Shoulder to shoulder:

Comparative functional morphology of the scapula across therians

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Abstract

The scapula (shoulder blade) in therian mammals is highly variable in its morphology, and understanding how this variation relates to biomechanical function can inform research in many fields, such as within palaeontology, where anatomical correlates are used to infer behaviours and ecology of extinct mammals. While the relationship between scapular morphology and function has been investigated across all major extant therian clades, taxonomic constraint and discrepancies in methodology make it near-impossible to synthesise this research into generalisable evidence of form-function relationships, especially in the context of locomotion behaviour. This thesis begins by quantifying locomotion behaviour in high resolution using a multivariate scoring system, producing both a data matrix and a mathematically-defined categorical variable, greatly surpassing traditional behavioural quantification methods. Next, scapula morphology across 201 species of extant therians (covering all extant orders) is quantified in 3D using 71 landmarks via geometric morphometric methods, and this is related to locomotion behaviour, allometry and clavicle presence within a phylogenetic framework, using a suite of multivariate statistics. The results demonstrate clear morphological correlates associated with allometry, clavicle loss, and certain locomotion behaviours (particularly climbing/aerial movement and running ability). Finally, these results are validated in the functionally-representative order, Rodentia, which demonstrates consistencies in the form-function relationships, and supports rodents as a suitable model order in the context of scapular functional morphology. The findings of this thesis provide a clade-wide investigation of scapular morphology in therians, which shows robust evidence of generalisable links between scapular form and function across therians based on the highest resolution shape and function datasets thus far in the field.

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Author's declaration

I declare that this thesis is a presentation of my original work. All sources are acknowledged as references, and any passages or figures copied from academic papers, books, etc. have been clearly identified and appropriately cited. This work has not previously been presented for a degree or other qualification at this University or elsewhere. This thesis does not contain any unacknowledged work from other sources.

Chapter I

Introduction:

The shoulder girdle is a window into mammal locomotor evolution

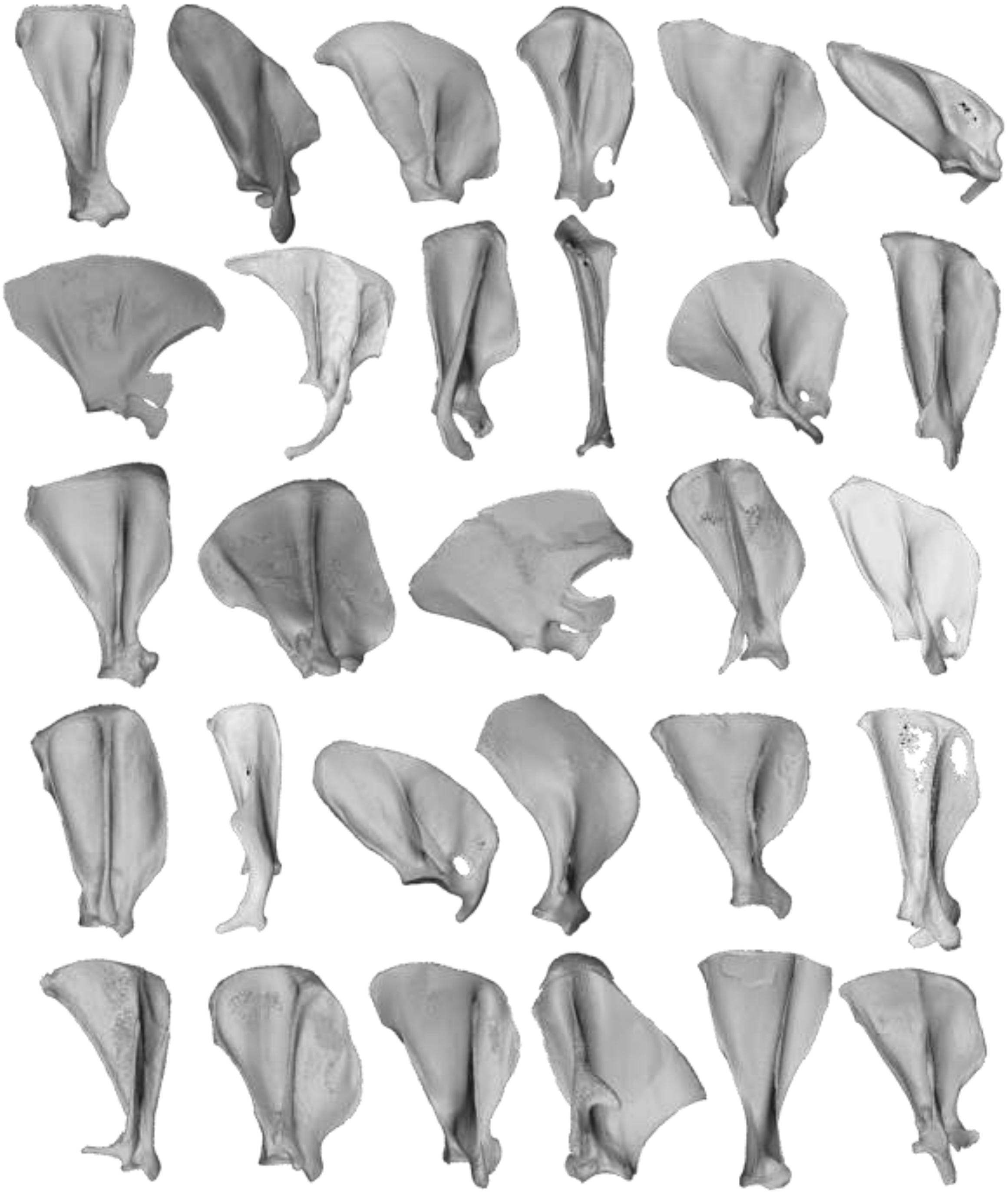

Figure I.1: Scapular variation in extant therians
*Examples of scapulae from extant therians included in this thesis. Images are not to scale. From left to right and top to bottom: African wild ass (*Equus africanus*) uant-bio-fun:EQasi01301; chimpanzee (*Pan troglodytes*) DU EA 155.4; Chinese pangolin (*Manis pentadactyla*) NHMUK 58.6.24.166/728.F; South American tapir (*Tapirus terrestris*) NHMUK 1847.4.6.1/709.d; ursine colobus (*Colobus vellerosus*) UMZC E.7309.A; little golden-mantled flying fox (*Pteropus pumilus*) UMMZ 156775; short-finned pilot whale (*Globicephala macrorhynchus*) NHMUK 1992.78; pink fairy armadillo (*Chlamyphorus truncatus*) FMNH 39468; common wombat (*Vombatus ursinus*) NHMUK 72.4499; star-nosed mole (*Condylura cristata*) YPM VZ Mam 014548; giant anteater (*Myrmecophaga tridactyla*) NHMUK 3.7.7.176; Hispaniolan solendon (*Solenodon paradoxus*) UMZC E.5418.A; pygmy hippopotamus (*Choeropsis liberiensis*) NHMUK 1967.3.20.1; brown bear (*Ursus arctos*) UMZC K.1181; harbour porpoise (*Phocoena phocoena*) UMZC C.87.G; crested porcupine (*Hystrix cristata*) UMZC E.3404; Linnaeus' two-toed sloth (*Choloepus didactylus*) NHMUK 1510.0_c/69.7.19.12; striped hyaena (*Hyaena hyaena*) NHMUK 75.1992/273; golden mole (*Amblysomus hottentotus*) MCZ 57045; brown-throated sloth (*Bradypus variegatus*) NHMUK 1904.7.4.111; dugong (*Dugong dugon*) NHMUK 1852.6.26.1/107.a; western tree hyrax (*Dendrohyrax dorsalis*) NHMUK 1910.6.11.3; greater dwarf lemur (*Cheirogaleus major*) AMNH 100843; European hare (*Lepus europaeus*) SCA personal collection; wolverine (*Gulo gulo*) UMZC K.2004; Indochinese rhesus macaque (*Macaca mulatta*) UMZC E.7503.A; African elephant (*Loxodonta africana*) MSCC-020; roan antelope (*Hippotragus equinus*) UMZC H.24363; aardvark (*Orycteropus afer*) NHMUK 72.4496.*

I.1. Thesis foundation

Therian mammals are unique among vertebrates. From fur to jaws, and from the diaphragm to milk production, therian mammals have a range of adaptations which are not present in other vertebrate groups, and which have contributed to their rise to dominance in the Cenozoic, the ‘Age of Mammals’. One of the few windows we have into vertebrate evolution and, therefore, into mammal evolution, is our understanding of the skeleton. With limited exceptions, the skeleton is all that remains as evidence of the long and complex evolutionary journey which has resulted in the extant animals we see today. Thus, it is the skill of palaeontologists, functional morphologists and others to ‘read’ the history laid down in the fossil record by rigorously relating skeletal anatomy to biomechanical function and phylogeny. This is why the study of functional morphology in extant animals is crucial to our understanding of evolutionary history. One skeletal element, the scapula (A.K.A. the shoulder blade), offers a particularly tantalising glimpse into therian mammal evolution thanks to its diverse morphology in this group. The evolution of therian mammals from non-mammalian synapsid ancestors to the thousands of extant species present today arguably cannot be understood without understanding shoulder girdle evolution. The scapula in extant therians is highly variable in its morphology (Fig. I.1), from a thin rod in some moles to a wide expanse in cetaceans, but the exact nature of the relationships between these morphologies and the biomechanical functions they are optimised for is not yet fully understood. Though much research has investigated the functional morphology of the therian scapula, the studies have largely focused on individual taxonomic groups and often with significantly different methodologies, making different studies challenging to compare and synthesise. Herein arises the overarching aim of this thesis: **to empirically relate scapular morphology to biomechanical function across therian mammals**. Succinct as this may sound, it belies the complexity and nuance of the challenges involved in studying a highly variable bone in a large and diverse group of animals. As will become apparent throughout this thesis, the therian scapula defies simple explanation. Instead, what unfolds is evidence of a structure which contains large quantities of functional and phylogenetic information, all layered and interwoven in branching interactions. Nevertheless, through the noise, it is possible to illuminate functional signatures in scapular morphology. First, however, we must establish the foundation from which we are working, beginning with the nature of therian mammals themselves.

