some previous authors have size-adjusted caudal vertebral measurements by dividing linear measurements by body-mass \(^{1/3}\) and areas by body-mass \(^{2/3}\) based on species mean body mass data from the literature (Fleagle 1988; Youlatos 2003; Russo 2014). However, Macropodinae exhibit indeterminate growth, and also substantial sexual dimorphism (Hume et al. 1989; Strahan 1995; Warburton, Bateman & Fleming 2013), so femur mid-shaft circumference was used as a proxy for body size. Helgen et al. (2006) demonstrated that femur mid-shaft circumference was an accurate predictor of body mass in Macropodinae, in line with other research which suggests that load-bearing bones, such as limb bones, and measurements derived from them, are appropriate for estimating body mass (Anderson, Hall-Martin & Russell 1985; Anyonge 1993). Femur mid-shaft circumference was derived by averaging circumferences calculated from the anterior-posterior and mediolateral diameters of the femur mid-shaft. Diameters were measured using digital calipers. Scatterplots and correlations were used to assess the relationship between the raw measurements and femur mid-shaft circumference.
**Table 4-4.** Functional measurements of the caudal vertebrae used to construct caudal vertebral profiles.

<table>
<thead>
<tr>
<th>Functional measurement/ratio</th>
<th>Calculation</th>
<th>Functional relevance</th>
</tr>
</thead>
</table>
| Relative centrum length              | RCL  2xCL/(DVPE+MLPE)             | Higher values: Flexibility of the centrum  
| Robusticity                          | R W/CL                             | More resistant to bending in the coronal plane  
|                                      |                                    | Lower values:  
|                                      |                                    | Stiffness of the centrum  
|                                      |                                    | Less resistant to bending in the coronal plane  
| Proximal endplate area               | PEA $\pi x (DVPE/2) x (MLPE/2)$   | Increased load bearing ability and resistance to axial compression  
| Sagittal bending                      | SB $DVPE^2 x MLPE$                 | Increased resistance to bending in the sagittal plane  
| Mammillary process length            | MPL Avg. of L and R MPL            | Longer lever for dorsal extensors  
| Relative distal transverse process length | RDTPL $DTPB – DVPE$               | Longer lever for lateral flexors  

Functional measurements are calculated from lengths derived from caudal vertebrae (Fig. 4-3, Table 4-3).
Morphometric Analysis
Size-adjusted lengths were used to derive six functional measurements (Table 4-4). All measurements except SB and PEA were subsequently multiplied by 100 to give whole numbers for the comparative analyses (Youlatos 2003; Organ 2010). Finally, to investigate morphometric variation along the tail, ‘vertebral profiles’ (Pierce, Clack & Hutchinson 2011) were constructed for each species by plotting the species mean of each functional measurement against caudal vertebral number, using the size-adjusted values. All species were plotted on the same graph to enable comparative analysis of vertebral profile shape. Note that quadrupedal bounders are abbreviated to bounders, and pentapedal macropodines are abbreviated to pentapedals in the results figures.

Results
General Osteology
The proximal region is comprised of four caudal vertebrae in all species, except D. lumholtzi and D. dorianus which have five (Table 4-1). The location (caudal vertebral number) of the longest caudal vertebrae, the length of the transitional region, and the location of the appearance proximal transverse process, vary between and within groups, except in the quadrupedal bounding macropodines (Table 4-1). All raw measurements from Ca1, Ca5, Ca10 and Ca15 are positively correlated with femur mid-shaft circumference (Table 4-5).

Table 4-5. Correlation coefficients and statistical significance of raw linear measurements and femur mid-shaft circumference.

<table>
<thead>
<tr>
<th></th>
<th>CL</th>
<th>W</th>
<th>DVPE</th>
<th>MLPE</th>
<th>MPL</th>
<th>DTPB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca1</td>
<td>0.95</td>
<td>0.87</td>
<td>0.69</td>
<td>0.97</td>
<td>0.91</td>
<td>0.82</td>
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<tr>
<td>Ca5</td>
<td>0.96</td>
<td>0.88</td>
<td>0.88</td>
<td>0.97</td>
<td>0.93</td>
<td>0.95</td>
</tr>
<tr>
<td>Ca10</td>
<td>0.94</td>
<td>0.93</td>
<td>0.97</td>
<td>0.97</td>
<td>0.75</td>
<td>0.93</td>
</tr>
<tr>
<td>Ca15</td>
<td>0.73</td>
<td>0.86</td>
<td>0.92</td>
<td>0.91</td>
<td>0.64</td>
<td>0.85</td>
</tr>
</tbody>
</table>

All p-values are <0.0001
CHAPTER FOUR

CAUDAL VERTEBRAL PROFILES

All values used for the caudal vertebral profiles have are the size-adjusted values.

CENTRUM LENGTH (CL)

All four groups and 14 species share a broadly similar profile of CL in the first 15 caudal vertebrae: there are small changes in the first three vertebrae, followed by a steep increase in size to a maximum length, usually at Ca8 and then a gradual decline from that position to the 15th vertebra (Fig. 4-4A,B).

CL is greatest in Ca1-3 in the pentapedal and quadrupedal bounding groups, and smaller in the rock-wallabies and tree-kangaroos, with the exception of D. dorianus which is near the lower end of the range of variation of the former two groups (Fig. 4-4C).

In the distal region, the rock-wallabies have highest CL, but these values overlap with some members of the pentapedal group (Fig. 4-4D). CL gradually reduces in the distal region but the rate is generally lower in tree-kangaroos than the other groups, although it is exceptionally low in O. unguifera (Fig. 4-4D,E-H). Throughout most of the distal region, the vertebral profile of S. brachyurus is markedly lower than all other species (Fig. 4-4D).
Figure 4-4 (A & B). Caudal vertebral profiles of centrum length for all species (A) and the means for each group (B).
Figure 4-4 (C & D). Centrum length of Ca1-Ca5 (C) and Ca5-Ca15 (D) in all species.
Figure 4-4 (E, F, G & H). Caudal vertebral profiles of centrum length for individual species in each group. A vertical line indicates the separation of proximal and distal vertebrae.
RELATIVE CENTRUM LENGTH (RCL)

All four groups and 14 species show a similar profile of RCL, with little change between Ca1 and CA3 followed by generally increasing values to maximum at Ca15 (Fig. 4-5A, B). There is a large amount of variation within the pentapedal macropodines, and the vertebral profiles of species from this group overlaps with other functional groups, while the vertebral profiles of the other functional groups are less variable (Fig. 4-5A,C,D).

In the proximal region, there is large overlap in RCL between all functional groups, except in Ca1-3 of the tree-kangaroos, where RCL is markedly lower than the other species (Fig. 4-5C).

In the distal region of the tail the variation in the pentapedal macropodines overlaps with all the other functional groups (Fig. 4-5D). In this region, O. unguifera shares a similar vertebral profile to rock-wallabies with a greater rate of increase (Fig. 4-5D). M. rufus and M. robustus have relatively low values, and the profile is flat in the distal region of the tail (Fig. 4-5D,E). M. fuliginosus and W. bicolor have different profiles to all other pentapedal macropodines, with the former having more complex profile that include a dip around Ca12-13. These two species have a less pronounced increase in values across the region with the values for M. fuliginosus declining quite markedly through most of the region (Fig. 4-5D,E). M. irma and M. agilis and show similar shaped profiles of RCL in the distal region of the tail, the values are higher than the quadrupedal bounders (Fig. 4-5D,E).

In the distal region of the tail, the vertebral profile of the larger pentapedal macropodines (M. rufus, M. fuliginosus and M. robustus) has a less steep increase in RCL, while the smaller pentapedal macropodines (W. bicolor, O. unguifera, M. agilis and M. irma) show a steeper increase in RCL (Fig. 4-5E-H).
Rock-wallabies have the highest values, tree-kangaroos the next highest values, and quadrupedal bounders the least highest of these three functional groups in the distal region of the tail (Fig. 4-5D). These groups also differ from one another in the steepness of the profiles in the distal region of the tail, rock-wallabies show a very steep incline in RCL between segments, followed by the tree-kangaroos, which are followed by quadrupedal bounders, which have the least steep profiles of these three groups (Fig. 4-5D). In contrast with the proximal region, there is also little overlap of values between quadrupedal bounders, rock-wallabies and tree-kangaroos (Fig. 4-5D).
Figure 4-5 (A & B). Caudal vertebral profiles of relative centrum length in all species (A) and the means for each group (B).
Figure 4-5 (C & D). Relative centrum length of Ca1-Ca5 (C) and Ca5-Ca15 (D) in all species.
Figure 4-5 (E, F, G & H). Caudal vertebral profiles of relative centrum length for individual species in each group. A vertical line indicates the separation of proximal and distal vertebrae.
ROBUSTICITY (R)

In all species robusticity is greatest in the proximal region of the tail, and declines toward the distal end of the tail (Fig. 4-6A,B). Robusticity in the proximal region of the tail is greatest in the rock-wallabies and tree-kangaroos, and these values decline steeply from Ca3-Ca6, beyond this point the decline is much less steep (Fig. 4-6A,B). Pentapedal macropodines and quadrupedal bounders have similar profiles that do not have such a large difference in robusticity from the proximal to distal regions as seen in the other two groups. Values for quadrupedal bounders are consistently higher than those for pentapedal macropodines (Fig. 4-6A,B).

In Ca1-4 pentapedal macropodines have the lowest values for robusticity and there is no overlap between this group and the other functional groups (Fig. 4-6C). From Ca5 onwards, there is overlap between pentapedal macropodines and other functional groups, but M. rufus, M. robustus, M. fuliginosus and W. bicolor generally have lower values, except for at Ca14, where M. fuliginosus, M. rufus and W. bicolor show an increase in robusticity (Fig. 4-6D,E). In contrast, values of robusticity in O. unguifera, M. agilis and M. irma are higher (Fig. 4-6D,E). The latter species have values that overlap with the robusticity values of tree-kangaroos, although they do not share the same pattern (Fig. 4-6D). The lowest values of robusticity are seen in M. rufus from Ca1-14 (Fig. 4-6B-H). The decline in values of robusticity from the proximal region to the distal region is less steep in pentapedal macropodines compared with other groups (Fig. 4-6A,B,E-F).

In the distal region, quadrupedal bounders have the highest values for robusticity, and do not overlap with other functional groups (Fig. 4-6D). Rock-wallabies and tree-kangaroos share the same shaped vertebral profile; robusticity is very high in Ca1-3, and steeply decreases between Ca3 and Ca4, and continues to decline in the distal regions (Fig. 4-6A,B,G&H). Rock-wallabies and tree-kangaroos differ in that robusticity is generally
higher in tree-kangaroos than rock-wallabies in both the proximal and distal regions (Fig. 6C,D,G&H).
**Figure 4-6 (A & B).** Caudal vertebral profiles of robusticity for all species (A) and the means for each group (B).
Figure 4-6 (C & D). Robusticity of Ca1-Ca5 (C) and Ca5-Ca15 (D) in all species.
Figure 4-6 (E, F, G & H). Caudal vertebral profiles of robusticity for individual species in each group. A vertical line indicates the separation of proximal and distal vertebrae.
PROXIMAL ENDPLATE AREA (PEA)

Among the pentapedal macropodines, the quadrupedal bounders and the rock-wallabies, the pattern of PEA across along the first 15 caudal vertebrae is similar, with increasing values from Ca1-Ca7/8 followed by a decline such that Ca15 is less than Ca1 (Fig. 4-7A,B). Tree-kangaroos on the other hand, show a generally steady decrease from Ca1-15 (Fig. 4-7A,E-H). Variation between and within pentapedal macropodines, the quadrupedal bounders and the rock-wallabies, corresponds mainly to variation in the amplitude of the curve in the caudal vertebral profile (Fig. 4-7B).

PEA is greatest in pentapedal macropodines (Fig. 4-7A,B,E-H). *M. fuliginosus* generally has the highest values of PEA, with a maximum at Ca6 (Fig. 4-7D). In pentapedal macropodines, rock-wallabies and *M. eugenii*, the highest values of PEA are usually Ca8, Ca7 and Ca7, respectively, beyond which PEA gradually declines (Fig. 4-7E-G). *O. unguifera*, *M. agilis* and *M. irma* have relatively lower amplitude of PEA along the tail, compared with the larger pentapedal macropodines (*M. rufus, M. fuliginosus, M. robustus* and *W. bicolor*) (Fig. 4-7E).

Quadrupedal bounding macropodines appear to have the smallest amplitude in the vertebral profile of all functional groups (Fig. 4-7A). Although *S. brachyurus* shows increased values of PEA from Ca6-Ca8, the overall vertebral profile shows declining PEA along the tail (Fig. 4-7A,E-H).

Rock-wallabies and tree-kangaroos have less within group variation compared to pentapedal macropodines and quadrupedal bounding macropodines (Fig. 4-7A,E-H).
Figure 4-7 (A & B). Caudal vertebral profiles of proximal endplate area for all species (A) and the means for each group (B).
Figure 4-7 (C & D). Proximal endplate area in Ca1-Ca5 (C) and Ca5-Ca15 (D) in all species.
Figure 4-7 (E, F, G & H). Caudal vertebral profiles of proximal endplate area of for individual species in each group. A vertical line indicates the separation of proximal and distal vertebrae.
SAGITTAL BENDING (SB)

Vertebral profiles of SB (Fig. 4-8A-H) are similar to those PEA. However, there is large variation within the pentapedal macropodines, and variation between and within pentapedal macropodines, the quadrupedal bounders and the rock-wallabies, mainly corresponds to variation in the amplitude of the curve.

*M. rufus, M. fuliginosus, M. robustus* and *W. bicolor* have the highest values and greater amplitude in the vertebral profile curve (Fig. 4-8E). *M. rufus* differs from other pentapedal macropodines in the proximal region by having a steep increase in SB between Ca3-5 (Fig. 4-8E). *O. unguifera, M. agilis* and *M. irma*, have much lower values, reduced amplitude and do not increase as much between Ca6-11 (Fig. 4-8E). The latter group of pentapedal species share the vertebral profile shape with rock-wallabies, and *M. eugenii*, although absolute values are lower in rock-wallabies (Fig. 4-8B,E-G).

*S. brachyurus* has a unique vertebral profile of SB, with very low values along the tail, and an overall decline in the values of SB along the tail, rather than a noticeable increase in any region (as seen in all other species, Fig. 4-8B,F).

The vertebral profile of SB in tree-kangaroos also differs from all other species, the values are greatest in the proximal region of the tail and decline towards the end of the tail (Fig. 4-8G). As in PEA, rock-wallabies and tree-kangaroos have less within group variation, compared to pentapedal macropodines and quadrupedal bounding macropodines (Fig. 4-8B,E-H).
Figure 4-8 (A & B). Caudal vertebral profiles of sagittal bending for all species (A) and the means for each group (B).
Figure 4-8 (C & D). Sagittal bending of Ca1-Ca5 (C) and Ca5-Ca15 (D) in all species.
Figure 4-8 (E, F, G & H). Caudal vertebral profiles of sagittal bending for individual species in each group. A vertical line indicates the separation of proximal and distal vertebrae.
MAMMARY PROCESS LENGTH (MPL)

All four groups and 14 species have a similar profile of MPL in the first 15 caudal vertebrae with increasing values from Ca1 to Ca3 followed by a decline to about Ca9 and then little change to Ca15 (Fig. 4-9A-H).

In the proximal region, quadrupedal bounders and rock-wallabies share similar shaped profiles, with similar values for MPL (Fig. 4-9C). In this region, pentapedal macropodines show a large amount of variation, and appear to be separated into two groups. M. agilis, M. irma and O. unguifera, all which have higher values for MPL, and M. fuliginosus, M. rufus, M. robustus and W. bicolor, that have lower values for MPL (Fig. 4-9C). These patterns are also apparent in the distal region of the tail (Fig. 4-9D).

In the distal region of the tail, quadrupedal bounders and rock-wallabies and O. unguifera have the highest values for MPL (Fig. 4-9D). The other eight species all sit below these species (Fig. 4-9D). In this region all pentapedal macropodines show similar patterns of MPL across Ca5-15, but vary in the absolute values of MPL (Fig. 4-9D).
Figure 4-9 (A & B). Caudal vertebral profiles of mammillary process length for all species (A) and the means for each group (B).
Figure 4-9 (C & D). Mammillary process length of Ca1-Ca5 (C) in Ca5-Ca15 (D) in all species.
Figure 4-9 (E, F, G & H). Caudal vertebral profiles of mammillary process length for individuals in each group. A vertical line indicates the separation of proximal and distal vertebrae.
RELATIVE DISTAL TRANSVERSE PROCESS LENGTH (RDTPL)

All four groups and 14 species have a similar profile of RDTPL in the first 15 caudal vertebrae (Fig. 4-10B-H). This profile is very much like that for MPL with high values in the proximal region, peaking at either Ca2 or Ca3, and rapidly declining from there to Ca7 then little change to Ca15. Across all functional groups Ca2 generally has the highest value for RDTPL (Fig. 4-10C). The largest variation between and within groups is in the proximal region of the tail, but functional groups do overlap in the distal region (Fig. 4-10C,D).

Generally, pentapedal macropodines have lowest values for RDTPL, but there is large variation within this group (Fig. 4-10A-E). *M. rufus, M. fuliginosus, M. robustus* and *W. bicolor* have the lowest values of RDTPL, located in the proximal region, and do not overlap with any other functional group in this region (Fig. 4-10C). In contrast, *O. unguifera, M. irma* and *M. agilis* overlap with tree-kangaroos in the proximal region (Fig. 4-10C). From Ca1-15, *M. rufus, M. fuliginosus, M. robustus* have lowest values of RDTPL compared to all other 11 species (Fig. 4-10E). Due to the low values of *M. rufus, M. fuliginosus, M. robustus* and *W. bicolor* in the proximal region of the tail, there is no steep decline in RDTPL in Ca5-7, as seen in all other 11 species (Fig. 4-10B-H).

Quadrupedal bounders and rock-wallabies have the highest values for RDTPL, located in the proximal region of the tail, and do not overlap with other functional groups within this region (Fig. 4-10C). In the distal region of the tail, there is relatively more overlap between smaller pentapedal macropodines *O. unguifera, M. irma, M. agilis* and *W. bicolor*, with the quadrupedal bounders, rock-wallabies and tree-kangaroos (Fig. 4-10D).

Tree-kangaroos are at the lower end of the range, while quadrupedal bounders and rock-wallabies are at the higher end of the range (Fig. 4-10D). Of the smaller pentapedal
macropodines, *M. irma*, *M. agilis* and *W. bicolor* show an interesting pattern of a relative plateauing of RDTPL from Ca8-9. *M. rufus*, *M. fuliginosus*, *M. robustus* do not overlap with other functional groups in the proximal and distal regions of the tail (Fig. 4-10D).
Figure 4-10 (A & B). Caudal vertebral profiles of relative distal transverse process length for all species (A) and the means for each groups (B).
Figure 4-10 (C & D). Relative distal transverse process length of Ca1-Ca5 (C) and Ca5-Ca15 (D) in all species.
Figure 4-10 (E, F, G & H). Caudal vertebral profiles of relative distal transverse process length for individual species in each group. A vertical line indicates the separation of proximal and distal vertebrae.
**DISCUSSION**

Caudal vertebral morphology in the Macropodinae reflects the divergent evolution for the role of the tail in the locomotor repertoire within this subfamily. The results from this study indicate that the role of the tail in pentapedal locomotion is characterised by morphology associated with load bearing and on the centrum in Ca5-Ca13, as indicated by a distinctively increased proximal endplate area and resistance to sagittal plane bending in these vertebrae. Variation within the pentapedal macropodines reflects the varied roles for the tail apart from pentapedal locomotion within this group.

**PENTAPEDAL LOCOMOTION**

The caudal vertebral morphology of pentapedal kangaroos and wallabies is distinguished from non-pentapedal taxa by two key features: the ability to resist bending in a sagittal plane and the relatively large proximal endplate area in Ca5-Ca13. This morphology reflects the role of the tail in supporting and propelling the body weight forwards during the tail support phase (when the hindlimbs are off the ground) during pentapedal locomotion (Dawson & Taylor 1973; O'Connor et al. 2014; Dawson et al. 2015). Resistance to sagittal plane bending reflects the role of the tail to resist the forces of acceleration and deceleration, and associated bending and torsion stresses during pentapedal locomotion (Currey 1967, cited in Alexander 2003). The propulsive force (O'Connor et al. 2014), likely from the sacrocaudal and ‘pelvi-caudal’ musculature (Dawson, Milne & Warburton 2014), would exert considerable pressure on the caudal vertebrae from the base of the tail to those in contact with the ground (likely Ca4/5–Ca13/14)(See Fig. 5-2). The contrasting decreased resistance to sagittal plane bending in the proximal region of the tail (Ca1–Ca4) in kangaroos may be a reflection of load bearing by the sacrocaudal musculature and mammillary processes, as has been suggested in other animals (Slijper 1946; Finch & Freedman 1986).
The large proximal endplate area in Ca5-Ca13 would also serve to bear the high axial load, and resist axial compression, associated with both supporting the body weight during the tail support phase of pentapedal locomotion, and the propulsion produced by the caudal musculature during pentapedal locomotion. Specifically; in *M. rufus* the tail exerts vertical force equivalent to 35% of the body mass of the individual on the ground, while the hindlimbs are off the ground, and also contributes 22% of the positive mechanical work during the pentapedal gait cycle (O'Connor et al. 2014). Proximal endplate area has been shown to be relatively greater in vertebrae from species where axial compression and load bearing is increased as a result of weight transmission associated with specific posture and large body mass, compared with close phyletic relatives that lack these features (Shapiro 2007).

Large joints indicate adaptation for increased ability to distribute load (e.g. MacConaill & Basmajian 1969, Kapandji 1970, Norkin and Lavangie 1983, Currey 1980 cited in Jungers 1988, Kapandji 2008), and there appears to be an allometric effect associated with proximal endplate shape and size (PEA and SB) in pentapedal macropodines. Larger pentapedal macropodines (*M. rufus, M. fuliginosus, M. robustus* and *W. bicolor*) have higher levels of resistance to sagittal plane bending and proximal endplate area compared to smaller pentapedal macropodines (*Onychogalea unguifera, M. agilis* and *M. irma*). *W. bicolor* appears to be the exception to this proposed allometric association, as it only reaches a maximum of 20kg in adult males, where the kangaroos and wallaroos are much larger (Table 5-1). To better understand this relationship between body size and caudal vertebral morphology, a force plate analysis study would have to be undertaken across pentapedal macropodines to quantify the forces produced by the tails belonging to these species during the pentapedal gait cycle.
BIPEDAL HOPPING

Among the pentapedal taxa, differences in caudal vertebral profile appear to reflect different adaptations for bipedal hopping. One adaptation is the reduced flexibility and reduced capability of movement in the coronal plane along the tail seen in large kangaroos (*M. rufus*, *M. fuliginosus* and *M. robustus*). The reduced flexibility/passive stiffness in kangaroos (as indicated by relatively low and constant centrum length) may reflect the role of the tail as a cantilever during bipedal hopping to counteract the rotational thrust produced by the heavy hindlimbs during bipedal hopping (Alexander & Vernon 1975; Baudinette 1994).

The movement of the tail during bipedal hopping is predominantly in the sagittal plane, with small amounts of rotation while the hindlimbs are off the ground (Alexander & Vernon 1975; Dawson 2012). This is consistent with observations that large kangaroos predominantly travel in a straight line, even when fleeing. Restriction of movement to the sagittal plane in the tail is reflected in the relatively short distal transverse processes, which gives rise to and receives the lateral flexor muscles along the tail (Dawson, Milne & Warburton 2014). As caudal vertebral stiffness and short distal transverse processes are not shared by smaller pentapedal macropodines and non-pentapedal macropodines, it is interpreted that passive stiffness and restriction of movement of the tail to the sagittal plane are adaptations only present in kangaroos. This corresponds to previous hypotheses that adaptations of the tail for biomechanical efficiency during bipedal hopping may be unique to kangaroos, and that smaller macropodines may not get significant benefits from such adaptations (Dawson & Taylor 1973; Dawson 1977; Baudinette 1994).

In contrast, smaller pentapedal wallabies and quadrupedal bounding macropodines share long distal transverse processes in the proximal region, high robusticity of the centrum in the proximal region and flexible distal regions of the tail. These morphological patterns
indicate adaptations for non-linear, jinking-and-weaving locomotion, in which fleeing animals make rapid, evasive changes in direction. This action may be aided by strong lateral movements of the tail acting as both a counterbalance and as a rudder, as described in cheetahs (Hildebrand 1959). The longer distal transverse processes provide longer levers for the lateral flexor muscle bellies. The processes provided attachment for strong lateral flexors capable of abducting the tail, and also a site of origin for lateral flexors which move the distal tail (Dawson, Milne & Warburton 2014). This capacity for lateral movements of the tail, together with a flexible distal tail (indicated by relative centrum length), would facilitate directional changes as part of jinking-and-weaving locomotion.

**Locomotion in three-dimensional environments**

Rock-wallabies (*Petrogale* spp.) and tree-kangaroos (*Dendrolagus* spp.) display a caudal skeletal morphotype consistent with other mammals adapted for locomotion in three-dimensional environments. Rock-wallabies and tree-kangaroos display much greater relative centrum length in the distal tail compared to the pentapedal macropodines and quadrupedal bounding macropodines. Previous works have highlighted that the length of the tail is associated with maintenance of balance in arboreal mammals (see Russo 2014 for discussion). The increased flexibility, due to the increased centrum length in the distal tail, would facilitate the role for the tail as a counterbalance for rock-wallabies while jumping and leaping (Strahan 1995), and in tree-kangaroos climbing (Martin 2005). The flexible nature of the tail in rock-wallabies and tree-kangaroos is further demonstrated by the fact that both genera have been noted to hold the tail in a ‘question mark’/arc shape when on flat ground, and sometimes during bipedal hopping (Martin 2005).

The differing caudal vertebral morphology between rock-wallabies and tree-kangaroos reflects differences between adaptations for leaping behaviours (rock-wallabies) and climbing behaviours (tree-kangaroos). Unlike tree-kangaroos, rock-wallabies have longer
distal transverse process length in the proximal region, which suggests a greater role for powerful lateral movements in the proximal tail in this group. In rock-wallabies, this likely reflects the use of strong lateral movements of the tail used to oppose, or counter, shifts in centre of mass when leaping and jumping, or to aid in landing, as seen in many other species (Hatt 1932; Siegel 1970; Hildebrand 1974; German 1982; Wada, Hori & Tokuriki 1993; Demes et al. 1996; Larson & Stern 2006).

Relatively reduced distal transverse process length in tree-kangaroos compared with rock-wallabies, may reflect the need for some lateral movement of the tail (presumably to counter lateral movement of the axial skeleton, as seen in other climbers) while they climb and walk along branches (Procter-Gray & Ganslosser 1986; Martin 2005; Menzies 2011). Larger lateral movements, perhaps similar to that which could be achieved by the long distal transverse processes in rock-wallabies, may compromise stability for tree-kangaroos or may even be unnecessary if tree-kangaroos engage in pedal grasping. Previous authors have highlighted that tree-kangaroos have flexible articular surfaces in the pes (Flannery 1982; Szalay 1994; Warburton & Prideaux 2010), which are indicative of engaging the feet in grasping behaviours (e.g. Procter-Gray & Ganslosser 1986), akin to other arboreal species (including marsupials), to aid in maintenance of balance (Cartmill 1985; Fleagle 1988; Argot 2002). It may also be that lateral movements of the pre-sacral skeleton, rather than the tail are more important in tree-kangaroos. In Chen, Milne and O'Higgins (2005) it was highlighted that the dorsoventrally expanded vertebral body and the laterally orientated transverse processes, are adaptations for lateral movement of the spine, as seen in other climbers (Johnson & Shapiro 1998).

Patterns of centrum robusticity along the tail appear to be associated with adaptations for lateral movement of the tail. For example, in species with long distal transverse processes, robusticity is high. This may reflect adaptations of the centrum to resist bending in the
coronal plane associated with these lateral movements, as seen in strepsirrhines (Shapiro, Demes & Cooper 2001). In contrast, kangaroos (M. rufus, M. fuliginosus and M. robustus) have relatively small distal transverse processes, and also have low and consistent values for robusticity along the tail. This reinforces that the tail is not adapted for movement in the coronal plane in kangaroos.

An additional source of morphological variation in the caudal vertebra of kangaroos, not investigated in this current study, is sexual dimorphism. Previous studies have highlighted the substantial sexual dimorphism in body size where male-male competition is frequent, in gregarious kangaroos (Jarman 1989). During male-male fighting males often ‘stand’ on their tail, freeing the hindlimb from supporting the body weight and enabling the use of the feet to kick the opponent (Ganslosser 1989; Jarman 1991). Given the presumably large amount of axial compression exerted on the caudal vertebrae during this posture, and the relationship between joint size and load size (discussed above), it may be that internal vertebral architecture and endplate morphology are sexually dimorphic. Studies by Warburton, Bateman and Fleming (2013) and Richards, Grueter and Milne (2015) show that forelimb musculature and length are significantly sexually dimorphic in kangaroos and wallaroos, highlighting that elements involved that are primarily locomotor apparatus can subject to sexual selection, and that this is evident in the morphology. Analysis of intraspecific variation to test these hypotheses will await a larger sample size.

CONCLUSIONS
It appears that within the Macropodinae, there has been divergent evolution of caudal vertebrae reflecting selection for either stability or mobility of the tail during locomotion. Specifically, stability is favoured where morphology is associated with the load-bearing role for the tail during pentapedal locomotion and specialisations of the tail as a cantilever
in bipedal hopping in kangaroos; while mobility provides a flexible appendage useful for weaving locomotion in small pentapedal macropodines and quadrupedal bounding macropodines; or as a long, flexible counterweight useful while negotiating three-dimensional environments in rock-wallabies and tree-kangaroos. The differential morphology of the tail among kangaroos and wallabies reflects the adaptive radiation of the Macropodinae and the subsequent locomotor adaptations associated with the evolutionary trajectory within this group.
CHAPTER FIVE

DID STHENURINES USE PENTAPEDAL LOCOMOTION? A GEOMETRIC MORPHOMETRIC ANALYSIS OF THREE CAUDAL VERTEBRAE IN THE MACROPODIDAE

The fourth study in this thesis, chapter five has not yet been published. In this chapter, Studies 1 and 2 are referred to as Dawson et al. (2015) and Dawson, Milne and Warburton (2014), respectively, and chapter four is referred to as Study 3.

ABSTRACT

Pentapedal locomotion is the use of the tail as a fifth leg during slow locomotion, and is adopted by several macropodines, but is not universal among the group. While we mostly understand the prevalence of pentapedal locomotion in extant species, it is unclear whether this gait was adopted by the extinct sister clade to the macropodines, the sthenurines. Establishing whether or not it was likely that sthenurines engaged in pentapedal locomotion will shed light on whether this gait is unique to the Macropodinae.