I.2. A brief overview of mammal evolution

The class Mammalia is a large and diverse vertebrate group, comprising nearly 6,500 extant species (Burgin et al. 2018), but the diversity we see today in extant mammals is a product of a long and complex evolutionary history. Mammals are the only living representatives of Synapsida, one of the two major amniote clades. They diverged from the other amniote clade, Sauropsida (which comprises reptiles and birds), in the mid-Carboniferous approximately 330-315 Mya (Benton 2005). From the late Carboniferous into the end Permian, the large-bodied synapsid pelycosaurs and therapsids dominated terrestrial ecosystems. However, the transition from the Permian to the Triassic approximately 259 Mya is defined by a catastrophic extinction event. The limited surviving lineages of therapsids went on to diversify through the Triassic and, by the late Triassic approximately 227-201 Mya, a group known as Mammaliaformes arose from a therapsid lineage called Cynodontia (Romer 1945; Benton 2005; Kemp 2016), which already showed clear evidence of characteristic mammalian traits, such as modification of the lower jaw. This group gave rise to true mammals, among other now extinct sister groups (Kermack et al. 1973; Benton 2005; Kemp 2016). Generally, these early mammaliaforms are believed to have been oviparous (egg-laying), though some may have given birth to live but significantly under-developed young which then developed in pouches (akin to marsupials) (Ferner et al. 2017). The only extant oviparous mammals are the Monotremata, comprising echidnas and the platypus, which diverged from the other mammals (Theria) sometime within the range 250-165 Mya (Álvarez-Carretero et al. 2022). Monotremes are, of course, represented by very few extant species, and these animals are unique among extant mammals in many ways, even beyond oviparity. Importantly in the context of this thesis, monotremes exhibit a sprawling limb posture and locomotion style more akin to the non-mammalian synapsid ancestors than other modern mammals (Gambaryan & Kuznetsov 2013; Regnault et al. 2020). In the late Cretaceous, therian ecomorphological diversity was increasing (Grossnickle & Newham 2016), but approximately 66 Mya the catastrophic K-Pg (Cretaceous-Paleogene) extinction event changed the course of life on Earth. Estimates suggest that, in some regions, as many as 86% of mammal genera became extinct during the K-Pg extinction (Longrich et al. 2016), with survivors tending to be small ecological generalists best able to adapt to the dramatic ecosystem changes (Grossnickle et al. 2019). Within just 300,000 years of the event, local diversity had reached twice pre-K-Pg levels (Longrich et al. 2016), and evidence suggests that the crown groups of all extant therian orders were present by this time (Carlisle et al. 2023). The subsequent and current geological time period, the Cenozoic, is often referred to as 'The Age of Mammals', thanks to the global radiation and dominance of mammals over the last 66 million years. While extant therians are highly diverse, there are some features which unite all therians, particularly viviparity and mammary glands which lead to teats. Notably, one of the key characteristics of therians which is etched in the fossil record is their shoulder girdle anatomy.

I.3. The shoulder girdle as a window into mammal evolution

The reptile shoulder girdle (Fig. I.2) comprises four main elements: scapula, procoracoid, clavicle and interclavicle. The procoracoid is ventral to the scapula (but is not necessarily an independent element), together forming the glenoid fossa which articulates with the proximal humerus. The clavicle articulates with the scapula on the cranial side, and passes ventrally to articulate with the interclavicle. The interclavicle lies on the ventral side of the girdle, in line with the midline of the body, and connects the two clavicles to the sternum (Romer 1945; Romer & Parsons 1977; Hildebrand 1995). In the early non-mammalian synapsids, pelycosaurs, a novel element arose – the coracoid – caudal to the procoracoid (Romer 1945; Romer & Parsons 1977; Luo 2015). The lateral side of the scapula was almost entirely composed of the infraspinous fossa, with no scapular spine or supraspinous fossa present (Romer 1945; Luo 2015). While these early groups had sprawling limbs, a transition begins to occur in the late Triassic towards a parasagittal posture. Advanced therapsids like gorgonopsids show evidence of adaptation towards a facultative parasagittal posture in the hindlimbs (Romer 1945; Pough et al. 1989), and some cynodonts like *Oligokyphus* had fully parasagittal hind- and forelimbs (Pough et al. 1989). There are many biomechanical advantages of a parasagittal posture over a sprawling posture. Particularly, stacking of the joints in line with ground reaction force reduces energy expenditure and shearing stress, and parasagittal limbs facilitate longer strides (Preuschoft et al. 2022). Notably, while vertebrates with sprawling limb postures locomote via lateral undulation of the trunk, parasagittal limbs facilitate locomotion via dorso-ventral undulation, associated with increased respiratory efficiency during locomotion (Carrier 1987). As part of this transition, musculature of the shoulder girdle shifted greatly, linked with dramatic shifts in morphology of the scapula and coracoid. Around this time, the scapular spine began to develop, as the cranial edge of the scapula turned out laterally to form a ridge (Romer 1945; Luo 2015). This is approximately the condition of the monotreme shoulder girdle (Fig. I.2). Though Romer described the monotreme shoulder girdle as “emphatically reptilian” (Romer 1945), it is better described as an intermediate, exhibiting both a coracoid and a reduced procoracoid, as well as a spinous crest which separates the lateral side of the blade into two fossae. However, the cranial fossa is the infraspinous fossa and the caudal fossa houses the *m. teres major* (Luo 2015). Therian shoulder girdles (Fig. I.2), on the other hand, continued to differentiate from early mammal-like relatives. The procoracoid is entirely lost in therians, as is the interclavicle. The coracoid (though present and variable in prominence) does not form part of the glenoid fossa, and a true scapular spine has formed which divides the lateral side of the blade into the infraspinous and supraspinous fossae to house the *m. infraspinatus* and *m. supraspinatus* respectively. The acromion, which articulates with the clavicle (if present), is at the joint-end of the scapular spine rather than on the cranial edge of the blade (Luo 2015). The therian shoulder girdle is unique among vertebrates, and this is directly associated with biomechanical advantages, particularly mobility, which enabled the impressive locomotor diversity observed in extant therians (Luo 2015; Kemp 2016). Firstly, the reduction of elements of the shoulder girdle facilitates increased mobility of the region (Luo 2015). Secondly, the separate clavicles (when present) are able to move independently in an arcuate motion, allowing each side of the shoulder girdle – and thus each forelimb – to move independently (Jenkins 1974; Preuschoft et al. 2022). Finally, the shallow, more ventrally-oriented glenoid fossa, stabilised by the rotator cuff muscles, also allows more freedom of movement at the glenohumeral joint, particularly parasagittally (Luo 2015). Additionally, there is evidence to indicate that evolutionary changes in the shoulder girdle facilitated regionalisation of the vertebral column (Jones et al. 2018), which has been significantly associated with therian locomotor diversity.