This study uses geometric morphometric methods to compare the morphology of caudal vertebra (Ca)1, Ca5 and Ca10 in four groups of extant Macropodinae with functionally different uses for the tail; to characterise adaptations associated with pentapedal locomotion; to test the hypothesis that sthenurines did not engage in pentapedal locomotion.

Ca1 and Ca5 of pentapedal macropodines differ in morphology from non-pentapedal macropodines, and the sthenurine species investigated in this study (Sthenurus spp.,
Simosthenurus occidentalis spp., and ‘Procoptodon’ gillii). As a group, pentapedal macropodines are characterised by adaptations for ventral flexion along the tail, and lateral flexion associated with the pelvi-caudal musculature in Ca5; features that are lacking in the sthenurines examined in this study. The morphology of Ca10 differed between macropodines who are adapted for locomotion in more typically ‘terrestrial’ environments, compared with those adapted for movement in three-dimensional habitats (Petrogale and Dendrolagus).

Additionally, sthenurines did not appear to share morphologies with any extant species, and evidently lack adaptations associated with the role of the tail during bipedal hopping. Rather, these sthenurine species show adaptations indicative of an upright bipedal posture and a striding gait.

These findings support the hypothesis that sthenurines did not engage in pentapedal locomotion, and highlight that this gait is unique to the Macropodinae. The contrasting locomotor repertoire of sthenurines to that of macropodines raises interesting questions about the evolutionary trajectory of these sister clades.
INTRODUCTION

As a group, kangaroos and wallabies (Macropodidae: Macropodinae) are united by their ability to engage in bipedal hopping. While all members engage in bipedal hopping during fast locomotion, gait selection during slow locomotion is variable within the group (Windsor & Dagg 1971; Dawson et al. 2015). Pentapedal locomotion is the use of the tail as a fifth limb to support the body and to propel the body forward during slow gait, and is adopted by kangaroos and medium-to-large wallabies (Dawson & Taylor 1973; O'Connor et al. 2014; Dawson et al. 2015). In contrast, smaller macropodines adopt a quadrupedal bounding gait during slow locomotion (Windsor & Dagg 1971; Baudinette 1977; Baudinette, Snyder & Frappell 1992; Dawson et al. 2015). It is proposed that pentapedal locomotion has arisen in kangaroos and medium-to-large wallabies due to specialisations of the bauplan for bipedal hopping, such as long hindlimbs, high crural index, and forelimb-hindlimb asymmetry, features that are not shared by smaller macropodines (Dawson 1977; O'Connor et al. 2014; Dawson et al. 2015). Pentapedal locomotion is a remarkable gait, and while we have elucidated some of the selective pressures associated with the evolution of it, it remains unclear whether pentapedal locomotion was adopted by other large macropodids, or is unique to the Macropodinae.

The subfamily Sthenurinae are the extinct sister group to the Macropodinae. This group is commonly referred to as ‘giant’ kangaroos, as some species were larger (up to 230kg) than extant kangaroos (maximum 90kg) (Helgen et al. 2006), although many of them likely grew up to 40-60kg as adults (Prideaux 2004). Diversity amongst the sthenurines peaked during the mid-Pleistocene; thus far twenty eight species belonging to eight genera have been identified (Cooke 1999; Kear 2002; Prideaux 2004; Prideaux & Warburton 2010). The demise of the sthenurines was part of a widespread megafaunal extinction across Australia, which saw the loss of 90% of the continent’s large mammals.
(Roberts et al. 2001; Prideaux et al. 2009). Generally, sthenurines depart from the macropodine bauplan with short crania, functional monodactyly of the pes, and adaptations of the upper limb that could permit reaching above the head, improving flexibility and manoeuvrability during browsing (Wells & Tedford 1995; Prideaux 2004) (Fig. 5-1).

Figure 5-1. Articulated skeletons of *Sthenurus stirlingi* (A) and *Macropus giganteus* (B). From Janis, Buttrill and Figueirido (2014), after Wells and Tedford 1995. The scale bar represents 20cm.
Due to their large size, and unique aspects of their postcranial skeleton, previous authors have postulated that sthenurines adopted a different locomotor repertoire to extant macropodine kangaroos (Adnams-Hodges 1988; Wells & Tedford 1995; Moore 2008; Janis, Buttrill & Figueirido 2014). Recently, Janis, Buttrill and Figueirido (2014) proposed that sthenurines adopted a bipedal striding gait rather than a bipedal hopping gait as previously proposed by Wells and Tedford (1995). While the preference for a bipedal striding gait versus a bipedal hopping gait remains debated, adaptations of the sthenurine manus and vertebrae appear prohibitive of the adoption of pentapedal locomotion. At the beginning of the pentapedal locomotion cycle, the hands are placed flat on the ground before the tail is used to support the body (Dawson & Taylor 1973). The sthenurine manus seems incapable of this, with limited dorsiflexion of the wrist, and long third phalanges unsuited for weight bearing (Wells & Tedford 1995; Janis, Buttrill & Figueirido 2014). Flexibility of the tail is also apparently compromised in sthenurines, with previous authors reporting common fusion of the sacrocaudal joint. Flexibility at this joint is presumably important during pentapedal locomotion, given that the tail needs to be drawn under the pelvis, prior to the tail supporting the body weight (Dawson & Taylor 1973).

In this study, the primary aim is to characterise the pentapedal morphotype in functionally significant caudal vertebrae, in order to test the hypothesis that sthenurines did not engage in pentapedal locomotion. While the results from Study 3 provide a baseline understanding of the functional morphology associated with pentapedal locomotion, to elucidate locomotor repertoire from extinct species, a more sophisticated approach is required. As such, a geometric morphometric approach is employed to characterise the pentapedal morphotype in three key caudal vertebrae (Ca1, Ca5 and Ca10). Ca1 was chosen as it articulates with the sacrum, which is reportedly modified in sthenurines.
(Wells & Tedford 1995; Janis, Buttrill & Figueirido 2014), while Ca5 and Ca10 will inform on the transitional and distal regions of the tail, which belong to the regions of the tail associated with the distinctive pentapedal caudal morphology (Study 3). Firstly, to establish the pentapedal morphotype, Ca1, Ca5 and Ca10 from pentapedal macropodines are compared with non-pentapedal macropodines to determine whether the shape is distinguishable. It is expected that non-pentapedal macropodines will show distinctive morphologies in the three vertebrae, associated with the locomotor roles for their tail, as demonstrated in Study 3. Due to their potentially divergent locomotor repertoire (Wells & Tedford 1995; Janis, Buttrill & Figueirido 2014), it is expected that sthenurine caudal morphology will also differ from that of non-pentapedal macropodines.

**MATERIALS AND METHODS**

**SAMPLE**

The sample comprised the first, transitional and tenth caudal vertebrae from individuals belonging to 30 different species (Table 5-1). Taxa included in this study were categorised into five groups based on the use of their tail as part of their locomotor repertoire (following Study 3) (Table 5-1).

- **Pentapedal** macropodines are defined as bipedal hopping terrestrial kangaroos and wallabies that engage in pentapedal locomotion at low speeds (Group 1).

- **Non-pentapedal** macropodines are categorised into three groups:
  - Quadrupedal **bounders** are bipedal hopping wallabies that use a quadrupedal bounding gait when moving at slow speeds (Group 2);
  - **Rock-wallabies** are bipedal hopping wallabies that use a quadrupedal bounding gait when moving at slow speeds, but are also adapted for vertical jumping and leaping over uneven habitats (Group 3);
Tree-kangaroos utilise a range of locomotor patterns (Table 5-1), but are non-pentapedal and are adapted for climbing and their arboreal habitats (Group 4).

The sthenurine group (Group 5) comprises five species assigned to three genera. Their phylogenetic position and relationships are indicated in supplementary material.

Specimens belonging to extant species belong to the dry mammal collections of the Western Australian and South Australian Museums, and all extinct species belong to the paleontological collections of the latter museum and Flinders University.
Table 5-1. Sample size details and summary of ecological and locomotory characteristics of the Macropodidae used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Body mass (kg)</th>
<th>Locomotor repertoire</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ca1</td>
<td>Ca5</td>
<td>Ca10</td>
<td>Male</td>
</tr>
<tr>
<td>Pentapedal macropodines</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Macropus agilis</em></td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>16-27</td>
</tr>
<tr>
<td><em>Macropus irma</em></td>
<td>7</td>
<td>6</td>
<td>7</td>
<td>7-9</td>
</tr>
<tr>
<td><em>Macropus fuliginosus</em></td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>3-53.5</td>
</tr>
<tr>
<td><em>Macropus robustus</em></td>
<td>16</td>
<td>16</td>
<td>14</td>
<td>7.3-46.5</td>
</tr>
<tr>
<td><em>Macropus rufogriseus</em></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>15-23.7</td>
</tr>
<tr>
<td><em>Macropus rufus</em></td>
<td>8</td>
<td>8</td>
<td></td>
<td>22-85</td>
</tr>
<tr>
<td><em>Onychogalea fraenata</em></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>5-6</td>
</tr>
<tr>
<td><em>Onychogalea unguifera</em></td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>6-9</td>
</tr>
<tr>
<td><em>Wallabia bicolor</em></td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>12.3-20.5</td>
</tr>
<tr>
<td>Non-pentapedal macropodines</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadrupedal bounders</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lagorchestes hirsutus</em></td>
<td>--</td>
<td>2</td>
<td>2</td>
<td>1.25-1.8</td>
</tr>
<tr>
<td><em>Macropus eugenii</em></td>
<td>8</td>
<td>11</td>
<td>8</td>
<td>6-10</td>
</tr>
<tr>
<td><em>Macropus parma</em></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>4.1-5.9</td>
</tr>
<tr>
<td><em>Setonix brachyurus</em></td>
<td>3</td>
<td>5</td>
<td>4</td>
<td>2.7-4.2</td>
</tr>
<tr>
<td><em>Thylagale billardierii</em></td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3.8-12</td>
</tr>
<tr>
<td>Rock-wallabies</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Petrogale brachyotis</em></td>
<td>8</td>
<td>1</td>
<td>8</td>
<td>3.2-5.6</td>
</tr>
<tr>
<td><em>Petrogale inornata</em></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3.4-5.6</td>
</tr>
<tr>
<td><em>Petrogale lateralis</em></td>
<td>7</td>
<td>11</td>
<td>12</td>
<td>2.3-7.1</td>
</tr>
<tr>
<td><em>Petrogale rothschildi</em></td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5.3</td>
</tr>
<tr>
<td>Species</td>
<td>Body Mass</td>
<td>Habitat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>--------------------------</td>
<td>-----------</td>
<td>-----------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Petrogale xanthopus</em></td>
<td>8</td>
<td>Rocky outcrops</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Tree-kangaroos</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dendrolagus bennettianus</em></td>
<td>2</td>
<td>Walking; quad. bound; Arboreal</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dendrolagus dorianus</em></td>
<td>1</td>
<td>7.5-14.5; 6.5-10; Arboreal</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dendrolagus lumholtzi</em></td>
<td>4</td>
<td>3.7-10; 5.2-7; Arboreal</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Sthenurines†</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'Procoptodon' <em>gilli</em></td>
<td>--</td>
<td>54 ± 15.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Simosthenurus occidentalis</em></td>
<td>2</td>
<td>118 ± 14.3; Slow gait is unlikely pentapedal; fast gait proposed as bipedal striding or bipedal hopping</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Simosthenurus sp.</em></td>
<td>1</td>
<td>--</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sthenurus stirlingi</em></td>
<td>2</td>
<td>173 ± 26.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sthenurus sp.</em></td>
<td>4</td>
<td>--</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


**Locomotor repertoire** slow gait is given first, followed by fast gait, additional descriptions are given only where relevant.

**Locomotor repertoire abbreviations:** Quad. bound = quadrupedal bound, bip. Hopping = bipedal hopping.


**Habitat abbreviations:** Open for./wood. = Open forest/woodlands, Den. under./thickets = dense understorey and thickets


†Denotes extinct species
IDENTIFICATION AND SERIATION OF CAUDAL VERTEBRAE

The transitional caudal vertebra is defined as having cranial zygapophyses, but no caudal zygapophyses (Ankel 1972; German 1982), and is the Ca5 in most macropodines, except in *D. lumholtzi* and *D. bennettianus*, where it is Ca6 in some cases (Russo 2014). For simplicity, in this study Ca5 will be used as a synonym for the transitional caudal vertebra (although Ca6 was measured in *D. lumholtzi* and *D. bennettianus*).

Seriation was achieved based on examining the relative development of the zygapophyses and haemal processes, zygapophyseal intrafacet distances, and relative transverse process breadth. Where possible, articulated tails were used to confirm seriation. Where the tail was not articulated, caudal vertebrae are differentiated from lumbar vertebrae based on the lack of a developed neural spine and neural arch, both of which are present in the lumbar region (German 1982; Youlatos 2003; Organ, Teaford & Taylor 2009; Organ 2010).

MENSURATION

Due to the changing morphology of the vertebrae along the tail, individual landmark sets are created for Ca1, Ca5 and Ca10 (Figs. 5-2A-C and Tables 5-2A-C). Three-dimensional coordinate data of these landmarks were collected using a hand digitiser (Microscribe 3D-X, Immersion Corporation, San Jose, CA).
**Table 5-2A.** Landmark set used in this study for digitizing Ca1. Refer to Fig. 5-2A.

<table>
<thead>
<tr>
<th>Number</th>
<th>Definition of landmarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 &amp; 15</td>
<td>Most proximal point of the lateral margin of the R &amp; L distal transverse processes</td>
</tr>
<tr>
<td>2 &amp; 14</td>
<td>R &amp; L most lateral points on the proximal endplate</td>
</tr>
<tr>
<td>3 &amp; 13</td>
<td>R &amp; L roots of the neural arch at the proximal end of the vertebra</td>
</tr>
<tr>
<td>4 &amp; 12</td>
<td>Most ventromedial point on the R &amp; L proximal articulating facets</td>
</tr>
<tr>
<td>5 &amp; 11</td>
<td>Most cranialateral point on the R &amp; L mammillary processes</td>
</tr>
<tr>
<td>6 &amp; 10</td>
<td>Most cranialateral point on the R &amp; L proximal articulating facets</td>
</tr>
<tr>
<td>7 &amp; 9</td>
<td>Nutrient foraminae at the root of the R &amp; L mammillary processes</td>
</tr>
<tr>
<td>8</td>
<td>Midpoint of the vertebral arch at the proximal end of the vertebra</td>
</tr>
<tr>
<td>16 &amp; 17</td>
<td>Most ventral point on the R &amp; L haemal processes</td>
</tr>
<tr>
<td>18 &amp; 29</td>
<td>Most caudal point on the lateral margin of the R &amp; L distal transverse processes</td>
</tr>
<tr>
<td>19 &amp; 28</td>
<td>Junctions between the R &amp; L distal transverse processes and the centrum</td>
</tr>
<tr>
<td>20 &amp; 27</td>
<td>R &amp; L root of the neural arch at the distal end of the vertebra</td>
</tr>
<tr>
<td>21 &amp; 25</td>
<td>Most ventromedial point on the R &amp; L distal articulating facets</td>
</tr>
<tr>
<td>22 &amp; 26</td>
<td>Most dorsolateral point on the R &amp; L distal articulating facets</td>
</tr>
<tr>
<td>23</td>
<td>Midpoint of the vertebral arch at the distal end of the vertebra</td>
</tr>
<tr>
<td>24</td>
<td>Most dorsal tip of the spinous process</td>
</tr>
<tr>
<td>30 &amp; 31</td>
<td>Most ventral point on R &amp; L the haemal grooves</td>
</tr>
</tbody>
</table>

**Figure 5-2A.** Landmarks used for digitising Ca1 shown from the dorsal, proximal and distal views of an *M. fuliginosus* Ca1. Landmarks are defined in Table 5-2A. Note that not all possibly visible landmarks are shown from each view.
**Table 5-2B.** Landmark set used in this study for digitizing Ca5. Refer to Fig. 5-2B.

<table>
<thead>
<tr>
<th>Number</th>
<th>Definition of landmarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 &amp; 10</td>
<td>Most distal point on the lateral margin of the R &amp; L mammillary processes</td>
</tr>
<tr>
<td>2 &amp; 9</td>
<td>Most cranial point on the lateral margin of the R &amp; L mammillary processes</td>
</tr>
<tr>
<td>3 &amp; 8</td>
<td>Most lateral point on the R &amp; L cranial articulating facets</td>
</tr>
<tr>
<td>4 &amp; 7</td>
<td>Most medial point on the R &amp; L cranial articulating facets</td>
</tr>
<tr>
<td>5</td>
<td>Most distal point on the dorsal surface of the neural arch</td>
</tr>
<tr>
<td>6</td>
<td>Most cranial point on the centrum along the midline of the vertebra on the dorsal surface</td>
</tr>
<tr>
<td>11 &amp; 12</td>
<td>R &amp; L most lateral points on the proximal endplate</td>
</tr>
<tr>
<td>13 &amp; 15</td>
<td>Most ventral points on the R &amp; L haemal processes</td>
</tr>
<tr>
<td>14</td>
<td>Most cranial point on the centrum along the mid-sagittal plane on the ventral surface</td>
</tr>
<tr>
<td>16 &amp; 25</td>
<td>R &amp; L margins of the narrowest part of the centrum</td>
</tr>
<tr>
<td>17 &amp; 26</td>
<td>Ventrocaudal-most point on the roots of the R &amp; L mammillary processes</td>
</tr>
<tr>
<td>18 &amp; 24</td>
<td>Most proximal point on the lateral margin of the R &amp; L distal transverse processes</td>
</tr>
<tr>
<td>19 &amp; 23</td>
<td>Most distal point on the lateral margin of the R &amp; L distal transverse processes</td>
</tr>
<tr>
<td>20 &amp; 22</td>
<td>R &amp; L most lateral points on the distal endplate</td>
</tr>
<tr>
<td>21</td>
<td>Most distal point on the centrum along the midline of the vertebra on the dorsal surface</td>
</tr>
<tr>
<td>27 &amp; 29</td>
<td>Most ventral point on the R &amp; L haemal grooves</td>
</tr>
<tr>
<td>28</td>
<td>Most distal point on the centrum along the midline of the vertebra on the ventral surface</td>
</tr>
</tbody>
</table>

**Figure 5-2B.** Landmarks used for digitising Ca5 shown from the dorsal, proximal and distal views of an *M. fuliginosus* Ca5. Landmarks are defined in Table 5-2B. Note that not all possibly visible landmarks are shown from each view.
Table 5-2C. Landmark set used in this study for digitising Ca10. Refer to Fig. 5-2C.

<table>
<thead>
<tr>
<th>Number</th>
<th>Definition of landmarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 &amp; 12</td>
<td>Lateral-most point on the R &amp; L proximal transverse processes</td>
</tr>
<tr>
<td>2 &amp; 13</td>
<td>Cranial-most point on the R &amp; L proximal transverse processes</td>
</tr>
<tr>
<td>3 &amp; 11</td>
<td>R &amp; L lateral most points of the proximal endplate</td>
</tr>
<tr>
<td>4 &amp; 8</td>
<td>Junction between the R &amp; L mammillary processes and the centrum</td>
</tr>
<tr>
<td>5 &amp; 9</td>
<td>Lateral most point on the R &amp; L mammillary processes</td>
</tr>
<tr>
<td>6 &amp; 10</td>
<td>Cranial most point on the R &amp; L mammillary processes</td>
</tr>
<tr>
<td>7</td>
<td>Most proximal point on the centrum along the midline of the vertebra on the dorsal surface</td>
</tr>
<tr>
<td>16 &amp; 14</td>
<td>Most ventral points on the R &amp; L haemal processes</td>
</tr>
<tr>
<td>15</td>
<td>Most proximal point on the centrum along the midline of the vertebra on the ventral surface</td>
</tr>
<tr>
<td>17 &amp; 18</td>
<td>R &amp; L lateral margins of the narrowest point of the centrum</td>
</tr>
<tr>
<td>19 &amp; 25</td>
<td>Most lateral points on the R &amp; L distal transverse processes</td>
</tr>
<tr>
<td>20 &amp; 24</td>
<td>R &amp; L most lateral points on the distal endplate</td>
</tr>
<tr>
<td>21 &amp; 23</td>
<td>Most distal points on the R &amp; L lips of the spinous process remnants</td>
</tr>
<tr>
<td>22</td>
<td>Most distal point on the centrum along the midline of the vertebra on the dorsal surface</td>
</tr>
<tr>
<td>26 &amp; 28</td>
<td>R &amp; L haemal processes on the distal end of the vertebra</td>
</tr>
<tr>
<td>27</td>
<td>Most distal point on the centrum along the midline of the vertebra on the ventral surface</td>
</tr>
</tbody>
</table>
CALCULATING INTRA-OBSERVER ERROR
To calculate intra-observer error, first, repeat digitisations were undertaken on the Ca1, Ca5 and Ca10 from two individuals of *M. rufus*. These repeated digitisations were undertaken once a day for six days, in a randomised order. Intra-observer error was calculated (von Cramon-Taubadel, Frazier & Lahr 2007) on selected reference landmarks (Table 5-3), and then, by extension this error is assumed for the entire shape. The landmarks were then submitted to a generalised Procrustes analysis (see below for description). Using the Procrustes registered coordinates for the reference landmarks, the standard deviation was then calculated for each landmark (σ) (where N is the number is the number of repeat digitisations) as:

$$\sigma = \sqrt{\frac{\sum_{i=1}^{N} (x_i - \bar{x})^2 + (y_i - \bar{y})^2 + (z_i - \bar{z})^2}{3N}}$$

Following this, the average reference landmark error (σ̄) was calculated (where d, e, f are the reference landmarks) as:

$$\bar{\sigma} = \sqrt{\frac{\sigma_d^2 + \sigma_e^2 + \sigma_f^2}{3}}$$

Average reference landmark error was between 0.14 and 0.30mm (Table 5-3), which is considered low (von Cramon-Taubadel, Frazier & Lahr 2007).

**Table 5-3.** Average error for reference landmarks.

<table>
<thead>
<tr>
<th>Reference landmarks</th>
<th>Ca1</th>
<th>Ca5</th>
<th>Ca10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average error (mm)</td>
<td>0.26</td>
<td>0.30</td>
<td>0.14</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Reference landmarks</th>
<th>Ca1, Ca2, Ca3</th>
<th>Ca4, Ca6, Ca7</th>
<th>Ca8, Ca9, Ca10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average error (mm)</td>
<td>0.26</td>
<td>0.30</td>
<td>0.14</td>
</tr>
</tbody>
</table>
GEOMETRIC MORPHOMETRIC ANALYSIS

The landmark configurations (raw 3D coordinates) of the caudal vertebrae were first subjected to a generalised Procrustes analysis (GPA), using morphologika 2.0 (O'Higgins & Jones 2006), which removes scale, rotation and translation information (non-shape information) and is followed by the analysis of shape variation (using principal components analysis, PCA) (Rohlf 1990; Bookstein 1991; O'Higgins & Jones 1998).

The first step in the GPA was the scaling of each individual configuration. During this step, the centroid size was made equal to 1. Centroid size is defined as the square root of the sum of squared Euclidean distances from each landmark to the centroid of the landmarks (Bookstein 1991; Dryden & Mardia 1993; O'Higgins & Jones 1998). Individual original centroid size for each configuration was retained to be used as a statistically unbiased measure of size for later analyses. Because of strong correlations between linear dimensions of these caudal vertebrae and mid-shaft femur circumference (Study 3), and the latter’s strong correlation with body mass (Helgen et al. 2006), centroid size was also used as a proxy for body mass in the present study. Usually, ‘centroid size’ will be simply referred to as ‘size’ in this chapter.

After the scaling step, the following step in the GPA process involves the translation to superimpose centroids. This is followed by rotation of the configurations such that the square root sum of the squared differences, between corresponding landmarks, the Procrustes chord distance, is minimised. At the end of this process (GPA), the scaled, translated and rotated coordinates are known as shape coordinates. Their arithmetic mean across individuals of a species is the mean shape, it was calculated for each species before commencing the PCA, e.g. Cardini et al. (2015).
Once mean shapes are calculated for the extant species, their shape coordinates, along with shape coordinates of individual sthenurines were subjected to GPA/PCA using morphologika 2.0 (O'Higgins & Jones 2006). The number of shapes submitted for the PCA was 27, 29 and 22 for Ca1, Ca5 and Ca10, respectively.

Shape variables in the form of principal component scores (PCs) and Procrustes distances were extracted from this GPA/PCA for tests of significance. To test whether functional groups are statistically different from each other, permutation tests, in which group membership was permuted 10,000 times, were used to assess the significance of the Procrustes distances between groups.

To test whether differences between groups co-vary with centroid size, a multivariate analyses of variance of shape variables (PC scores) between groups with centroid size as a co-variate (MANCOVA) was carried out. Because the number of PCs was very large, PCs below Jolliffe’s cut-off value were submitted for the MANCOVA. Jolliffe’s cut-off value was calculated in PAST 3.0 (Hammer, Harper & Ryan 2001), e.g. Blanco, Jones and Milne (2013). MANCOVA and subsequent ANCOVAs on individual PCs were undertaken in GenStat (VSN International 2015).

To investigate whether sthenurine caudal vertebrae share adaptations associated with the pentapedal species, mean shapes were created for the five groups at each caudal vertebral level (Ca1, Ca5 and Ca10). This was done by calculating the arithmetic mean shape for each group in an approach similar to Cobb and O'Higgins (2007). Creating these means enabled pair-wise comparisons between the pentapedal mean shape and the mean shape of the other groups. This also permitted an assessment of whether the sthenurine mean shape differed from the pentapedal mean shape in a similar way to other extant mean shapes. Once the mean shapes were calculated for each group, two shapes (pentapedal
and one other, at a time) were submitted for GPA/PCA, which produced one PC, thus reducing the morphospace (and all associated shape differences) to one axis of variation. In this PC, the relative warp method was used to extract wireframe diagrams that contained all the shape variation, between the pentapedal mean shape and the other mean shapes. Importantly, this prevented shape variation being spread across multiple PCs, which becomes an issue when three shapes, i.e. Ca1, Ca5 and Ca10, are involved. Relative shape changes were not exaggerated.

PHYLOGENETIC ANALYSIS
At present there is no phylogeny that includes all the taxa in this study sample, however, the Cardillo et al. (2004) phylogeny includes all of the extant taxa in this study. Using this phylogeny, significance of phylogenetic signal in the PC scores and centroid size was investigated in the extant taxa. This was done by mapping this data onto the phylogeny and running a permutation test (set to 10,000 repeats) in MorphoJ (Klingenberg 2011), following Klingenberg and Gidaszwewski (2010). For Ca1, Ca5 and Ca10 all PC scores were submitted for the permutation tests.

INTRASPECIFIC VARIATION
Intraspecific variation was investigated in species with different functional roles for the tail in locomotion; M. robustus, a pentapedal kangaroo and M. eugenii a quadrupedal bounding wallaby (Dawson et al. 2015). To quantify the magnitude of size-related shape variation that is responsible for shape variation within a species, shape variables (all PC scores) were regressed onto centroid size for both M. robustus and M. eugenii (separately), using multivariate regression (MVR) in morphologika 2.0 (O’Higgins & Jones 2006). Analyses were undertaken separately for Ca1, Ca5 and Ca10.
RESULTS

FIRST CAUDAL VERTEBRA (CA1)

STATISTICAL DIFFERENCES BETWEEN GROUPS

There was strong evidence that all five groups differ in their Ca1 shapes. Pair-wise comparisons of mean Procrustes distances between groups had $p$-values of less than or equal to 0.06 (Table 5-4). The largest difference was between the pentapedals and sthenurines (Table 5-4). The pentapedals are statistically different to all the non-pentapedal macropodines, pentapedals are most similar to the bounders, and most different to the tree-kangaroos (Table 5-4).

Table 5-4. Procrustes distances between groups for Ca1 and probability values for test of significance from zero.

<table>
<thead>
<tr>
<th>Procrustes distances</th>
<th>Pentapedals</th>
<th>Bounders</th>
<th>Rock-wallabies</th>
<th>Tree-kangaroos</th>
<th>Sthenurines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pentapedals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bounders</td>
<td>0.099*</td>
<td>0.141**</td>
<td>0.181*</td>
<td>0.208***</td>
<td></td>
</tr>
<tr>
<td>Rock-wallabies</td>
<td>0.02</td>
<td>0.06</td>
<td>0.134</td>
<td>0.144**</td>
<td></td>
</tr>
<tr>
<td>Tree-kangaroos</td>
<td>&lt;0.01</td>
<td>0.06</td>
<td>0.06</td>
<td>0.144***</td>
<td></td>
</tr>
<tr>
<td>Sthenurines</td>
<td>&lt;0.001</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>0.05</td>
<td></td>
</tr>
</tbody>
</table>

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

The first 8 PCs (of 26) were below the Jolliffe’s cut-off value, and were thus submitted for MANCOVA with centroid size as a co-variate. The MANCOVA revealed that differences between groups were significant after being adjusted for centroid size, and centroid size had a significant effect on shape variation in Ca1 (Table 5-5).

Table 5-5. Results from MANCOVA of shape variables PCs1-8 in Ca1 testing differences between groups with centroid size as a co-variate.

<table>
<thead>
<tr>
<th></th>
<th>$p$</th>
<th>Wilks’ $\lambda$</th>
<th>% cumulative variance of PCs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groups</td>
<td>$&lt; 0.0001$</td>
<td>0.01</td>
<td>85.3</td>
</tr>
<tr>
<td>Centroid size</td>
<td>0.006</td>
<td>0.32</td>
<td></td>
</tr>
</tbody>
</table>
Investigation of individual PCs using ANCOVA show that groups differed on PCs 1 and 4 (Table 5-6). Centroid size is not significantly associated with PC1 or PC4, and for those PCs that do vary with centroid size (PCs 2 and 6) there are no significant shape differences between groups (Table 5-6).

Table 5-6. Results from ANCOVA of shape variables (PCs) from Ca1 testing differences between groups with centroid size as a co-variate.

<table>
<thead>
<tr>
<th>PC</th>
<th>% variance explained</th>
<th>Groups (p)</th>
<th>Centroid size (p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>41.2</td>
<td>&lt;0.001*</td>
<td>0.19</td>
</tr>
<tr>
<td>2</td>
<td>15.0</td>
<td>0.67</td>
<td>0.005**</td>
</tr>
<tr>
<td>3</td>
<td>7.9</td>
<td>0.15</td>
<td>0.62</td>
</tr>
<tr>
<td>4</td>
<td>6.3</td>
<td>0.001*</td>
<td>0.34</td>
</tr>
<tr>
<td>5</td>
<td>5.4</td>
<td>0.61</td>
<td>0.11</td>
</tr>
<tr>
<td>6</td>
<td>3.9</td>
<td>0.14</td>
<td>0.009**</td>
</tr>
<tr>
<td>7</td>
<td>3.0</td>
<td>0.63</td>
<td>0.83</td>
</tr>
<tr>
<td>8</td>
<td>2.6</td>
<td>0.40</td>
<td>0.67</td>
</tr>
</tbody>
</table>

* p < 0.05 ** p < 0.01 *** p < 0.001

The pentapedal-sthenurine difference is highlighted on PC1 where they occupy opposite extremes of the range of variation, as is the similarity between sthenurines and tree-kangaroos (Fig. 5-3). The similarities between non-pentapedal macropodines are also evident by their occupation of similar ranges on PC1 and 2 (Fig. 5-3). Differences between groups are less clear on PC4 (Fig. 5-3).
Figure 5-3. Plots of PCs 1 and 2 (A) and PCs 1 and 4 (B) from PCA of Cal. Combined, PCs 1 and 2 explain 56.2% of shape variation, and PCs 1 and 4 explain 47.5% of the shape variation.