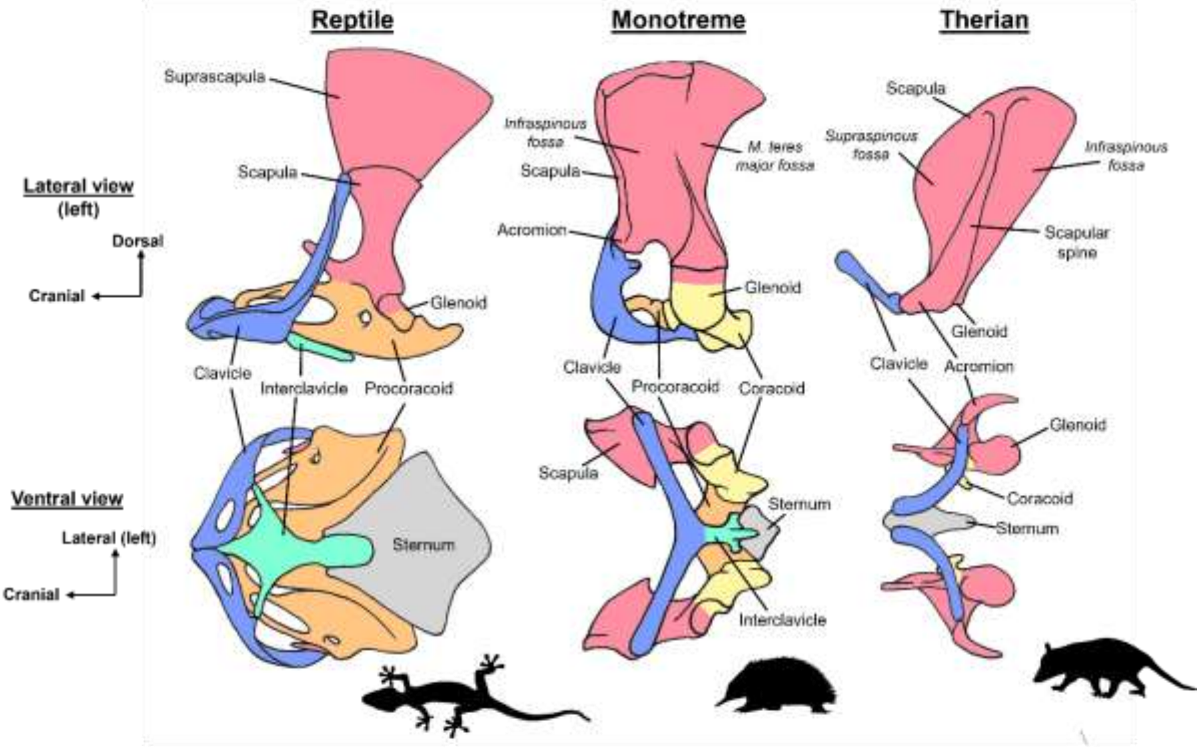

Figure I.2: Comparison of the shoulder girdle in reptiles, monotremes and therians
An illustration of the skeletal elements of the shoulder girdle in reptiles, monotremes and therians. The diagrams show the shoulder girdle in lateral view (left side) and ventral view. The reptile shoulder girdle representation is primarily based on a specimen of Gecko gecko *(UF 14993 via sketchfab.com), the monotreme representation is primarily based on figures of* Tachyglossus aculeatus *from Regnault et al. (2020), and the therian representation is primarily based on a specimen of* Trichosurus vulpecula *(Natural History Museum University of Pisa C 131 via sketchfab.com).*

I.4. Therian locomotor and functional diversity

Most therian survivors of the K-Pg extinction have been reconstructed as small generalist insectivores/omnivores (Grossnickle et al. 2019). This kind of animal has an inherent advantage in changing and unpredictable conditions, such as those following the asteroid impact at the K-Pg boundary, thanks to not relying on particular environmental and ecosystem conditions associated with specialisations. However, these small generalists relatively rapidly diversified into a variety of niches which had been left vacant by the loss of other dominant groups in the extinction event. There are many factors which have been associated with therian success and diversification in the Cenozoic. Endothermy provides a buffer to harsh environmental temperatures, large brains enable complex behavioural adaptations, and placentation and milk production for offspring allow longer and more stable developmental periods (Pough et al. 1985; Smith 2015; Kemp 2016). Behavioural adaptability in therians has undoubtedly been a key feature of their success, with therian groups thriving in a vast number of niches worldwide. For example, the earliest known bats arise in the fossil record around 52 Mya, less than 15 million years after the K-Pg asteroid impact, at which point they were already capable of powered flight (Simmons et al. 2008; Amador et al. 2019; Rietbergen et al. 2023). By the mid-Eocene around 48 Mya, ancestral cetaceans were undergoing dramatic transformations as the lineage transitioned from terrestrial to aquatic life (Gingerich 2015). Advanced climbing behaviours have arisen across many therian groups throughout the Cenozoic, and specialised behaviours like brachiating and gliding for traversing forest canopies far above the ground make therian representatives extremely adept in these environments. Rapid terrestrial movement is certainly of great advantage for both prey and predator species, and many therians excel in this regard. The cheetah (*Acinonyx jubatus*) is the fastest terrestrial animal and has been reported to reach speeds of over 120 km/h (Sunquist & Sunquist 2002), but the cheetah is certainly not alone among therians in being able to move rapidly.

The examples above barely scratch the surface of therian locomotion, but are indicative of their locomotor aptitudes and diversity, much of which can be directly attributed to unique postcranial morphology. There are three main features of therian postcranial anatomy which release them from the functional constraints present in other vertebrate groups: parasagittal limbs, vertebral regionalisation, and a mobile shoulder girdle. Together, these features dramatically increase therian locomotor adaptability in life and through evolution, and they are all linked with therian scapular morphology. As discussed previously, parasagittal limbs reduce long bone stress in response to ground reaction forces, and increase stride length (Preuschoft et al. 2022). Regionalisation of the vertebral column into cervical, thoracic and lumbar regions facilitates increased respiratory efficiency during locomotion, dramatically increasing energetic efficiency of movement, as well as allowing independent specialisations of hind- and forelimbs (Carrier 1987; Buchholtz et al. 2012; Jones et al. 2018). Finally, the therian shoulder girdle allows independent movement of the two forelimbs, significantly increasing the nuance of locomotion, especially when navigating uneven terrain or small platforms (Biewener 2003).

Therian mammals are capable of arguably the most diverse locomotor behaviours of any vertebrate group. This is inherently linked to their unique postcranial anatomy and its biomechanical advantages, which align to create a group of vertebrates particularly well-equipped for versatility, adaptability and efficiency in locomotion.

I.5. Previous research on therian scapular functional morphology

Shoulder girdle morphology has been closely linked to locomotor capacity throughout the evolution of therian mammals, and today we see not only extensive diversity of locomotion within extant therians, but striking morphological diversity in the scapula. Is morphological diversity of the scapula directly linked to facilitating diverse locomotor behaviours in extant therians? There has been extensive research on the functional morphology of the therian scapula, spanning every major extant group: **marsupials** (Stein 1981; Argot 2001; Sears 2004; Astúa 2009), **afrotherians** (Domning 1977; Thewissen & Badoux 1986; Shoshani et al. 1988; Salton & Sargis 2008), **xenarthrans** (Monteiro & Abe 1999), **primates** (Young 2004; Taylor & Slice 2005; Voisin 2006; Preuschoft et al. 2010; Voisin et al. 2014), **rodents** (Lehman 1963; Jenkins 1974; Swiderski 1993; Morgan 2008; Wölfer et al. 2019; Carvalhaes et al. 2022; de Oliveira et al. 2025), **chiropterans** (Vaughan 1970; Gaudioso et al. 2020), **carnivorans** (Müller 1967; Taylor 1974; Gálvez-López 2014), **ungulates** (Müller 1967), and **cetaceans** (Smith et al. 1994; Cooper et al. 2007). However, not only do these studies vary greatly in their taxonomic composition, they also vary greatly in the research goals/questions, and methods of scapular shape quantification. In particular, the differences in methodology (2D versus 3D, landmarks versus linear measurements, decisions of landmark number and placement, etc.) make it challenging to synthesise research on therian scapula morphology into a cohesive narrative. For example, Sargis' (2002) results in tupaiids based on four linear measurements cannot readily be compared to Gálvez-López's (2014) results in carnivorans based on 34 landmarks in 3D. Nevertheless, there are some consistent themes across research on the therian scapula. First, several regions/aspects are consistently identified as the sources of greatest scapular shape variation: **blade width** (Argot 2001; Sargis 2002; Astúa 2009; Wölfer et al. 2019; Carvalhaes et al. 2022), **ratio of the lateral fossae** (Müller 1967; Monteiro & Abe 1999; Sargis 2002; Taylor & Slice 2005; Salton & Sargis 2008; Voisin et al. 2014; Gálvez-López 2014; Carvalhaes et al. 2022), **vertebral border** (Taylor 1974; Argot 2001; Sargis 200; Seckel & Janis 2008; Preuschoft et al. 2010; Gálvez-López 2014), **caudal angle and attachment for *m. teres major*** (Lehman 1963; Stein 1981; Taylor 1974; Monteiro & Abe 1999; Astúa 2009), **acromion region** (Lehman 1963; Taylor 1974; Sears 2004; Seckel & Janis 2008; Salton & Sargis 2008; Astúa 2009; Voisin et al. 2014; Gálvez-López 2014; Wölfer et al. 2019; Carvalhaes et al. 2022), and **coracoid process** (Lehman 1963; Argot 2001; Sargis 2002; Salton & Sargis 2008). Secondly, patterns of developmental and morphological modularity and integration appear to be consistent in broad strokes across multiple studies: the **blade and scapular spine are integrated** (Timmons et al. 1994 [mice]; Pellegrini et al. 2001 [mice]; Young 2004 [hominoid primates]; Sears et al. 2013 [opossum, mouse and bat]), while the **coracoid is independent or associated with the glenoid region** (Timmons et al. 1994 [mice]; Pellegrini et al. 2001 [mice]; Young 2004 [hominoid primates]; Luo 2015 [tetrapods]; Young et al. 2019 [tetrapods]). Finally, though the influence of specific locomotor behaviours on scapular morphology appears to vary in different studies, some aspects of scapular morphology are consistently identified as being associated with increased climbing ability: **vertebral border expansion** (Argot 2001; Sargis 2002; Astúa 2009; Gálvez-López 2014), **enlarged supraspinous fossa** (Monteiro & Abe 1999; Sargis 2002; Taylor & Slice 2005; Salton & Sargis 2008; Astúa 2009; Gálvez-López 2014), **enlarged attachment for *m. teres major*** (Taylor 1974; Monteiro & Abe 1999; Argot 2001; Astúa 2009; Gálvez-López 2014), **prominent acromion** (Taylor 1974; Argot 2001; Salton & Sargis 2008; Astúa 2009; Voisin et al. 2014; Gálvez-López 2014), and **prominent coracoid** (Argot 2001; Sargis 2002). These adaptations facilitate enlarged musculature involved in raising the thorax through the shoulder girdle against gravity, and stabilising a mobile shoulder joint moving in 3D environments – features crucial for effective climbing behaviour.