SHAPE DIFFERENCES BETWEEN THE PENTAPEDAL MEAN CA1 AND THAT OF OTHER GROUPS (FIG. 5-4)

The pentapedal Ca1 is characterised by a long centrum (relative to quadrupedal bounders, rock-wallabies and tree-kangaroos), short mammillary processes, caudally projecting and tapered distal transverse processes.

The sthenurine Ca1 centrum is relatively larger than the pentapedal Ca1. Most notably, the sthenurine Ca1 is relatively short and wide in overall appearance, owing to the relatively large centrum width compared to the pentapedal Ca1. The sthenurine Ca1 also differs from the pentapedal Ca1 with a relative reduction in the mediolateral length of distal transverse process, relatively shorter mammillary processes and a relatively longer spinous process. The proximal zygapophyses of the sthenurine Ca1 have a more sagittal orientation, and a smaller intermammillary distance compared to the pentapedal Ca1. The sthenurine Ca1 displays a relative deepening of proximal endplate, but a relatively shallower distal endplate, with relatively reduced ventral wedging compared to the pentapedal Ca1. Sthenurines do not share the curved proximal articular facets displayed by pentapedal Ca1.

The pentapedal and bounder Ca1 shapes are similar, with the exception of the shape of the distal transverse and mammillary processes. The bounder Ca1 has a relatively less caudally projecting and less tapered distal transverse process in bounders, and also display a relative lengthening of the mammillary processes which have a more cranial orientation compared with the pentapedal Ca1. The rock-wallaby Ca1 differ from the pentapedal Ca1 with a relatively short and wide centrum and, relatively long distal transverse and mammillary processes. The tree-kangaroo Ca1 differs from the pentapedal Ca1 with a relatively short centrum, relatively square shaped distal transverse processes,
relatively long and more dorsally orientated mammillary processes (with a relatively wider intermammillary distance) and relatively wider proximal and distal endplates.
Figure 5-4. Warped wireframes displaying the mean shape of the pentapedal macropodines, and the shape differences between the pentapedal shape and the other groups for Ca1. Relative shape changes were not exaggerated. C = centrum, MP = mammillary process, PrZ = proximal zygapophyses, DZ = distal zygapophyses, DTP = distal transverse process, SP = spinous process, PrEP = proximal endplate, DEP = distal endplate and NA = neural arch.
**TRANSITIONAL CAUDAL VERTEBRA (CA5)**

**STATISTICAL DIFFERENCES BETWEEN GROUPS**

As for Ca1, there was strong evidence that all five groups differ in their Ca5 shapes. Pairwise comparisons of mean Procrustes distances between groups had \( p \)-values of less than or equal to 0.04 (Table 5-7). The largest difference was between the sthenurines and tree-kangaroos (Table 5-7). Pentapedals are most different to sthenurines and most similar to rock-wallabies (Table 5-7).

**Table 5-7.** Procrustes distances between groups for Ca5 and probability values for test of significance from zero.

<table>
<thead>
<tr>
<th></th>
<th>Pentapedals</th>
<th>Bounders</th>
<th>Rock-wallabies</th>
<th>Tree-kangaroos</th>
<th>Sthenurines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pentapedals</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bounders</td>
<td>0.102*</td>
<td>0.101**</td>
<td>0.160**</td>
<td>0.161****</td>
<td></td>
</tr>
<tr>
<td>Rock-wallabies</td>
<td>&lt; 0.01</td>
<td>0.02</td>
<td>0.142*</td>
<td>0.209***</td>
<td></td>
</tr>
<tr>
<td>Tree-kangaroos</td>
<td>&lt; 0.01</td>
<td>0.01</td>
<td>0.04</td>
<td></td>
<td>0.225**</td>
</tr>
<tr>
<td>Sthenurines</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.01</td>
<td></td>
</tr>
</tbody>
</table>

* \( p < 0.05 \)  ** \( p < 0.01 \)  *** \( p < 0.001 \)  **** \( p < 0.0001 \)

The first 8 PCs (of 29) were below Jolliffe’s cut-off value, and were thus submitted for MANCOVA with centroid size as a co-variate. The MANCOVA revealed that differences between groups were significant after being adjusted for centroid size, and centroid size did not have a significant effect on shape variation in Ca5 (Table 5-8).

**Table 5-8.** Results from MANCOVA of shape variables PCs1-8 in Ca5 testing differences between groups with centroid size as a co-variate.

<table>
<thead>
<tr>
<th></th>
<th>( p )</th>
<th>Wilks’ ( \lambda )</th>
<th>% cumulative variance of PCs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groups</td>
<td>&lt; 0.0001</td>
<td>0.007</td>
<td>86.7</td>
</tr>
<tr>
<td>Centroid size</td>
<td>0.528</td>
<td>0.7114</td>
<td></td>
</tr>
</tbody>
</table>
Investigation of the individual PCs using ANCOVA show that groups differed on PCs 1, 2 and 3 (Table 5-9, Fig. 5-5). Centroid size is not significantly associated with PCs 1, 2 and 3, and where a PC does vary with centroid size (PC 7), there are no significant shape differences between groups (Table 5-9).

**Table 5-9.** Results from MANCOVA of shape variables PCs1-8 in Ca5 testing differences between groups with centroid size as a co-variate.

<table>
<thead>
<tr>
<th>PC</th>
<th>% variance explained</th>
<th>Groups (p)</th>
<th>Centroid size (p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>34.6</td>
<td>&lt; 0.001***</td>
<td>0.98</td>
</tr>
<tr>
<td>2</td>
<td>18.9</td>
<td>0.041*</td>
<td>0.96</td>
</tr>
<tr>
<td>3</td>
<td>11.2</td>
<td>0.005**</td>
<td>0.12</td>
</tr>
<tr>
<td>4</td>
<td>6.7</td>
<td>0.07</td>
<td>0.96</td>
</tr>
<tr>
<td>5</td>
<td>6.1</td>
<td>0.13</td>
<td>0.42</td>
</tr>
<tr>
<td>6</td>
<td>3.7</td>
<td>0.04</td>
<td>0.45</td>
</tr>
<tr>
<td>7</td>
<td>3.3</td>
<td>0.33</td>
<td>0.03*</td>
</tr>
<tr>
<td>8</td>
<td>2.3</td>
<td>0.73</td>
<td>0.83</td>
</tr>
</tbody>
</table>

*p < 0.05  **p < 0.01  ***p < 0.001

PC1 highlights the difference between sthenurines and all macropodines, and similarities between the macropodines (Fig. 5-5). On PC1 the difference between sthenurines and tree-kangaroos is emphasized by position of these groups at the opposite extremes of the range (Fig. 5-5). Although there is overlap of sthenurines and pentapedals with the other groups on PC2, rock-wallabies and bounders appear to occupy opposite ends of the range on this PC (Fig. 5-5). PC3 highlights the difference between tree-kangaroos and the other taxa, but the differences between groups are less clear on PC6 (Fig. 5-5).
Figure 5-5. Plots of PCs 1 and 2 (A) and PCs 3 and 6 (B) from PCA of Ca5. Combined, PCs 1 and 2 explain 53.5% of shape variation, and PCs 3 and 6 explain 14.9% of the shape variation.

Sthenurines: 1 Si. Occidentalis 2 Si. Occidentalis 3 Simosthenurus sp. 4 Sth. stirlingi 5 Sthenurus sp. 6 P. gilli 7 P. gilli Pentapedals: 8 M. agilis 9 M. irma 10 M. fuliginosus 11 M. robustus 12 M. rufogriseus 13 M. rufus 14 O. fraenata 15 O. ungufera 16 W. bicolor
Bounders: 17 L. hirsutus 18 M. eugenii 19 M. parma 20 S. brachyurus 21 T. billardieri
Rock-wallabies: 22 P. brachyotis 23 P. inornata 24 P. lateralis 25 P. rothschildi 26 P. xanthopus
Tree-kangaroos: 27 D. bennettianus 28 D. dorianus 29 D. lumholtzi

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SHAPE DIFFERENCES BETWEEN THE PENTAPEDAL MEAN CA5 AND THAT OF OTHER GROUPS
(Fig. 5-6)

The pentapedal Ca5 is characterised by laterally tapering distal transverse processes, relatively large and ventrally projecting mammillary processes and elliptical proximal and distal endplates.

The sthenurine Ca5 differs from the pentapedal Ca5 with distal transverse processes that have a relatively greater dorsal projection, increased tapering of the distal transverse process (relatively narrower lateral margin), larger proximal zygapophyseal roots, flatter mammillary processes, reduced intermammillary process distance, a shorter, wider centrum, and, larger proximal and distal endplates.

The pentapedal Ca5 and the quadrupedal bounder Ca5 have very similar morphology, although the bounder Ca5 has a relatively smaller mammillary processes, with a wider root of the proximal zygapophyses, a relatively longer centrum and relatively wider proximal endplates than the pentapedal Ca5. The rock-wallaby Ca5 differs from the pentapedal Ca5 with a relatively more slender, longer centrum and relatively smaller mammillary processes and articulating facets. The rock-wallaby Ca5 also has mammillary processes that have a relatively more coronal orientation, and relatively shorter (in the dorso-ventral direction) proximal and distal cranial endplates compared to the pentapedal Ca5. The tree-kangaroo Ca5 differs from the pentapedal Ca5 with a relatively more slender and longer centrum, relatively flat mammillary processes, articulating facets that are relatively more coronal orientation, and relatively wider and coronally orientated mammillary processes and wider distal transverse processes that taper cranially.
**Figure 5-6.** Warped wireframes displaying the mean shape of the pentapedal macropodines, and the shape differences between the pentapedal shape and the other groups for Ca5. Relative shape changes were not exaggerated. C = centrum, MP = mammillary process, PrZ = proximal zygapophyses, DTP = distal transverse process, SP = spinous process, PrEP = proximal endplate and DEP = distal endplate.
TENTH CAUDAL VERTEBRA (CA10)

STATISTICAL DIFFERENCES BETWEEN GROUPS

Differences between groups were less clear in Ca10 than in Ca1 or 5. Pentapedals differed from rock-wallabies and tree-kangaroos, but not from bounders (Table 5-10). Rock-wallabies and tree-kangaroos differed from pentapedals and bounders, but did not differ from each other (Table 5-10). Sthenurines were only represented by one specimen, and did not differ from any other group (Table 5-10).

Table 5-10. Procrustes distances between groups for Ca10 and probability values for test of significance from zero.

<table>
<thead>
<tr>
<th></th>
<th>Procrustes distances</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pentapedals</td>
</tr>
<tr>
<td>Pentapedals</td>
<td></td>
</tr>
<tr>
<td>Bounders</td>
<td>0.17</td>
</tr>
<tr>
<td>Rock-wallabies</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Tree-kangaroos</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Sthenurines</td>
<td>0.085</td>
</tr>
</tbody>
</table>

* p < 0.05   ** p < 0.01   *** p < 0.001

The first 6 PCs (of 21) were below the Jolliffe’s cut-off value, and were thus submitted for MANCOVA with centroid size as a co-variate. The MANCOVA revealed that differences between groups were significant after being adjusted for centroid size, and centroid size had a significant effect on shape variation in Ca10 (Table 5-11).

Table 5-11. Results from MANCOVA of shape variables PCs1-6 in Ca10 testing differences between groups with centroid size as a co-variate.

<table>
<thead>
<tr>
<th></th>
<th>p</th>
<th>Wilks’ λ</th>
<th>% cumulative variance of PCs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groups</td>
<td>&lt; 0.0001</td>
<td>0.0014</td>
<td>86.3</td>
</tr>
<tr>
<td>Centroid size</td>
<td>0.02</td>
<td>0.344</td>
<td></td>
</tr>
</tbody>
</table>
Investigation of the individual PCs using ANCOVA show that groups differed on PCs1 and 5 (Table 5-12, Fig. 5-7). Centroid size is associated with PC1, though not with PC2 or 5 (Table 5-12).

**Table 5-12.** Results from ANCOVA of shape variables (PCs) from Ca10 testing differences between groups with centroid size as a co-variate.

<table>
<thead>
<tr>
<th>PC</th>
<th>% variance explained</th>
<th>Groups (p)</th>
<th>Centroid size (p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>59.5</td>
<td>&lt; 0.01**</td>
<td>0.04*</td>
</tr>
<tr>
<td>2</td>
<td>9.1</td>
<td>&lt; 0.001***</td>
<td>0.1</td>
</tr>
<tr>
<td>3</td>
<td>5.5</td>
<td>0.21</td>
<td>0.1</td>
</tr>
<tr>
<td>4</td>
<td>5.2</td>
<td>0.19</td>
<td>0.4</td>
</tr>
<tr>
<td>5</td>
<td>4.1</td>
<td>&lt; 0.001***</td>
<td>0.9</td>
</tr>
<tr>
<td>6</td>
<td>2.9</td>
<td>0.13</td>
<td>0.4</td>
</tr>
</tbody>
</table>

* p < 0.05  ** p < 0.01  *** p < 0.001

In the PCA of Ca10 PC1 is separating all macropodines from the sthenurine individual (Fig. 5-7). The separation of pentapedals and bounders from rock-wallabies and tree-kangaroos, but overlap within these pairings is highlighted on PCs1 and 2 (Fig. 5-7). On PC5 bounders and tree-kangaroos occupy a similar range, as do pentapedals and rock-wallabies (Fig. 5-7).
Figure 5-7. Plot of PCs 1 and 2 (A) and PCs 3 and 6 (B) from PCA of Ca10. Combined, PCs 1 and 2 explain 68.6% of shape variation, and PCs 1 and 5 explain 63.6% of the shape variation.

SHAPE DIFFERENCES BETWEEN THE PENTAPEDAL MEAN CA10 AND THAT OF OTHER GROUPS (FIG. 5-8)

The pentapedal Ca10 differs from all other Ca10 shapes with relatively longer haemal processes.

The sthenurine Ca10 centrum is relatively shorter and wider mediolaterally than the pentapedal Ca10 centrum. The sthenurine Ca10 differs from the pentapedal Ca10 with the relatively large transverse processes, which aren’t as ventrally projecting as the pentapedal Ca10.

The bounder Ca10 has relatively shorter mammillary processes and haemal processes compared to the pentapedal Ca10. The rock-wallaby Ca10 has a relatively longer and more slender centrum, with smaller and shorter mammillary and proximal and distal transverse processes compared to the pentapedal Ca10. The differences between the tree-kangaroo and the pentapedal Ca10 are similar to the differences between the rock-wallaby and the pentapedal Ca10. The tree-kangaroo Ca10, however, has relatively smaller haemal, proximal, and distal transverse processes, with a notably more cylindrical centrum compared to the pentapedal Ca10. The rock-wallaby Ca10 and tree-kangaroo Ca10 both have relatively longer and narrower centra compared to the pentapedal Ca10.
Figure 5-8. Warped wireframes displaying the mean shape of the pentapedal macropodines, and the shape differences between the pentapedal shape and the other groups for Ca10. Relative shape changes were not exaggerated. C = centrum, MP = mammillary process, PTP = proximal transverse process, DTP = distal transverse process, SP = spinous process, PrEP = proximal endplate, DEP = distal endplate, HP = haemal process and HL = haemal lip.
PHYLOGENETIC ANALYSIS
PC scores, centroid size and log centroid size of the extant species showed the presence of phylogenetic signal across all three vertebrae (Table 5-13).