The relative contributions of size, evolutionary history, and function (generally locomotion) on scapular morphology in therians varies considerably across studies. Several identify **size** as the dominant influence (Sears 2004; Astúa 2009; Wölfer et al.

2019), while others find it to be the least influential factor (Monteiro & Abe 1999; Morgan 2008; de Oliveira et al. 2025). Many studies find **evolutionary history** to be the most influential factor (Oxnard 1968; Leamy & Atchley 1984; Swiderski 1993; Monteiro & Abe 1999; Morgan 2008; Gaudioso et al. 2020; Carvalhaes et al. 2022; de Oliveira et al. 2025), while some find evolutionary history to be the least influential (Young 2004; Astúa 2009; Wölfer et al. 2019). The influence of **locomotor behaviour** is consistently found to be superseded by that of other factors, or its influence cannot be disentangled from size or evolutionary history effects (Oxnard 1968; Swiderski 1993; Monteiro & Abe 1999; Young 2004; Morgan 2008; Astúa 2009; Wölfer et al. 2019; Gaudioso et al. 2020; de Oliveira et al. 2025). These results are evidently dependent upon the make-up of the datasets used, with rodent datasets reliably indicating a dominant effect of evolutionary history (Leamy & Atchley 1984; Swiderski 1993; Morgan 2008; Carvalhaes et al. 2022; de Oliveira et al. 2025), for example. Additionally, interactions of these factors are frequently identified as problematic for interpretation (Morgan 2008; Ásua 2009; Wölfer et al. 2019).

I.6. The study of functional morphology

I.6.1. Quantifying shape

Questions regarding the relationship of form and function arise across biology, from plant stems (e.g. Speck & Speck 2021), to insect wings (e.g. Wootton 1992), to the mammal skeleton as discussed here. Morphological variation in elements of the skeleton can provide valuable insight into functional capabilities of mammals, such as inferring diets from dental morphology (Pineda-Munoz et al. 2017), inferring dominant locomotor modes from linear measurements of postcranial bones (Chen & Wilson 2015), or body mass estimation based on humeral circumference (Campione & Evans 2012).

Foundational to the study of functional morphology is mathematical quantification of shape. Arguably the most influential text regarding the study of biological form is ‘On Growth and Form’ (Thompson 2014, originally published 1917), which discusses the diversity of organisms and develops ways of quantifying and comparing differences in form. Though Thompson lamented the complexity of understanding the relationships between form and function, he was of the opinion that bone provides a subject which is “so far simplified and particularised that we may to some extent deal with it”. Thompson’s great innovation in this text is the development of Cartesian Transformation – a method for comparing biological forms in two dimensions based on their relative warping of a Cartesian grid. Through the first half of the 20th Century, methodologies were developed which utilised linear measurements and ratios to quantify biological form, which were then used as inputs for multivariate statistical analyses to investigate specific research hypotheses and questions (Reyment 1985; Zelditch et al. 2012). This is generally referred to as ‘traditional’ morphometrics. This type of morphometrics can be used to address many research questions, often with relatively minimal time spent on data collection. However, traditional morphometrics usually captures form in relatively low resolution, and does not differentiate the components of form – size and shape (Kendall 1977). That is, groups or individuals may be differentiated in multivariate analyses, but the influence of differences in absolute size are not separate from differences in shape (Reyment 1985; Zelditch et al. 2012). The use of ratios instead of absolute measurements can minimise the influence of size, but ratios come with statistical complications (Humphries et al. 1981; Reyment 1985; Zelditch et al. 2012; Gálvez-López 2021). Geometric morphometric methods (GMM), however, use homologous landmarks on objects to represent form, i.e. on every specimen in the dataset, the same loci are identified and recorded as Cartesian coordinates. This captures far more of the geometry of an object than traditional morphometrics, with the potential to use large numbers of landmarks (arguably at the expense of interpretability). The resulting landmark configurations can still not be said to differentiate size from shape, but a mathematical procedure called Generalised Procrustes Analysis (GPA) provides the most popular solution to separate both components, though it was not originally developed for shape data (Gower 1975). Firstly, this procedure standardises size across the landmark configurations by scaling each landmark’s coordinates based on centroid size (square root of the sum of squared distances from each landmark to the centroid – the geometric centre of the configuration). Additionally, the landmark configurations are translated in Euclidean space to align their centroids, and rotated to maximise alignment of the configurations. The outputs – Procrustes coordinates – represent quantified shape, independent of size (Bookstein 1991; Zelditch et al. 2012). Centroid size values obtained from the original configurations can then be used in addition to investigate questions of allometry. GMM is considered standard practice for quantifying shape in studies of functional morphology today, providing the opportunity to capture shape in extremely high resolution should the researcher desire, and allowing the differentiation of size and shape. Thus, this is the method used within this thesis, quantifying the ‘morphology’ aspect of functional morphology.

I.6.2. Multivariate statistical analyses

Here, both shape and function data are complex and multivariate, so interpreting them requires a suite of statistical techniques. Below are descriptions of key analyses used throughout this thesis which are not otherwise described within individual chapters. All statistical analyses were carried out in R v. 4.2.2 - 4.5.1 (R Core Team 2022-2025), and an annotated R script covering all data chapters is available in supplementary material (S.1). The alpha value for significance is $p \leq 0.05$ throughout this thesis.

General Linear Models (GLM): This term refers to an umbrella of statistical methods used to model the relationship between one or more dependent variables and one or more independent variables by fitting a linear equation to observed data, under an assumption of normal distribution in the variables. Familiar methods such as linear regression, ANOVA, ANCOVA and MANOVA are all encompassed under this umbrella. The *lm* function within the R package *stats* v. 3.6.2. (R Core Team 2019) was used to carry out such tests on linear variables (e.g. centroid size), and the *procD.lm* function within the *geomorph* v.4.0.10 package (Adams et al. 2025) was used for sets of interdependent variables (e.g. Procrustes coordinates). GLMs are used over PGLS (described below) when phylogenetic influence is assumed to be minimal and/or not relevant to interpretation.

Modelling within a phylogenetic framework: Given the taxonomically broad nature of the dataset, it is necessary to account for the influence of shared evolutionary history in analyses here, as the data of different species are not independent and, specifically, this means that the error distribution is not a normal distribution (Felsenstein 1985). Phylogenetic Generalised Least Squares (PGLS) offers a way to assess linear relationships between variables within a framework of known phylogenetic structure (i.e. phylogeny). A relationship investigated using a GLM may be significant, but may be non-significant when investigated within a phylogenetic framework, thus the latter provides a more biologically accurate interpretation of the data. PGLS is a variant of Generalised Least Squares (GLS), which is a method used for estimating unknown parameters (slopes and intercepts) in linear models, specifically in cases where there is correlation in the residuals of the model. In PGLS, information from a phylogenetic tree is included as part of the model, filling in some information which is otherwise represented by the unknown parameters. As in the *lm* function, the *pgls* function within the R package *caper* v.1.0.4 (2023) is used to model linear variables. There is an option in the *pgls* function to use maximum likelihood to generate a value of Pagel's lambda (λ) associated with each model (Pagel 1999), providing a measure of phylogenetic signal contained in the residuals. This value ranges from 0.0 to 1.0, where 0.0 indicates no effect of phylogeny in the model (residual covariance between individuals is not related to their phylogenetic distance), and 1.0 indicates maximum effect of phylogeny in the model (residual covariance between individuals is directly proportional to their phylogenetic distance). For shape data, linear models are performed within a phylogenetic framework through the use of the function *procD.pgls* in the R package *geomorph* v. 4.0.10 (Adams et al. 2025). This function, unlike the *pgls* function, does not allow for a value of Pagel's lambda (λ) to be calculated and outputted for each regression – a lambda value must be included in the model structure. Therefore, the value of lambda for the Procrustes coordinates was established using the *physignal.z* function in the *geomorph* R package, and this value is used in subsequent models.

Principal Components Analysis (PCA): PCA offers a method for reducing the dimensionality of high-dimensionality data, and visualising said data. This is utilised here to reduce the dimensionality of the locomotor scoring matrix (Chapter II) and Procrustes coordinates (Chapters III & IV). PCA can investigate the multidimensional data space and determine 'slices' through the space which represent the most to least relevant sources of variation, numbered numerically in order of decreasing percentage variance accounted for (i.e. PC1 accounts for the greatest variation in the dataset). Each principal component (PC) is a linear combination of multiple variables in the dataset (such as the five different locomotor abilities in Chapter II's scoring matrix) to varying extents. As part of the analysis, each variable (e.g. locomotor ability) is given a loading value in each PC which represents its relative importance in determining a specimen's position on that axis. A specimen's position on an axis is determined by multiplying that species' score values by the loading values of the axis, and producing a subsequent total – the final value being the coordinate value for that observation on that axis in the PCA. In the context of this thesis, scatter plot visualisations of the PCA are referred to as behavioural spaces for the analysis of locomotor scoring data, and as morphospaces for the analysis of shape data (as is common practice in the literature [Zelditch et al. 2012]). Within these spaces, species with similar locomotor profiles or scapular shapes relative to the axes being visualised will appear closer together and those which are least similar will appear distant.