Table 5-13. P-values from permutation tests for phylogenetic signal in shape data (PC scores) and size data within the sample used for this study and tree lengths (TL) in Ca1, Ca5, Ca10.

<table>
<thead>
<tr>
<th>PC scores</th>
<th>TL</th>
<th>p</th>
<th>TL</th>
<th>p</th>
<th>TL</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.24</td>
<td>&lt;.0001</td>
<td>0.08</td>
<td>&lt;0.001</td>
<td>0.27</td>
<td>&lt;.0001</td>
<td></td>
</tr>
<tr>
<td>Centroid size</td>
<td>6683.8</td>
<td>0.012</td>
<td>11861.2</td>
<td>0.03</td>
<td>11551.5</td>
<td>0.011</td>
</tr>
<tr>
<td>Log centroid size</td>
<td>1.12</td>
<td>0.008</td>
<td>1.65</td>
<td>0.05</td>
<td>1.74</td>
<td>0.016</td>
</tr>
</tbody>
</table>

INTRASPECIFIC VARIATION
Of the MVRs of shape and centroids size from PCAs of the Ca1, Ca5 and Ca10 in *M. robustus* and *M. eugenii*, none are significant, although some PCs are significantly associated with size (Table 5-14).

Table 5-14. Results from MVR of shape variables (PCs) and centroid size to investigate intraspecific variation associated with size in *M. eugenii* and *M. robustus* in Ca1, Ca5 and Ca10.

<table>
<thead>
<tr>
<th>M. eugenii</th>
<th>M. robustus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ca1</td>
</tr>
<tr>
<td>n</td>
<td></td>
</tr>
<tr>
<td>PCs</td>
<td>7</td>
</tr>
<tr>
<td>p</td>
<td>0.32</td>
</tr>
<tr>
<td>PC1</td>
<td>37.2</td>
</tr>
<tr>
<td>PC2</td>
<td>18.3</td>
</tr>
<tr>
<td>PC3</td>
<td>12.8</td>
</tr>
<tr>
<td>PC4</td>
<td>10.6</td>
</tr>
<tr>
<td>PC5</td>
<td>8.3</td>
</tr>
<tr>
<td>PC6</td>
<td>7.7</td>
</tr>
<tr>
<td>PC7</td>
<td>5.2</td>
</tr>
<tr>
<td>PC8</td>
<td>--</td>
</tr>
<tr>
<td>PC9</td>
<td>--</td>
</tr>
<tr>
<td>PC10</td>
<td>--</td>
</tr>
<tr>
<td>PC11</td>
<td>--</td>
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<tr>
<td>PC12</td>
<td>--</td>
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<tr>
<td>PC13</td>
<td>--</td>
</tr>
<tr>
<td>PC14</td>
<td>--</td>
</tr>
<tr>
<td>PC15</td>
<td>--</td>
</tr>
</tbody>
</table>

*p < 0.05  ** p < 0.01
**DISCUSSION**

This study revealed a suite of morphological adaptations for the role of the tail in macropodines and sthenurines. Indeed, pentapedal macropodines show distinctive morphologies of Ca1 and Ca5 compared with non-pentapedal macropodines and sthenurines. That ‘pentapedal’ features are not evident in the caudal vertebrae from the sthenurines investigated in this study (*Sthenurus stirlingi, Sthenurus* sp., *Simosthenurus occidentalis, Simosthenurus* sp., and ‘Procoptodon’ gilli), corroborate postulations by Janis, Butrill and Figueirido (2014) and Wells and Tedford (1995) that these species did not engage in pentapedal locomotion. Furthermore, sthenurines examined here displayed morphologies that are prohibitive of bipedal hopping, and correlate with adaptations for an upright bipedal posture, and a striding gait. Combined, these features support the hypothesis that sthenurines engaged in bipedal striding gait, as proposed by Janis, Buttrill and Figueirido (2014).

**STHENURINE CAUDAL MORPHOLOGY IS NOT CONSISTENT WITH PENTAPEDAL LOCOMOTION OR BIPEDAL HOPPING**

Ventral flexion of the tail is a key movement during pentapedal locomotion; and occurs when the proximal tail is pulled under the pelvis, prior to the when the tail supports the body weight and propels the body forward (Dawson & Taylor 1973). In this study, mechanical advantage to the ventral flexors is demonstrable in the pentapedal morphotype of Ca1, as it is long in the craniocaudal direction, which increases both leverage and surface area for muscle attachment. Ventral flexion of the tail is also performed by the lateral flexors which originate from the pelvis and attach to the lateral margins of Ca2-Ca7 (m. coccygeus, m. intertransversarius lateralis caudalis, m. sacrocaudalis ventralis lateralis) (Dawson, Milne & Warburton 2014). The importance of these muscles are highlighted in the pentapedal morphotype of Ca5, which have transverse processes that have long attachments sites for this musculature, and well-
developed haemal processes. Sthenurines did not share these morphologies on Ca1 and 5, rather, they demonstrated reduced mechanical advantage to the ventral flexors in Ca1 and 5, and the lateral flexors in Ca1. Given that sthenurines had reduced ability to draw the tail under the pelvis, in addition to the fact that sthenurines skeletal remains show limited ability to dorsiflex the wrist, phalanges unsuited to weight bearing and reduced tail length (Wells & Tedford 1995; Janis, Buttrill & Figueirido 2014) it is unlikely that sthenurines engaged in pentapedal locomotion.

During bipedal hopping in kangaroos, the tail counters the rotational thrust produced by the heavy hindlimbs by rotating in the opposite direction to the hindlimbs, and also reduces the forward pitching of the body by and moving up and down (Alexander & Vernon 1975). The ability to extend and rotate the tail are both important during bipedal hopping (Alexander & Vernon 1975; Baudinet 1994; Usherwood & Hubel 2012). Although the extensors of the tail (i.e. sacrocaudalis dorsalis lateralis) are responsible for these actions (Dawson, Milne & Warburton 2014), the relatively narrow centra and curved proximal articulating facets in the proximal and transitional region of the tail, as seen in pentapedal macropodines in this study, allow the necessary range of motion for both extension and rotation of the tail during bipedal hopping (Boszczyk, Boszczyk & Putz 2001). These features, however, are not evident in sthenurines. Rather, the wide centrum of the sthenurine Ca1 indicates a high degree of stiffness (Long et al. 1997; Pierce, Clack & Hutchinson 2011). Although some stiffness is necessary to keep the tail extended (stretched out), rather than curled up (as in a prehensile tail); some flexibility is necessary to move tail up and down whilst hopping (Alexander & Vernon 1975; Hopwood & Butterfield 1990; Dawson 2012). In turn, the shorter Ca1 centra in sthenurines, reduces the distance between zygapophyses, which also reduces the range of movement dorsally and increases the stability in the region (Boszczyk, Boszczyk & Putz 2001). Range of motion is further limited by the strictly sagittal orientation of the
proximal zygapophyses, and cranial articulating facets, which permits no movement in the coronal plane (Rockwell, Evans & Pheasant 1938; Boszczyk, Boszczyk & Putz 2001). Without some orientation in the coronal plane, vertebrae are unable to rotate (Boszczyk, Boszczyk & Putz 2001), which is necessary for countering the thrust of the hindlimbs during the hopping cycle (Alexander & Vernon 1975; Baudinette 1994).

Although kangaroos and wallabies often stand upright, during pentapedal locomotion and bipedal hopping they adopt a pronograde-like posture. This makes sense in pentapedal locomotion, as that gait is merely an extension of the quadrupedal bounding gait adopted by smaller macropodines, with the additional support of the tail. In bipedal hopping this posture may correspond to the idea that this gait is thought to be a modified version of galloping. Sagittal flexion of the spine is an important aspect of both galloping and bipedal hopping (Gál 1992; Schilling 2011; Schilling & Carrier 2013), and its significance in bipedal hopping in kangaroos and wallabies is highlighted by the strong development of the epaxial musculature (Grand 1990; Dawson, Milne & Warburton 2014). The results from this study show that while pentapedal macropodines demonstrate adaptations for sagittal flexion at C1, sthenurines do not. Sagittal flexion at the sacrocaudal joint is precluded by dorsoventral expansion of the centrum and the long spinous process of C1 in sthenurines, unlike kangaroos that have relatively smaller and more cylindrical proximal endplates, and shorter spinous processes, permitting movement in all planes (Slijper 1946; Putz 1985; Finch & Freedman 1986; Boszczyk, Boszczyk & Putz 2001; Shapiro & Simons 2002; Chen, Milne & O'Higgins 2005; Kapandji 2008; Russo & Shapiro 2011; Deane et al. 2014; Russo 2014). Moreover, sthenurines lack ventral wedging of the C1 centrum, an adaptation associated with flexion in the sagittal plane in quadrupeds (Alexander & Vernon 1975; Boszczyk, Boszczyk & Putz 2001), which was observed in pentapedal macropodines in this study. The lack of these
adaptations for sagittal flexion in sthenurines highlights the unlikeliness of these species adopting either pentapedal locomotion or bipedal hopping habitually.

STHENURINE CAUDAL MORPHOLOGY CONSISTENT WITH HYPOTHESIS OF BIPEDAL STRIDING GAIT

The morphologies that support the hypothesis that sthenurines engaged in a bipedal striding gait as proposed by Janis, Buttrill and Figueirido (2014), include weight bearing adaptations and the ability to make powerful lateral movements of the tail.

The adoption of a habitually upright bipedal posture is strongly related to load bearing adaptations in lumbar and sacral vertebrae in humans and is reflective of the high axial loads associated with this posture. In particular, increased endplate area is associated with reducing forces of axial compression in vertebrae that experience high loads (Basmajian & Slonecker 1989; Boszczyk, Boszczyk & Putz 2001; Chen, Milne & O'Higgins 2005). Indeed, the sthenurine Ca1 proximal endplate is very large compared with pentapedal macropodines. This contrasts with the comparatively small proximal endplate in Ca1 seen in pentapedal macropodines, which corresponds to the more pronograde-like posture during bipedal hopping (Dawson 2012). This observation, in addition to reports by Janis, Buttrill and Figueirido (2014) and Wells and Tedford (1995) on the co-option of Ca1 into the sacrum in some sthenurines, highlights two key adaptations of this region of the spine in sthenurines. Firstly, for increasing the weight bearing capacity of the sacrum, and, secondly, the load bearing capability of the sacroiliac joints, both of which are associated with habitual adoption of an upright posture and bipedal locomotion (Kapandji 2008).

Additionally, the spinous process of Ca1 in sthenurines is very long, corresponding to well-developed m. multifidus lumborum as reported by Janis, Buttrill and Figueirido (2014). The m. multifidus lumborum is important in stabilising the trunk in humans, and is associated with their adoption of a habitually upright posture (Lickley 1904; Slijper
1946; Dofferhof & Vink 1985; Macintosh & Bogduk 1986; Basmajian & Slonecker 1989; Schilling 2011). These adaptations also support hypotheses that *Sthenurus* spp. and *Simosthenurus occidentalis* were ‘stand-up browsers’ that reached up into the trees using their highly mobile forelimbs as proposed by Wells and Tedford (1995).

Ability to move the tail in the lateral plane in sthenurines is indicated by the relatively long and narrow distal transverse processes of Ca5. This morphology indicates increased mechanical advantage of the lateral flexors in the transverse plane, as opposed to the mechanical advantage in the sagittal plane offered by distal transverse process that are long in the craniocaudal direction, as seen in pentapedal macropodids (Boszczyk, Boszczyk & Putz 2001). Adaptations of the transverse processes in the Ca5 of sthenurines, correspond to the adaptations of the Ca1 discussed above. Lateral movement of the tail may be beneficial if sthenurines engaged in bipedal striding. Particularly in the instance where one foot is off the ground during the bipedal striding gait, movement of the tail in the contralateral direction of this may offer additional balance. This would be similar to the role of the abductors in humans, which in the limb that is on the ground, prevent the slumping of the pelvis toward the unsupported side (Basmajian & Slonecker 1989). Janis, Buttrill and Figueirido (2014) also report that sthenurines have modification of the pelvis where the m. caudofemoralis attaches, which may reflect an adaptation for balancing the body over one limb.

**Sthenurine caudal vertebral morphology is not consistent with that of non-pentapedal macropodines**

The role for the tail as part of the locomotor repertoire in non-pentapedal macropodines corresponds to the use of the tail as a mobile, flexible appendage utilised in jinking-and-weaving locomotion in quadrupedal bounders, and traversing three-dimensional habitats in rock-wallabies and tree-kangaroos (Study 3). Sthenurines did not share any similarities in morphology with the non-pentapedal macropodines, and although the mean Procrustes
distances of sthenurines and tree-kangaroos Ca1 shapes were just outside statistical significance, there were no similarities in morphology between these groups.

Adaptations of the non-pentapedal caudal vertebrae highlight the significance of mobility of the tail in Ca1 and Ca5 in all three groups, whereas differences in morphology between non-pentapedal macropodines highlights the need for a flexible tail in Ca10. In Ca1 the non-pentapedal macropodines have relatively longer (mediolaterally) distal transverse processes and mammillary processes. These modifications enable coronal and sagittal plane movement, and permit mobility of the tail. Interestingly, the mammillary processes in rock-wallabies are exceptionally long, as are the cranial articulating facets. These morphologies may be interpreted as an adaptation for load bearing (Adams & Hutton 1980; Pal & Routal 1987; Chen, Milne & O'Higgins 2005), and could be related to the vertical jumping and leaping unique to rock-wallabies (Sharman & Maynes 1983; Strahan 1995). In contrast to Ca1, in Ca5 non-pentapedal macropodines have shorter mammillary processes compared to pentapedal macropodines. This likely corresponds to the strong development of the mm. sacrocaudalis dorsalis, as seen in *M. fuliginosus*, which is responsible for extension of the tail during bipedal locomotion (Dawson, Milne & Warburton 2014). That this morphology isn’t shared by the non-pentapedal macropodines reflects the specialisation of the role for the tail in bipedal hopping in kangaroos and large wallabies (Grand 1990; Study 3). In Ca5, rock-wallabies have very long and narrow distal transverse processes, while tree-kangaroos are slightly reduced, this supports the hypothesis in Study 3 that tree-kangaroos may not rely on as powerful lateral movements of the tail, as required by rock-wallabies. While mobility at the base of the tail is important in all macropodines, the longer and more slender Ca10 centrum in rock-wallabies and tree-kangaroos indicates that flexibility is favoured in these species (Study 3). That this Ca10 morphology separates quadrupedal bounding and pentapedal macropodines from rock-wallabies and tree-kangaroos, further highlights the importance of a long, flexible
ANALYSIS OF CA1, CA5, CA10 IN MACROPODINES AND STEHENURINES

tail, as an adaptation for movement in a more complex dimensional structure of habitat, as used by rock-wallabies and tree-kangaroos (Sharman & Maynes 1983; Martin 2005; Russo 2014). The findings from the present study further emphasise that caudal vertebral morphology is strongly associated with habitat use in the Macropodinae.