I.7. Rationale and overview of this thesis

The discrepancies across datasets and shape quantification in previous therian scapular research preclude confident conclusions, especially regarding the relationships between scapular morphology and locomotor function, even though some consistencies can be identified across the literature. In order to clarify the functional morphology of the scapula in therians, and discover how successfully patterns within constrained datasets generalise, it is necessary to undertake a study including representatives of as many therian groups as possible with high resolution shape quantification. This is the rationale for this thesis.

A key component of this study is quantifying function, primarily locomotor behaviour. As is discussed thoroughly in Chapter II, locomotion is generally captured as a categorical variable in which each species in the dataset is assigned to one of a series of predetermined locomotor categories, such as 'arboreal' or 'fossorial'. This system fails to capture a great deal of an animal's broad and varied locomotor capabilities by implying that a single behaviour defines the functional demands on their skeleton, and it introduces considerable subjectivity into the data regarding decisions about which categories to include and how to assign each species to them. This is the rationale for the work described in Chapter II, which develops a novel methodology for quantifying behaviour for use in functional morphology. The method is demonstrated for quantification of mammal locomotor behaviour, using a scoring system in which each species is scored on its ability to perform a series of five locomotor abilities, which produces a scoring data matrix. This is additionally used to produce a mathematically-defined categorical variable via Ward's hierarchical clustering. Thus, locomotor behaviour – function – is successfully quantified as both a multivariate data matrix and as a categorical variable, both of which are utilised in multivariate statistical analyses in subsequent chapters to address the question of the relationship between scapular morphology and locomotor behaviour in therians.

Chapter III forms the core of this thesis. In this chapter, morphology in a dataset of scapulae from 201 specimens, representing 74% of all extant therian families/subfamilies, is quantified using 71 landmarks in 3D. Locomotor quantification data from Chapter II, as well as data on centroid size, evolutionary history and clavicle presence, are used to directly test associations between form, evolutionary history, and biomechanical function in the therian scapula via a suite of multivariate statistical analyses. Using a taxonomically broad dataset, with shape quantified at a high number of landmarks, and locomotor behaviour quantified via the novel scoring and clustering method, makes this study the highest resolution investigation of therian scapular morphology to date.

However, one of the dataset's strengths – its taxonomical breadth – is also a drawback. The interaction of evolutionary history with other factors undeniably influences the results of this study. For example, all chiropterans fly and they are the only mammals capable of doing so, while all ungulates are aclaviculate, and all eulipotyphlans are relatively small (the largest being solenodons which are up to 1kg in body mass [Nowak 1999]). Therefore, it is necessary to identify a subgroup of therians, which can be considered functionally representative of Theria as a whole, in order to validate the findings of Chapter III. In Chapter IV, rodents are utilised as this exemplar group for a number of reasons:

- Rodentia is the most speciose group of extant therians, representing almost 40% of extant therian species.
- Though no individual group spans the full range of therian size (eight orders of magnitude, from a few grams up to hundreds of tonnes [Grossnickle et al. 2019]), rodents have a particularly large size range (four orders of magnitude, from a few grams to 60+ kg [Nowak 1999]), outdone only by carnivorans.
- Most rodents are claviculate, but clavicle loss has occurred in some species of hystricomorphs.

- Rodents engage in nearly every type of locomotor behaviour exhibited across therians, the only exceptions being that no rodents are capable of powered flight or obligate aquatic life.
- While several studies have been conducted investigating scapular functional morphology in rodents, these are taxonomically constrained and there is currently no published study which includes the full spectrum of rodent taxonomy and behaviour.
- Rodents have previously been proposed as a useful model order within functional morphology research (Fabre et al. 2012; Hautier & Cox 2015).

The 87 rodent species included in Chapter IV span the ranges of extant rodent taxonomy, size, clavicle presence and locomotor behaviour. Not only does this provide the opportunity to validate the findings of Chapter III, it offers greater insight into the use of rodents as a functionally representative microcosm of therian mammals in the context of the scapula.

This thesis provides unique insight into scapular functional morphology in therians, being both broader and deeper than previous work. Beginning with a novel method for locomotor quantification creates a robust and information-rich representation of extant therian locomotor behaviour, transcending the limitations of a traditional categorical locomotor variable. The dataset of therian mammals is selected to be both broad and representative, and to allow direct comparisons of morphology across this large group of vertebrates. Using 71 landmarks in 3D captures the scapula in unprecedented high resolution for such a broad dataset. In combination, these factors facilitate the testing of functional hypotheses with greater insight than has previously been possible. Subsequently validating the therian results within Rodentia both instils increased confidence in the findings, and demonstrates the potential for utilising Rodentia as a representative microcosm of Theria in the context of scapular functional morphology. The insights arising from this thesis add to our understanding of this fundamentally important skeletal element in therian mammals, which may be useful in a number of research contexts, including biomechanics, evolutionary development and palaeontology.

Chapter II

On the move:

A novel method for quantifying mammal locomotion

A version of this chapter has been published in Proceedings of the Royal Society B (25/02/2026) under the title, ‘A novel approach to quantifying mammal locomotor repertoires using scoring and cluster analysis’, doi.org/10.1098/rspb.2025.2515.

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Research Degree Thesis Statement of Authorship

Note that where a paper has multiple authors, the statement of authorship can focus on the key contributing/corresponding authors.

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Title of the work (paper/chapter)	Chapter title – On the move: Quantifying mammal locomotion Paper title - A novel approach to quantifying mammal locomotor repertoires using scoring and cluster analysis	
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(i) the candidate has accurately represented their contribution to the work;

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*The description of the candidate and co-authors contribution to the work may be framed in a manner appropriate to the area of research but should always include reference to key elements (e.g. for laboratory-based research this might include formulation of ideas, design of methodology, experimental work, data analysis and presentation, writing). Candidates and co-authors may find it helpful to consider the CRediT (Contributor Roles Taxonomy) approach to recognising individual author contributions.

Glossary of terms

Behavioural repertoire: *all the behaviours (in this case, specifically locomotor behaviours) which a specific species is capable of in nature.*

Locomotor categories: *categories used to classify species in traditional behaviour classification systems.*

Locomotor group/cluster: *a set of species which have been mathematically grouped via hierarchical cluster analysis.*

Locomotor mode: *the aspects of locomotion behaviour relating to animal movement associated with a particular medium and having specific functional demands (e.g. swimming in water, aerial movement, climbing).*

Locomotor ability: *a numerical variable representing skill level in a particular locomotor mode (e.g. swimming).*

Locomotor profile: *a set of scores on the locomotor abilities studied here.*

Locomotor variable: *a variable capturing locomotor behavioural information – either a categorical variable or a data matrix.*

II.1. Introduction

Studies of macroevolution and functional morphology, among other fields, frequently utilise categorical variables to represent behavioural information, such as diet, locomotor mode, or habitat preference. This is in pursuit of relating anatomical form to the biomechanical demands of behaviour, often to infer ecological adaptations and niche occupation in extinct species. In the case of tetrapod locomotion, the current classification system can be traced back to Eisenberg (1981), and to a certain extent Taylor (1974) almost a decade earlier. Eisenberg proposed eight locomotor categories, which continue to appear in the literature almost unchanged to this day: Terrestrial, Arboreal, Scansorial, Fossorial, Semifossorial, Volant, Aquatic, and Semiaquatic. Work by Van Valkenburgh (Van Valkenburgh 1985; Van Valkenburgh 1987) subsequently demonstrated the value of locomotion as a categorical variable in traditional morphometric studies on mammals, citing both Taylor (1974) and Eisenberg (1981). While alternatives to this traditional classification system have been proposed (e.g. Miljutin 2009), the wider community has continued to use it in subsequent work, modifying the number and identity of the categories as appropriate (e.g. [Samuels &

Van Valkenburgh 2008; Samuels et al. 2013; Chen & Wilson 2015; Gálvez-López 2021; Maher et al. 2022]). However, this reduction of behavioural repertoire into categorical variables has long suffered from certain caveats which remain unresolved; a sentiment put into words early on by Eisenberg himself: “Mammals, like all other living organisms, have a perverse tendency to defy exact classification.” (Eisenberg 1981).

II.1.1. Caveats of traditional behavioural categorisation

The core issue arising from the traditional method of coding behaviours as categorical variables is that behaviour is not categorical. This is the case whether it be locomotion, diet, etc., and whether in mammals or other taxonomic groups. Very few taxa engage in a single locomotor behaviour at all times (though an exception could be argued for obligately aquatic species such as cetaceans), so assigning them to a single locomotor category inherently fails to represent each animal’s behavioural repertoire accurately. For example, water shrews (*Neomys fodiens*) live in self-excavated burrows but are also exceptionally good swimmers (Nowak 1999). In fact, water shrews are not alone in this behaviour combination – water voles (*Arvicola amphibius*), beavers (*Castor spp.*), and otters (Lutrinae), among others, are all proficient diggers and swimmers (Nowak 1999). As standard practice, these animals are usually placed in a ‘semiaquatic’ category (e.g. [Samuels et al. 2013; Chen & Wilson 2015; Verde Arregoitia et al. 2017; Gálvez-López 2021; Woodman 2023]), removing any information on their burrowing ability despite the fact that this may be functionally relevant. The issue of loss of behavioural repertoire information has been noted by several authors (Ripley 1967; Van Valkenburgh 1985; Carrano 1999; Chen & Wilson 2015; Verde Arregoitia et al. 2017; Püschel et al. 2018; Woodman 2023), and it is generally taken as a caveat of the traditional method. In the context of dietary quantification, several authors have utilised scoring or ranking systems in order to determine the relative importance of different food types (Rojas et al. 2011; Kissling et al. 2014; Wisniewski et a. 2023). These authors go on to utilise the dietary matrices they create to determine a series of levels for a dietary categorical variable which, though based on substantial comparative data, is essentially at the discretion of the authors. No such scoring method appears to have been used in the literature in the context of locomotor behaviour, perhaps due to this information being less readily available or less detailed than dietary information in many taxa.