FUTURE CONSIDERATIONS
One aspect of variation not fully explored here, is allometric variation associated with caudal vertebral shape in the Macropodidae. While preliminary results indicate that centroid size is associated with shape (in both intraspecific and interspecific investigations) in this group, a broader, larger-scaled analysis is required to fully understand this relationship. This was outside the scope of this study, due to the many factors that must be considered when investigating size within the Macropodidae. However, examining these factors would be informative. Foremost of these factors, is the influence of sexual selection on tail use and body mass, particularly in kangaroos and larger wallabies. During male-male fighting in the larger members of the Macropodinae, males use their tails to support their body weight, so as to free the hindlimbs to kick their opponents (Jarman 1991; Dawson 2012). This complicates the issue of scale in this family because smaller macropodines do not utilise the tail in this manner, and, further to this, body mass becomes increasingly dimorphic (between sexes) as species size increases within the Macropodinae (Jarman 1989; Weckerly 1998 cited in Richards, Grueter & Milne 2015). Considering this behaviour is clearly important, as increasing evidence highlights that the forelimb, which is a locomotor apparatus (like the tail), is subject to significant sexual section in male kangaroos and large wallabies (Warburton, Bateman & Fleming 2013; Richards, Grueter & Milne 2015). Additionally, because macropodines exhibit indeterminate growth (Hume et al. 1989), in any investigation of size in this group age should be considered, as has been done by many previous authors (Milne & O'Higgins 2002; Hadley, Milne & Schmitt 2009; Dawson & Milne 2012; Richards, Grueter & Milne 2015).
Lastly, phylogenetic signal was also strong in both shape and size variables of extant macropodines, and should also be considered in any potential future investigations of allometry associated with caudal vertebral shape within the Macropodidae.

Finally, in this study, all the landmarks used were either ‘type II’ or ‘type III’ landmarks, meaning that they are more diverse in location than more discrete landmark types (type I), such as the junction between two sutures (Bookstein 1991). This may have influenced the shape variation in Ca5, particularly because landmarks 18 and 24 (Fig. 5-2A and Table 5-2A) on Ca5 are both type III landmarks. That the lateral margin (where these landmarks are located) is variable, and hard to define may be a potential source of shape variation in Ca5. As such, future studies of vertebrae should utilise sliding landmarks in order to retain more shape information (Bookstein 1991, Bookstein 1997 cited in Adams, Rohlf & Slice 2004), given that most landmarks on vertebrae are likely to be either type II or III.

**CONCLUSIONS**

The caudal vertebral morphology of sthenurines investigated here supports previous hypotheses that sthenurines adopted a locomotor repertoire divergent from extant macropodines. That it is highly unlikely that sthenurines engaged in pentapedal locomotion lends further support to the idea this gait is unique to the Macropodinae. Importantly, the findings from the present study highlight the functional-adaptive evolution of the tail as part of the locomotor repertoire across the Macropodidae.
**Figure 5-S1.** Proposed phylogeny of the sthenurines based on osteological characters, taken from Prideaux (2004).
CHAPTER SIX

GENERAL DISCUSSION AND CONCLUSIONS

SUMMARY OF MAJOR FINDINGS

This is the first study of the behavioural and morphological correlates of pentapedal locomotion across the Macropodidae. As a result of these investigations, this project demonstrates the following significant and new information:

- Pentapedal locomotion is not universal within the Macropodidae
- Pentapedal locomotion in kangaroos and wallabies can be characterized by the tail repositioning phase, a fixed distal tail and stable pelvis during the hindlimb swing phase
- The adoption of pentapedal gait for locomotion at slow speed is associated with the lengthening of the tibia relative to the femur, and corresponding adaptations to more open environments in the Macropodinae
- Pentapedal macropodines demonstrate a distinctive morphology in several aspects of caudal anatomy
- Variation in caudal vertebral morphology across the Macropodidae more broadly reflects the diverse role for the tail as part of the locomotor repertoire within this group. Importantly:
  - Kangaroos display adaptations associated with the role of the tail during bipedal hopping
  - Rock-wallabies and tree-kangaroos demonstrate caudal morphology that reflects adaptation to life in three-dimensional habitats
Sthenurine kangaroos did not demonstrate caudal vertebral morphology indicative of the use of the tail as a fifth leg during pentapedal locomotion or as a dynamic cantilever during bipedal hopping.

These new discoveries can be grouped into three major contributions:

1) Establishment of the anatomical correlates of pentapedal locomotion in kangaroos and wallabies;

2) A detailed understanding of the selective pressures associated with the evolution of pentapedal locomotion within the Macropodidae; and

3) The association between ecology, locomotor repertoire, and tail use across the Macropodidae.

As such, this chapter is comprised of three sections, one to address each of these major contributions. In closing, I suggest areas for future research, followed by a general conclusion.

ANATOMICAL CORRELATES OF PENTAPEDAL LOCOMOTION IN KANGAROOS AND WALLABIES

During slow gait, the use of the tail to support the body weight and propel the body weight forward has previously been clearly defined in the red kangaroo, *M. rufus* (O'Connor et al. 2014). As part of this project, I have expanded and elaborated on the description of pentapedal locomotion for a further seven species of macropodines, which includes kangaroos and medium-to-large wallabies (Dawson et al. 2015). In the analysis of slow locomotion across the Macropodinae, kangaroos and wallabies demonstrate two aspects of the gait cycle that indicate the tail is being used as a fifth leg:

- ‘Tail repositioning phase’, where the tail is drawn under the pelvis prior to the tail support phase (Dawson & Taylor 1973; Dawson et al. 2015).

- ‘Tail support phase’, where the distal tail is fixed, and the pelvis remains at a constant height (Dawson et al. 2015). This likely provides necessary friction and
stability so that the tail may support the body weight while the hindlimbs are drawn forward, and the body weight is shifted forward (O’Connor et al. 2014).

These two phases of the gait cycle are reflected in the caudal musculature of the western grey kangaroo, *M. fuliginosus* (Dawson, Milne & Warburton 2014). More importantly, the current project demonstrates the skeletal morphology that corresponds to this musculature, and the use of the tail as a fifth leg, is shared by all species identified as pentapedal macropodines (Dawson et al. 2015), and is absent in non-pentapedal species.

**TAIL REPOSITIONING PHASE**

The repositioning of the tail under the animal’s centre of mass, which is around the hindquarters, at the beginning of the pentapedal cycle (tail repositioning phase) is likely achieved by the highly developed, and relatively large ventral and lateral flexor musculature (m. pubococcygeus, m. sacrocaudalis ventralis lateralis, m. coccygeus) (Dawson & Taylor 1973; Dawson, Milne & Warburton 2014; O’Connor et al. 2014; Dawson et al. 2015). That mechanical advantage is given to these muscles in all pentapedal species is reflected in the morphology of the distal transverse processes of the Ca1 and Ca5 (Study 4). These processes are long in the craniocaudal direction, indicating that movement in the sagittal planes is important. Although the transverse processes are relatively shorter in the mediolateral direction, the lateral flexors that attach to this site are fleshy (Study 2), suggesting that movement in the coronal plane is also important in pentapedal species. Together, these features reflect the action of drawing the tail under the body (Study 1), as part of the tail repositioning phase.

**TAIL SUPPORT PHASE**

Pentapedal species display increased resistance to axial compression and increased ability to bear load in the proximal endplates of Ca5-Ca13, compared to non-pentapedal species (Study 3). This region of the caudal skeleton is between the point at which the tail bends
toward the ground and the point where the tail touches the ground. Thus, these adaptations of the proximal endplate correspond to the role of the tail to support the body weight while the hindlimbs are being swung forward (Dawson & Taylor 1973; O'Connor et al. 2014; Dawson et al. 2015). During the tail support phase, it is thought that through eccentric muscle action, the proximal extensor mass of the tail prevents the tail from ‘over-flexing’ under load bearing, while the flexors may prevent further flexion of the mid-distal tail under load (Dawson, Milne & Warburton 2014). In Ca5-13 pentapedal macropodines also display high resistance to sagittal plane bending (Study 3). This can be attributed to the need to resist buckling and the forces of deceleration and acceleration associated with propulsive action of the caudal musculature during the tail support phase (Currey 1967, cited in Alexander 2003).

THE NEED FOR A FIFTH LEG: THE EVOLUTION OF PENTAPEDAL LOCOMOTION IN KANGAROOS AND WALLABIES

During locomotion all macropodines, apart from tree-kangaroos, must move paired limbs in unison (asymmetrical gait) whilst moving at any speed, rather than striding or walking (symmetrical gait). They use bipedal hopping for fast locomotion, and either quadrupedal bounding or pentapedal gait during slow locomotion (Windsor & Dagg 1971; Dawson & Taylor 1973; Hildebrand 1977; 1980; Dawson et al. 2015). What varies between species during slow gait is the use of the tail to support and propel the body weight – the use of the tail as a fifth leg – in addition to moving the paired limbs in unison (Dawson & Taylor 1973; O'Connor et al. 2014; Dawson et al. 2015). As highlighted by Dawson (1977), this is not due to the inability of kangaroos to move the limbs independently, as they are able to do so while swimming (Wilson 1974). Rather, the inefficacy of a striding gait is attributed to the disparity in length between the forelimbs and hindlimbs (forelimb-hindlimb asymmetry) that inhibits stability, which is of particular importance during slow gait (Dawson & Taylor 1973; Dawson 1977; O'Connor et al. 2014). Tree-kangaroos are
able to engage in striding gait because they have relatively equal forelimb-hindlimb length, owing to adaptations of the forelimb necessary for climbing and life in the trees (Windsor & Dagg 1971; Grand 1990; Martin 2005; Warburton et al. 2011).

WHY BEING GOOD ON TWO LEGS MAKES YOU BAD ON FOUR: THE KANGAROO’S TRADE-OFF

The evolution of pentapedal locomotion has long been attributed to the inefficiency of bipedal hopping at slow speeds while the extreme specialisation of the body plan for bipedal hopping in kangaroos, precludes a quadrupedal gait at slow speeds as an alternative. One such specialisation is the elongation of the hindlimb in kangaroos. This adaptation enables increased stride length without increasing stride rate (Bennett 1987), and is driven by the increased length of the tibia relative to the femur (McGowan, Skinner & Biewener 2008). Indeed, in Dawson et al. (2015) it was found that species that engaged in pentapedal locomotion had a higher crural index than those that did not. While this supports the hypothesis that hindlimb length is associated with pentapedal locomotion, diversity in gait selection in medium-to-large wallabies requires further discussion of other aspects of body plan specialization that were not directly tested in this project.

O'Connor et al. (2014) suggested that the susceptibility for an animal with a posterior end as heavy as a kangaroo’s to fall backwards while the hindlimbs are off the ground may be a driving factor in the co-option of the tail as a fifth leg. This propensity to fall backwards is attributed to the large proportion of weight at the rear of the kangaroo (Grand 1990; Dawson et al. 2004; O'Connor et al. 2014). In kangaroos, this posterior weight (mainly around the pelvis) comprises 80% of the muscle mass and about 40% of the animal’s total body weight (Grand 1990; Dawson et al. 2004). This specialization of the body plan in kangaroos is due to the more heavily muscled hindquarters and tail (Hopwood & Butterfield 1976; Dawson, Milne & Warburton 2014), compared to smaller wallabies (Grand 1990). This, along with a small head, places the centre of gravity to the
posterior of the animal, and minimizes the tendency of the body to rotate at the end of take-off as well as at touch down (Grand 1990; Baudinette 1994). Combined, these features, among others, act to minimize the cost of bipedal hopping at high speeds in kangaroos (Baudinette 1989).

Minimizing the cost of locomotion at high speed is a major selective pressure that drives body plan specialization in vertebrates (Christiansen 2002). Macropodines, like many vertebrate groups (Hildebrand 1974; Romer & Parsons 1986; Christiansen 2002) become more specialized for locomotion as body mass increases (McGowan, Skinner & Biewener 2008). All members of the Macropodinae, no matter the size (~3-90kg), engage in bipedal hopping in some capacity (Windsor & Dagg 1971; Dawson & Taylor 1973; Baudinette 1989; Flannery 1990; Strahan 1995). But, kangaroos, the largest of the group, have the longest and most muscular hindlimbs, which enable longer, more powerful strides (Howell 1944; Grand 1990; Lodder 1991; Dawson et al. 2004; Kear et al. 2008; McGowan, Skinner & Biewener 2008). As such, kangaroos are capable of attaining the highest speeds, independent of stride rate, and are thus the most efficient during fast locomotion among the macropodines (Dawson & Taylor 1973; Bennett 1987; Baudinette, Snyder & Frappell 1992; Baudinette 1994). While these specialisations may constrain slow gait in large-bodied kangaroos, medium-sized macropodines appear to be less limited, likely due to less extreme adaptations of the body plan.

**DIVERSITY IN BODY PLAN AND SLOW GAIT IN MEDIUM-SIZED MACROPODINES**

Among medium-sized macropodines there is diversity in both hindlimb morphology and, consequently, gait selection at slow speed (Dawson et al. 2015). An apt example is the comparison of *T. billardierii* and *M. irma*. Both species can be classed as medium-sized wallabies (*T. billardierii*: 10-12kg, *M. irma*: 7-9kg) but differ in hindlimb morphology. Both species engage in bipedal hopping during fast locomotion (Windsor & Dagg 1971;
Strahan 1995), but *M. irma* is apparently more specialized for bipedal hopping, with a CI of 1.63 compared to *T. billardierii*, which has a CI of 1.25 (Dawson et al. 2015). During slow gait, *M. irma* engages in pentapedal locomotion, while *T. billardierii* engages in a quadrupedal bound (Dawson et al. 2015). That *T. billardierii* is in fact slightly larger than *M. irma* suggests that it is body plan, rather than body size, that may drive medium-sized macropodines species to adopt pentapedal locomotion.

As part of a study on sexual dimorphism of limb proportions in the Macropodidae, Richards, Grueter and Milne (2015) investigated forelimb-hindlimb asymmetry. This was measured by intermembral index (IMI; radius + humerus/tibia + femur), where a lower value represents a greater disparity between limbs. Results from that study showed that *M. irma*, had a relatively greater forelimb-hindlimb asymmetry (IMI) (M=0.408, F=0.391) than *T. billardierri* (M=0.566, F=0.496). On one hand, this would support the hypothesis that forelimb-hindlimb asymmetry contributes to the instability associated with specializations of the body plan for bipedal hopping. On the other hand, in some kangaroos (*M. rufus, M. giganteus, M. fuliginosus*) there is a reduction in forelimb-hindlimb asymmetry compared with medium-to-large wallabies (see supplementary material of Richards, Grueter & Milne 2015). While this is due to the lengthening of the humerus relative to the radius, and can be attributed to sexual selection in males, females from larger *Macropus* spp. also have reduced forelimb-hindlimb asymmetry, compared to smaller species (Richards, Grueter & Milne 2015).

That forelimb-hindlimb asymmetry does not necessarily increase with body size within the subfamily Macropodinae, suggests that this aspect of body plan specialization is not the major driving factor responsible for the evolution of pentapedal locomotion in kangaroos and wallabies, as has been previously proposed (e.g. Dawson 1977, O’Connor et al. 2014). It may be that there are other contributing factors associated with the
evolution of pentapedal locomotion in medium-to-large sized wallabies, compared to kangaroos. I propose that the positioning of body mass to the back of the animal may contribute most to the propensity to fall backwards in kangaroos, whereas forelimb-hindlimb asymmetry may be the cause of instability in medium-to-large sized wallabies. That sthenurine kangaroos were unlikely to have adopted pentapedal locomotion is consistent with suggestions that their body plan was not specialized for bipedal hopping (Janis, Buttrill & Figueirido 2014).

**Does having five legs allow you to be better on two?**

Pentapedal locomotion is generally considered to be no more than a clumsy, albeit less energetically costly, alternative to bipedal hopping at slow speeds, but, has the evolution of this gait allowed kangaroos to increase efficiency on two legs? The specialisations of the body plan that are associated with the co-option of the tail during slow gait correspond to refinements of the musculoskeletal system that allow greater speeds to be achieved independent of stride rate, thus increasing the efficiency of bipedal locomotion (Bennett 1987; Baudinette 1989; Baudinette, Snyder & Frappell 1992; Baudinette 1994). That kangaroos can engage the tail as a fifth leg prevents: 1) resorting to hopping at slow speeds, or 2) compromising hindlimb length for stability at slow speeds. Because these compromises aren’t required, adaptations that inhibit stability at slow speeds, but enhance the efficiency of bipedal hopping (i.e. heavy posterior and long hindlimbs), are sustainable aspects of the kangaroo’s body plan. Such adaptations might not have been viable in kangaroos if stability at slow speed was not provided by the tail. Moreover, as has been pointed out by many authors, adaptations of the body plan usually reduce unnecessary energy costs during locomotion. Reduction of energy costs is not only important during fast locomotion, but also during slow locomotion (see Christiansen 2002 for discussion), and, indeed, pentapedal locomotion offers a less costly alternative to bipedal hopping at slow speeds (Dawson & Taylor 1973). Perhaps we should regard the
evolution of pentapedal locomotion not only as a by-product of specialisation of the body plan for fast locomotion, but as part of the suite of adaptations that allow kangaroos to be so efficient during bipedal hopping.

**ECOLOGY, LOCOMOTOR REPertoire AND TAIL USE IN THE MACropodidae**

Kangaroos and wallabies have radiated into a variety of niches and habitats. Adaptations to these environments have resulted in some remarkable specialisations of the macropodid bauplan. While a great number of authors have previously paid attention to the specialisations of the main locomotor apparatus, the hindlimb (e.g. Hopwood & Butterfield 1976; Flannery 1982; Bennett 1987; Hopwood & Butterfield 1990; Lodder 1991; Kram & Dawson 1998; Bennett 1999; Dawson et al. 2004; McGowan et al. 2005; McGowan, Baudinette & Biewener 2006; Kear et al. 2008; McGowan, Skinner & Biewener 2008; Warburton & Prideaux 2010), and a few studies have focussed on the forelimbs (Harvey & Warburton 2010; Warburton et al. 2011), this research is the first to document how the *tail* has specialized for locomotion in specific habitats and niches within the Macropodidae.

Across the mammalian radiation, the tail can be co-opted into the locomotor repertoire when four limbs simply do not provide enough support (e.g. the grasping, prehensile tail of New World monkeys; Garber & Rehg 1999; Schmitt et al. 2005), or to provide some mechanical advantage during a particular movement (e.g. cheetahs when running; Hildebrand 1959). In the Macropodidae, it seems that the tail is incorporated into the locomotor repertoire when stability is compromised during a particular movement, or, to reduce the costs or increase efficacy associated with a particular gait or posture.

In some macropodines, stability at slow speed is compromised due to specialisations of the hindlimb for bipedal hopping (e.g. Dawson et al. 2015). Previous research has
highlighted the link between arid and open habitats and hindlimb structure in the subfamily Macropodinae (Flannery 1982), and, we know that bipedal hopping is an adaptive response to arid conditions in mammals more generally (Webster & Dawson 2004). Indeed, it is those species that live in open forest, woodlands and grasslands, that show the greatest lengthening of the tibia relative to the femur (crural index), which, in turn is strongly associated with the adoption of pentapedal locomotion in the Macropodinae (Dawson et al. 2015). And, of the pentapedal macropodines, it is those that display the most extreme adaptations for arid conditions (the kangaroos), which also show the greatest specialization of the tail in its role during bipedal hopping (Studies 3 and 4).

Although bipedal hopping is the mainstay of fast locomotion in kangaroos and typical wallabies (Windsor & Dagg 1971; Dawson & Taylor 1973; Baudinette 1977; Bennett 1987; Baudinette, Snyder & Frappell 1992; McGowan et al. 2005), selection of gait during slow locomotion appears to be more dependent on habitat preference and the nature of the substrate the macropodine is moving on (Dawson et al. 2015). Species that are adapted to less open environments, or that have less predictable terrain (e.g. Petrogale and Dendolagus spp.) do not engage in pentapedal locomotion, as they show less extreme adaptations of the bauplan for bipedal hopping compared with kangaroos and large wallabies (Dawson et al. 2015).

Of those species (Petrogale, Dendolagus and Sthenurinae spp.) that do not utilise pentapedal locomotion, nor have modifications of the tail that indicate specialisation for its role in bipedal hopping, the tail is adapted to increase stability associated with locomotor strategy. In tree-kangaroos and rock-wallabies, flexibility and mobility of the tail is favoured, likely to provide stability in the relatively unpredictable environments of the tree-tops and rocky outcrops they reside in (Studies 3 and 4). In contrast, in sthenurines the tail appears to be adapted to minimise movement in the sagittal plane, in
addition to bearing weight (Study 4), reflecting a potentially orthograde posture adopted when they engaged in stand-up browsing (Wells & Tedford 1995). Though *Petrogale* spp., *Dendolagus* spp., and subfamily Sthenurinae do not demonstrate adaptations for the tail consistent with the better known roles for the tail during bipedal hopping, the tails are nonetheless specialised for the locomotor repertoire utilised by these macropodids. Importantly, the diversity in the adaptations of the tail strongly reflect the ecological niches and habitats occupied by the Macropodidae.

**FUTURE DIRECTIONS**

The studies undertaken as part of this project provide a baseline knowledge of the functional morphology associated with the tail in the Macropodidae. From this, it is evident that there is a significant role for the tail as part of the locomotor repertoire across this family. In establishing this, it is clear that there are some areas where the role of the tail during gait, and the gait more generally should be further clarified.

In particular, it has been highlighted that many macropodines share aspects of the slow gait cycle with kangaroos, for which the role of the tail has been quantified during pentapedal locomotion. In *M. rufus* it is known that the tail supports the body weight, but also propels the body weight forward. While other macropodines demonstrate features that would indicate that propulsion is part of the slow gait cycle, this needs to be tested using force plate analysis. Comparative muscle dissections across the Macropodinae would complement this, and could also shed light on how the tail is adapted for its use as part of the locomotor repertoire within this group.

The results of the examination of muscular anatomy and the vertebral anatomy of kangaroos further highlight that the tail is highly specialized in kangaroos compared with the smaller macropodines. However, we still understand little about the actual role of the tail as part of fast bipedal hopping. Since Alexander and Vernon (1975), Bennett (1987),
Baudinette (1989) undertook their studies on hopping in kangaroos there have been major advances in quantitative *ex vivo* analyses of locomotion, such as moving 3D x-ray technology. This may allow a definitive understanding of the action of the tail during hopping.

One of this studies in this project demonstrates that the morphology of sthenurine caudal vertebrae is consistent with the adoption of an upright stance and striding. The next logical element to investigate would be the sacrum. The adaptations of the sacrum for bipedal locomotion in humans has been extensively noted (see Abitbol 1988 and Russo & Shapiro 2013 for discussion). Thus, any future comparative approach taken to elucidate the capability of the sacrum to bear load in sthenurines should be done via a comparison with other macropodids, and humans. Importantly, size needs to be addressed thoroughly in extant macropodids to instruct an informed hypothesis regarding the adaptations of the sacrum. To gain a more comprehensive understanding of the locomotor repertoire in sthenurines, a multi-element approach (i.e. including sacrum, limb bones, vertebrae in analyses) would be best, e.g. Christiansen (2002). Elucidating the likely locomotor repertoire of sthenurines is key, because, if sthenurines did engage in a bipedal striding gait as suggested by this study, this is truly remarkable among the mammalian radiation. It would beg the question, what selective pressures lead to the evolution of bipedal striding in one clade, versus bipedal hopping in another?

**Conclusion**

Prior to the studies carried out in this project there was a major gap in the literature regarding one of the remarkable aspects of biology in kangaroos and wallabies; the use of the tail in pentapedal locomotion. In light of the findings of this research, there is now a clearer picture of the use of pentapedal locomotion within the Macropodinae, and the factors that may have driven the evolution of the gait within this family. Specialisations
of the kangaroo and wallaby body plan, such as the relative lengthening of the tibia, appear to be more important drivers of the co-option of the tail as a fifth leg in macropodines, while previously suggested aspects of body plan specialisation, such as forelimb-hindlimb asymmetry, may be less so. That pentapedal locomotion is not universal within the Macropodinae, and given that sthenurines are unlikely to have adopted pentapedal locomotion as part of the locomotor repertoire, suggests that pentapedal locomotion is unique to the Macropodinae. Moreover, the variation in caudal morphology across the Macropodidae reflects the diverse role for the tail as part of the locomotor repertoire within this group.
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APPENDICES
Appendix A – Research Approval for Observation of Animals

Government of Western Australia
Zoological Parks Authority

Our Ref: ZA4981-8 #06935
Your Ref:
Enquiries: Pamela Smith, Caroline Lawrence 9474 0355

Perth Zoo

14 August 2013

Rebekah Dawson
PhD Candidate
School of Anatomy, Physiology and Human Biology
University of Western Australia
M309, 35 Stirling Highway
CRAWLEY WA 6009

Dear Rebekah

Project Title: 2013-9 Investigating the functional morphology of the tail in kangaroos and their kin

This letter is to confirm that the Perth Zoo Research and Animal Ethics Committees have approved the above named project.

Investigators are reminded that the duration of research activities must be no longer than required to meet the aim(s) of the project, and must be compatible with supporting and safeguarding animal wellbeing. Approval for your project is given for the period 14 August 2013 to 31 August 2013.

An annual report (attached) must be lodged with the Zoo at the end of each calendar year and a new application submitted after 31 August 2013. The Animal Ethics Committee must be informed prior to any changes being made to the procedures stated in the original application.

Additional applications should be made to the Committees for specific experimentation beyond the scope of this application.

With best wishes for success in your work.

Yours sincerely

Susan Hunt PSM
Perth Zoo Chief Executive Officer; and
Chair, Perth Zoo Animal Ethics Committee

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Dear Ms Dawson

Please find attached a copy of the Notification which was ratified at the Animal Ethics committee meeting of November 4, 2011.

Best wishes,

IN CONFIDENCE

THE UNIVERSITY OF WESTERN AUSTRALIA

ANIMAL ETHICS COMMITTEE

NOTIFICATION OF OBSERVATIONAL STUDIES

Studies involving the observation of free living animals have the potential to interfere with normal behaviour (section 5.1 of the Code). This form should not be used when the handling of animals will occur or there is potential to interfere with normal behaviour, in such cases a full application would be required. For further information, please refer to the Animal Ethics website at:

http://www.research.uwa.edu.au/staff/animals/ethics-committee

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1. PROTOCOL DETAILS

   Project Title:
   Investigating the functional morphology and evolution of the tail in kangaroos and their kin

   Proposed Start date: 01/12/2011
   Expected completion date: 01/08/2012

2. CHIEF INVESTIGATOR DETAILS

   Title: last name: first name
   Staff / Student number (UWA only)
   Rebeckah Dawson
   20410015

   Work / mailing address / school (include UWA MBDP)
   School of Anatomy and Human Biology M309, University of Western Australia

   Email: dawsonreb@student.uwa.edu.au
   Phone: 6488 8645
   Mobile: 0422 860 348

3. SPECIFY THE ANIMAL SPECIES AND NUMBERS TO BE OBSERVED (species name and common name)
   - Red Kangaroos (Macropus rufus)
   - Eastern Grey Kangaroos (M. giganteus)
   - Western Wallabies (M. robustus)
   - Tammar wallabies (M. eugenii)
   - Dama/Farma wallabies (M. parma)
   - Agile wallabies (M. agilis)
   - Bennett’s wallabies, Red-necked wallabies (M. rufogriseus)
   - Yellow-footed rock wallabies (Petrogale xanthopus)
   - Quokkas (Setonix brachyurus)

4. DESCRIPTION OF THE PROPOSED STUDY

   Must be written in English and include details of any potential animal welfare concerns


updated September 2010

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Tails are common in terrestrial, arboreal and aquatic mammals and functional adaptations for the tail are vast and varied. Although aquatic and arboreal mammals commonly use their tails in locomotion, it is a far rarer occurrence in terrestrial mammals. Aquatic mammals such as dolphins and manatees rely heavily on the tail in locomotion for propulsion and directionality in the water (Reidenberg, 2007). New world monkeys commonly have prehensile tails which aid them in arboreal locomotion. Among the terrestrial mammals there are few which engage their tails in locomotion. Kangaroos and their kin are a family of terrestrial mammals who incorporate their tails in locomotion (Windsor and Dagg, 1971).

Kangaroos and their kin, or macropodids, are a diverse family comprised of more than thirty living species in seven different genera (Strahan, 1995). These animals inhabit a vast range of habitats from the rainforest to the open plains of the desert and everything in between. This expansive geographic range has led to multiple different ecological niches being occupied by the macropodids. Along with these variations in habitat, there are great variations in body form, posture and locomotion, all of which have resulted in functional variation of the tail within this family. The proposed study aims to investigate what musculoskeletal adaptations have developed to support the function of the tail in macropodids.

The proposed study will have an observational component. In order to obtain detailed accounts of how macropodids use their tail in locomotion. Previous studies have briefly described the use of the tail in locomotion within the macropodid family; however this study requires much more detailed accounts. Representatives from multiple genera from different habitats, with different body forms will be observed to investigate if these factors affect the role of the tail in locomotion. Novel muscular and skeletal investigations will provide insight into anatomical adaptations related to the use of the tail. This knowledge of function and form in the living macropodids may then be applied to extinct macropodids, and it may be possible to infer how the macropodids of the past relied on this key locomotor organ.


5. DETAILS OF THE LOCATION OF THE STUDY

Caversham Wildlife Park, Caversham WA 6068 1984

Please confirm the manager/owner of the property/site location has been contacted and approval has been given for the use of this location. Yes [X] No []

Permits may be required from the Department of Environment and Conservation (DEC) for entry.

### 6. HEALTH AND SAFETY

Identify concerns for the health and safety of either staff, students and/or other animals. Ensure that the appropriate approvals have been obtained. For further information, refer to the safety and health website at www.safety.uwa.edu.au.

There will be no handling of animals by the observer. The observer will be aware of and comply with emergency procedures at each location.

### 7. DECLARATION

I have read and agree to abide by the conditions and constraints of the Animal Welfare Act 2002 (WA) Regulations, which include the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes available from www.srahc.gov.au/publications/synopsis/synopsis.htm.

Chief Investigator
Rebekah Dawson

PRINT NAME: REBEKAH DAWSON
SIGNATURE: [Signature]
DATE: 03/08/2011

Please forward one (1) signed copy to: Animal Ethics Committee – M459
The University of Western Australia
35 Stirling Highway, CRAWLEY WA 6009
aceo@admin.uwa.edu.au

http://www.research.uwa.edu.au/val/cover/research_services/ethics/minimal_ethics/forms_information

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<td>Richard Pelling</td>
<td>23/02/2014</td>
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## APPENDIX C – DETAILS OF STHENURINE MATERIAL USED FOR THIS STUDY

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<th>Species name</th>
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Flinders Palaeo = collection held at the Flinders University Palaeontology Laboratory
SAM = South Australian Museum