The second major issue that has been raised regarding traditional behavioural categories is subjectivity. The number and identity of the levels (i.e. categories) within the locomotor variable are determined prior to assigning the animals into categories. The choice is largely influenced by the taxa included and the interpretability of the results (fewer levels may be more interpretable, but less accurately represent the variation in the dataset), with most studies using three to eight levels in their locomotor variable (Van Valkenburgh 1985; Van Valkenburgh 1987; Samuels & Van Valkenburgh 2008; Samuels et al. 2013; Gálvez-López 2014; Chen & Wilson 2015; Verde Arregoitia et al. 2017; Püschel et al. 2018; Grossnickle 2020; Weaver & Grossnickle 2020; Woodman 2023). Following this, there is considerable subjectivity in the assignment of species to a locomotor category. Many authors will use ecological and behavioural literature to inform their judgement directly (Taylor 1974; Eisenberg 1981; Van Valkenburgh 1985; Chen & Wilson 2015; Gálvez-López 2021; Woodman 2023), but an animal’s assignment to one group or another is still at the discretion of the author. In other cases, authors will follow the judgement of preceding authors and utilise previously published locomotor assignments (Samuels & Van Valkenburgh 2008; Verde Arregoitia et al. 2017; Püschel et al. 2018). Almost all usages of locomotor category assignments can be traced, directly or indirectly, to Taylor 1974 and Eisenberg 1981. While this increases the consistency in the literature, it does not address the subjectivity of the original assignments. Lintulaakso et al. (2022) used cluster analysis on dietary data (from literature review of both general behavioural descriptions and studies using scat samples or stomach contents) to produce a mathematically derived categorical variable, thus reducing the subjectivity associated with selecting and assigning categories. While their method is extremely thorough, including large quantities of dietary repertoire information, the enormous quantity of data required means that the method would not be appropriate as standard practice for dietary classification systems, let alone other types of behavioural quantification.

II.1.2. The search for a solution

These caveats have often been acknowledged within the literature (Eisenberg 1981; Van Valkenburgh 1985; Van Valkenburgh 1987; Samuels & Van Valkenburgh 2008; Samuels et al. 2013; Chen & Wilson 2015; Verde Arregoitia et al. 2017; Woodman 2023), and steps have been taken to standardise the categorisation process within the work – by recording, for example, the most frequently used locomotor behaviour (Samuels & Van Valkenburgh 2008; Gálvez-López 2021; Püschel et al. 2018), the preferred form of locomotion for fleeing (Ripley 1967; Van Valkenburgh 1985; Van Valkenburgh 1987), or the preferred form of locomotion when acquiring food (Van Valkenburgh 1987; Woodman 2023). However, no satisfactory method has yet been developed to produce a locomotor variable which avoids substantial loss of information on locomotor repertoire and minimises subjectivity. The quantification of locomotion is a necessary part of many functional morphology studies including subsequent chapters of this thesis and, thus, the aim of this chapter is to improve upon traditional behaviour categorisation methods by developing an alternative that increases the behavioural repertoire information in the variable while reducing subjectivity. The method developed here is used to quantify the locomotor behaviour of 250 extant mammal species via ability scoring and cluster analysis, acting as a proof of concept for successfully producing a data matrix of scores containing far more information than a single variable (akin to Kissling et al. 2014, Rojas et al. 2021, and Wisniewski et al. 2023), as well as a mathematically derived categorical variable produced via cluster analysis (akin to Lintulaakso et al. 2022) for use in many of the multivariate analyses common to functional morphology studies. The method represents a replicable technique for quantifying animal behaviour and subsequently deriving categorical variables which is not only applicable to mammal locomotion, but has the potential to be tailored to analyse a variety of other behaviours and taxonomic groups for widespread use across evolutionary and ecological research.

II.2. Materials & methods

II.2.1. Sample

A total of 250 extant mammal species were included in this study (S.II.1). Taxonomic levels follow Burgin et al. (2018), and species names follow VertLife.org (Upham et al. 2019). The studied species were selected to represent one species per subfamily, or family where such divisions have not been defined. Decisions regarding which particular species within their subfamilies would be scored were largely based on the availability of locomotor information within the literature to avoid introducing missing data into the scoring matrix. In the case of Chiroptera, generally one species from each family was used, regardless of the presence of many subfamilies within the order, because the Chiroptera broadly represent a single behavioural repertoire which would be overrepresented if all subfamilies were included. Similarly, not all rodent subfamilies were included as it would risk overrepresenting this very large order. Note, however, that the reduced coverage still represents the whole locomotor variation within Rodentia.

II.2.2. Procedure

II.2.2.1. Ability scoring

Each species was given a score from 0 to 4 in each of five locomotor modes: swimming, climbing, digging, running, and aerial movement. A score of 0 represents an animal being physically unable to engage in a behaviour (e.g. a whale cannot run), while a score of 4 represents an animal being able to perform this behaviour highly proficiently (e.g. whales are extremely good swimmers). The criteria for scoring are given in Table II.1; these were determined prior to scoring and based on function rather than frequency (i.e. an animal’s ability to perform a behaviour informs its score in that mode, not the frequency of use of that behaviour). Strict adherence to these criteria is essential, and thus the wording of the criteria is intended to give as little room for ambiguity as possible in order to reduce subjectivity. Definitions of each locomotor mode and example taxa are provided to further clarify and differentiate the scoring levels. Interobserver repeatability of scoring was investigated across eight participants and found to be satisfactory (Appendix II.1). Ability in each locomotor mode was scored from 0 to 4 for consistency so that no single locomotor variable would contain numerically higher values than the others, which could result in that variable being disproportionately weighted in the subsequent cluster analysis. Scoring was based on information from articles in the American Society of Mammalogists' journal *Mammalian Species*, *Walker's Mammals of the World* (6th edition, Nowak 1999), and *The Kingdon Field Guide to African Mammals* (Kingdon 2013). The full scoring for each species and references used are given in S.II.1.A.

Table II.1: Criteria for mammal locomotor ability scoring.
Detailed criteria for how mammal locomotor ability was scored in this chapter. Criteria are given for every score from 0 to 4 in each of the five abilities, as well as definitions of the locomotor modes and example taxa which were given said score.

Ability	Definition	Score	Criteria	Examples
Swimming	Locomotion in water in which the body is supported only by buoyancy	0	Physically unable to swim	N/A
		1	Struggles to paddle out of water	Bat
		2	Adept at swimming for traversing environment, fleeing, and/or acquiring food. Diving only at shallow levels if at all.	Sloth, wildebeest
		3	Skilled swimmer and deep diver, but able to move terrestrially	Otter, pinniped
		4	Swimming as main mode of locomotion, which often results in inability to move terrestrially	Cetaceans, sirenians
Climbing	Vertical ascension and descension of objects such as trees and rock faces.	0	Physically unable to climb	Whale
		1	Able to scramble up simple obstacles relative to body size	Armadillo
		2	Adept at climbing some obstacles (e.g. bent trees or rocky outcrops) for traversing environment, fleeing, and/or acquiring food	Wolf, badger
		3	Able to climb vertical supports as part of traversing environment, fleeing, and/or acquiring food	Opossum, raccoon
		4	Capable of highly specialised climbing behaviours (clinging and leaping, headfirst descent, suspensory behaviours)	Squirrel, tarsier, gibbon
Digging	Breaking up and displacement of substrate using teeth or limbs	0	Physically unable to dig	Whale
		1	Very limited digging ability (e.g. superficial scratching)	Capybara, marmoset
		2	Adept at digging at shallow levels and/or as part of acquiring food	Rat, elephant shrew
		3	Able to dig burrows (either for living or just parturition), but leaves to acquire food etc.	Giant pangolin, armadillo
		4	Highly proficient at digging and lives (almost) exclusively underground, moving through self-dug burrows	Moles

Running	Gaits faster than walk which include an aerial phase in which at least two feet are lifted from the ground	0	Physically unable to run	Whale, moles
		1	Slow-moving and would only perform gaits faster than walk under extreme circumstances, e.g. fleeing	Pangolin
		2	Capable of performing running gaits comfortably, and will use them for short durations to flee or chase readily	Rhinoceros, capybara
		3	Uses synchronous running gaits (trotting, ambling, hopping) for extended durations	Camel, kangaroo
		4	Uses asynchronous running gaits (gallops, bounds) for extended durations	Horse, cheetah
Aerial	Locomotion in which the animal moves unsupported through air	0	Physically unable to perform aerial behaviours	Dog, horse
		1	Capable of long-distance vertical and/or horizontal leaps (relative to body size)	Gazelle, puma, jerboa
		2	Capable of some control over aerial descent directionality during long-distance leaps between high platforms	Spider monkey
		3	Capable of controlled and slowed aerial descent (e.g. gliding)	Colugo, sugar glider
		4	Capable of powered (flapping) flight	Bats only

II.2.2.2. Transforming the scoring matrix using polychoric correlations

As defined, the scoring matrix consists of ordinal data, as each locomotor mode has ordered levels but the distance between each level is not necessarily equal. Many statistical methods assume continuous data input, including Ward’s hierarchical clustering and those relying on covariance matrix estimations (e.g. Principal Components Analysis, PCA). Thus, the ordinal scoring matrix must be transformed into continuous variables for it to be appropriate as the input for these methods. Several ways of addressing this have been discussed in the literature (e.g. treating ranked ordinal data as continuous, or using Pearson-correlation matrices as input for PCA), generally in fields of psychology and social sciences where ordinal survey data and Likert scales are commonly used (Žiberna et al. 2004; Chen & Wang 2014). However, these methods do not sufficiently address the issue of inconsistency in the distance between variable levels. In contrast to those methods, transformations based on polychoric correlations do not assume that data are continuous, and they have been demonstrated to be the most effective and accurate correlation method to use for ordinal data (Holgado-Tello et al. 2010). Based on that, Wisniewski et al. (2023) transformed their ordinal scoring data on carnivoran diet by computing a PCA of their scoring matrix based on the polychoric correlation matrix, generating a new set of continuous variables to summarise their ecological data. This chapter uses the same approach for transforming the scoring matrix. The R package *polycor* (Fox & Dusa 2022) was used to produce the polychoric correlation matrix from the locomotor scoring data.

II.2.2.3. Clustering using Ward’s method

The polychoric PCA matrix can be used as any other data matrix without further manipulation in subsequent analyses. However, it is desirable to reduce the dimensionality of the data matrix in order to construct a locomotor categorical variable from it. This is achieved here using cluster analysis. Ward’s hierarchical clustering method (Ward 1963) (also known as Ward’s minimum variance method) was used to group animals into discrete clusters. This clustering method is agglomerative, or ‘bottom up’ and, uniquely, uses a classical sum of squares criterion to produce clusters which maximise between-cluster variance and thereby minimise within-cluster variation (Ward 1963; Murtagh & Legendre 2014). The input for Ward's method is a squared distance matrix produced from the matrix of polychoric PC scores. The output of Ward's method includes a list of cluster assignments for the observations at each cluster number, and the changes in cluster composition were visualised here using a dendrogram. The *hclust* function within the R package *stats* (R Core Team 2024) was used to perform the clustering.

II.2.2.4. Optimising cluster number using cluster validation

While Ward's method aims to maximise between-cluster variation and minimise within-cluster variation at each iteration, not every iteration will 'succeed' at this optimisation to the same extent. As other hierarchical clustering algorithms, Ward's is generally a 'greedy' algorithm, meaning that it focuses on local optima by making the most optimal clustering choices at each iteration rather than focusing on global optima. Therefore, there will be certain cluster numbers which are better optimised than others. There are a number of ways of establishing optimal cluster number for the model, collectively known as 'validation methods'. Due to the agglomerative nature of Ward's clustering method, any measure of optimisation will tend towards its optimum at k=n. Thus, the optimal cluster number is determined to be the lowest k at which there begins to be diminishing returns as k increases. Here, a consensus for optimal cluster number was established following the results of three different validation methods described below (elbow method, silhouette score, and Dunn index). At least one of these methods should be used to assess optimal cluster number, at the discretion of the researcher. Here, it was important to produce a number of clusters appropriate for biological interpretability, and thus optima below k=20 were explored. Researchers aiming for a more nuanced interpretation may wish to investigate higher optima.

The **elbow method** (Thorndike 1953) involves plotting total within-cluster sum of squares (as proxy for explained variation) against cluster number (Fig. II.1A). The 'elbow' in the plot occurs where diminishing returns begin. This method is somewhat simplistic because it does not consider between-cluster variation, but it provides a base for interpretation of further validation methods.

The **silhouette score** (Rosseeuw 1987) gives a measure of how similar an individual is to its assigned cluster. The silhouette score (s) for any individual is calculated as

$$s = \frac{b - a}{max\ (a, b)}$$

where *a* is the average similarity to individuals within its own cluster, and *b* is the minimum average dissimilarity to other clusters (Fig. II.1B). The silhouette score can range from -1 to +1, where +1 indicates perfect cluster assignment. Local optima are then determined by the presence of higher silhouette scores than the surrounding points. The *fviz_nbclust* function in R package *factoextra* was used to perform the elbow method and acquire silhouette scores (Kassambara & Mundt 2022).

The **Dunn index** (Dunn 1973) is calculated by dividing between-cluster distance by cluster size in a Euclidean context (Fig. II.1C). Specifically, cluster size is the maximum distance between two points within a cluster, and between-cluster distance is the distance between the closest two points in each cluster. As above, we are seeking to identify the lowest cluster number where diminishing returns begin. The *dunn* function in the R package *clValid* was used to acquire Dunn index values (Brock et al. 2021).

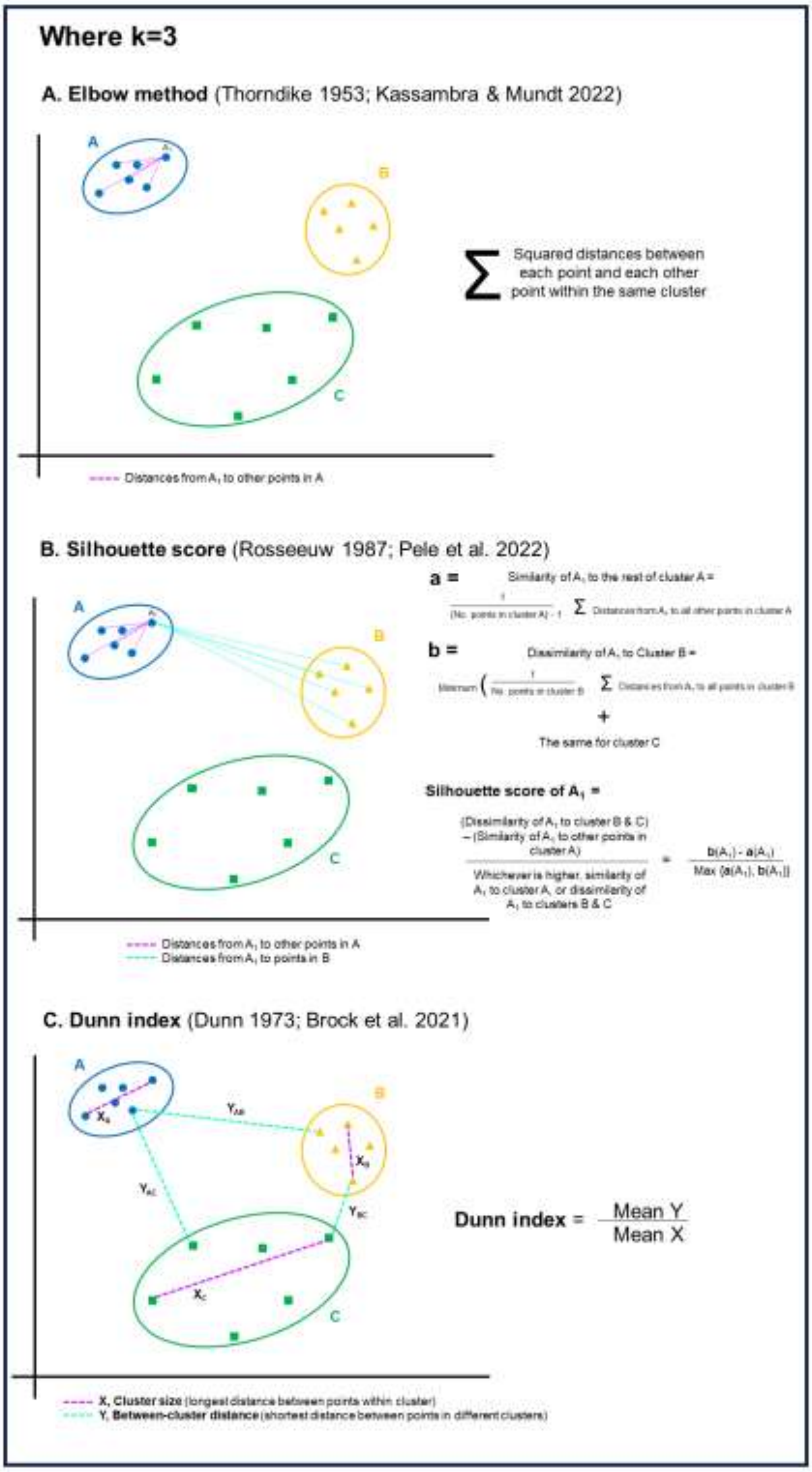

Figure II.1: Visual explanations of methods for determining optimal cluster number

Diagrammatic representations of the three methods used to determine optimal cluster number in this chapter, shown in the case of k=3 for simplicity.

II.2.2.5. Inspecting the behavioural space using Principal Components Analysis

As with any PCA, the axes produced while creating the matrix of polychoric PC scores can be used to summarise and visualise locomotor variation in the sample by creating a behavioural space, showcasing which species have the most similar locomotor profiles (i.e. their set of scores for all locomotor abilities) and highlighting gradients between extremes of locomotor specialisation.

II.3. Results

The scoring matrix produced for this dataset can be seen in S.II.1.A.1. A high overall score (i.e. sum of all scores) indicates that an animal may be considered a highly mobile generalist (similar to the all-terrain category of Gálvez-López 2021), being adept but not entirely specialised for a range of behaviours. For example, the grey wolf (*Canis lupus*) has one of the highest overall scores at 11, scoring 2 or more in every locomotor mode except aerial movement. Meanwhile, low overall scores indicate that an animal is either highly specialised in one ability (such as the bearded seal, *Erignathus barbatus*, which scores 3 in swimming and 0 everywhere else), or a lower mobility generalist (such as the northern brown bandicoot, *Isoodon macrourus*, which scores 5 overall: 1/1/2/1/0 (Swim/Climb/Dig/Run/Aerial)).

While the scoring system allows for a possible 3,125 unique locomotor profiles (5 scoring levels per mode to the power of 5 locomotor modes), only 81 unique profiles were identified in the dataset of 250 species.

II.3.1. Optimal cluster number

The results of the different validation methods are as follows:

- Elbow Method (Fig. II.2A): Total within-cluster sum of squares reaches a point of diminishing returns within the k = 5 to k = 8 interval, with larger k values being increasingly optimal.
- Silhouette Score (Fig. II.2B): A local maximum occurs at k = 6, followed by a second one from k = 8 to k = 10.

- Dunn Index (Fig. II.2C): A local maximum occurs at k = 10 and k = 11 before the final plateau of diminishing returns.

Overall, k = 8 to k = 10 appear to provide the most consistently optimal clustering across the three metrics. Based on inspection of the clusters at these k values, **k = 9** is the most biologically informative set of clusters, as at k = 8 the swim-dig and subterranean clusters merge while at k = 10 generalists are split in two uninformative clusters (see below).

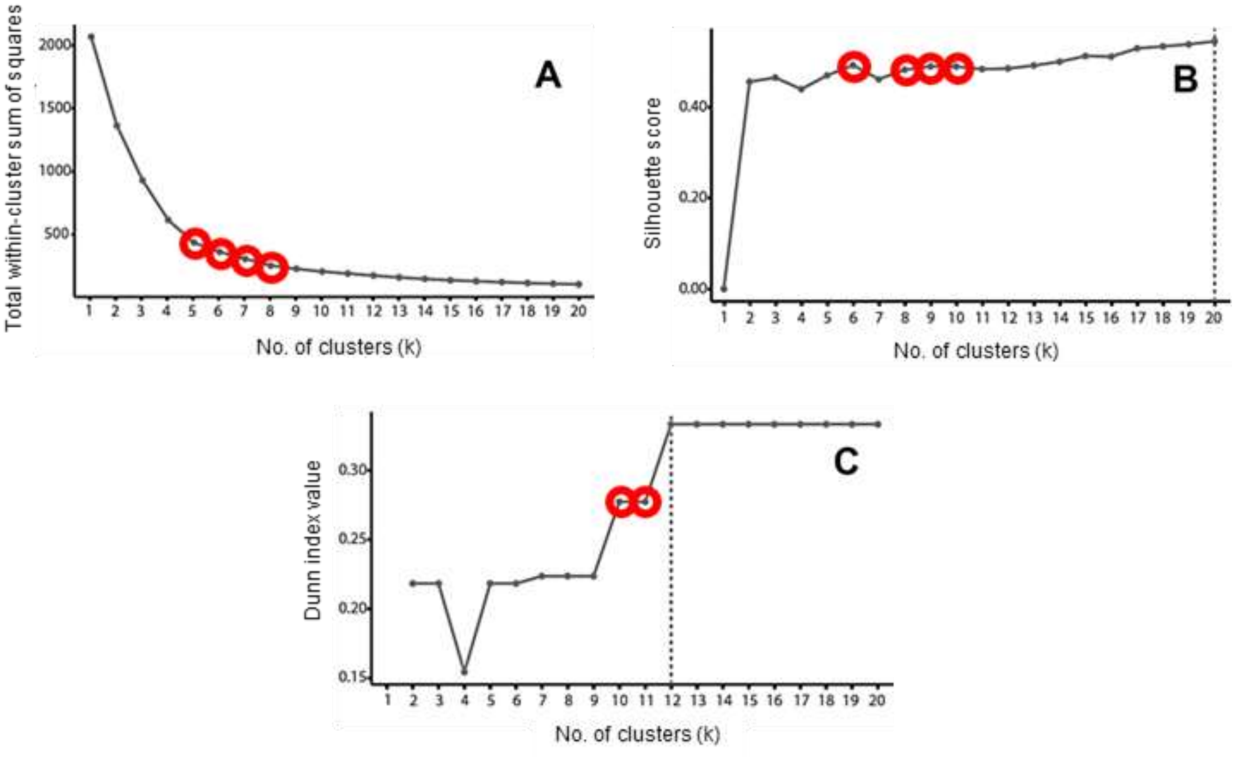

Figure II.2: Results of the cluster validation methods used
Results of A) Elbow method; B) Silhouette method; and C) Dunn Index values against cluster number. All plots show results for up to k = 20 with local optima indicated with red circles.

II.3.2. Clustering results

The results of Ward's hierarchical clustering on this dataset of locomotor profiles are illustrated with a dendrogram in Fig. II.3 and S. II.3 (labelled with species binomials). Each cluster is given a biologically informative descriptor based on the highest median scores in that cluster (Fig. II.3B). These descriptors are simply a way to discuss the clusters, and should not be considered a complete descriptor of the locomotor profiles of the species within them (Fig. II.3C). The clusters can be described as follows:

1. ‘Volant’ (n = 32): This cluster exclusively contains all the chiropterans, being the only taxa capable of powered flight. Species in this cluster are defined by their score of 4 in aerial movement ability, though they also score 4 in climbing ability.
2. ‘Aquatic’ (n = 27): This cluster contains the obligately aquatic cetaceans and sirenians, the pinnipeds, and the pygmy hippo (*Choeropsis liberiensis*). Species in this cluster are defined by their high scores in swimming ability in addition to scores of 1 or 0 in all other locomotor modes. The giant otter shrew (*Potamogale velox*), for example, scores 3 for swimming ability but also scores 3 for digging ability and, as such, it is not placed in the ‘Aquatic’ cluster.
3. ‘Aerial acrobats’ (n = 21): This cluster is defined by aerial scores of 2 or 3, and high climbing scores (median = 4). This includes gliders and brachiating primates, among others.
4. ‘Climbers’ (n = 46): This cluster is defined by scores of 3 or 4 in climbing ability, not associated with aerial movement ability (i.e. scoring 0 for that variable). This includes many of the primates, arboreal marsupials such as possums, and arboreal rodents such as squirrels.
5. ‘Dig-run’ (n = 25): This cluster is defined by a running score of 3 or 4, and high digging scores (median = 3). This includes saltatorial rodents such as the lesser Egyptian jerboa (*Jaculus jaculus*), and versatile terrestrial carnivores such as the grey wolf (*Canis lupus*).
6. ‘Runners’ (n = 23): This cluster is defined by scores of 4 in running ability not accompanied by high digging scores (digging scores range from 0 to 2). This cluster is dominated by ungulates, as well as fast-moving carnivores such as the cougar (*Puma concolor*).
7. ‘Generalists’ (n = 44): This cluster is characterized by medium to high scores (ranging from 1 to 3) in all locomotor modes except aerial movement. This includes

species with strong climbing and digging abilities, such as the Chinese pangolin (*Manis pentadactyla*), as well as generalists with moderate abilities in most locomotor modes, such as the brown bear (*Ursus arctos*). Three species that appear to be outliers were also included here via the agglomerative clustering process: the African elephant (*Loxodonta africana*), the Bactrian camel (*Camelus bactrianus*) and the black rhino (*Diceros bicornis*). These three species have extremely limited locomotor abilities (scores of 0 or 1 in all but running and, for some, swimming), contrary to all other species in this cluster. Due to the ‘greedy’ nature of agglomerative clustering, these potential outliers were absorbed into a larger cluster rather than defining their own cluster. Depending on the context of the study, researchers should consider excluding these three species from this cluster and treating them independently.

8. ‘Subterranean’ (n = 8): This cluster is defined by a score of 4 in digging ability, which is also associated with scores of 0 across all other abilities except swimming where the scores do not exceed 2. This represents subterranean species such as the star-nosed mole (*Condylura cristata*) and the naked mole rat (*Heterocephalus glaber*).
9. ‘Swim-dig’ (n = 24): This cluster is defined by high digging ability (scores of 3 or 4) associated with medium to high scores in swimming (ranging from 1 to 3). This is exemplified by species such as the water vole (*Arvicola amphibius*), the North American beaver (*Castor canadensis*) and the web-footed tenrec (*Limnogale mergulus*), which score 3 in both swimming and digging

Table II.2: Polychoric PCA loadings
For each PC, the loadings of each locomotor variable are provided.
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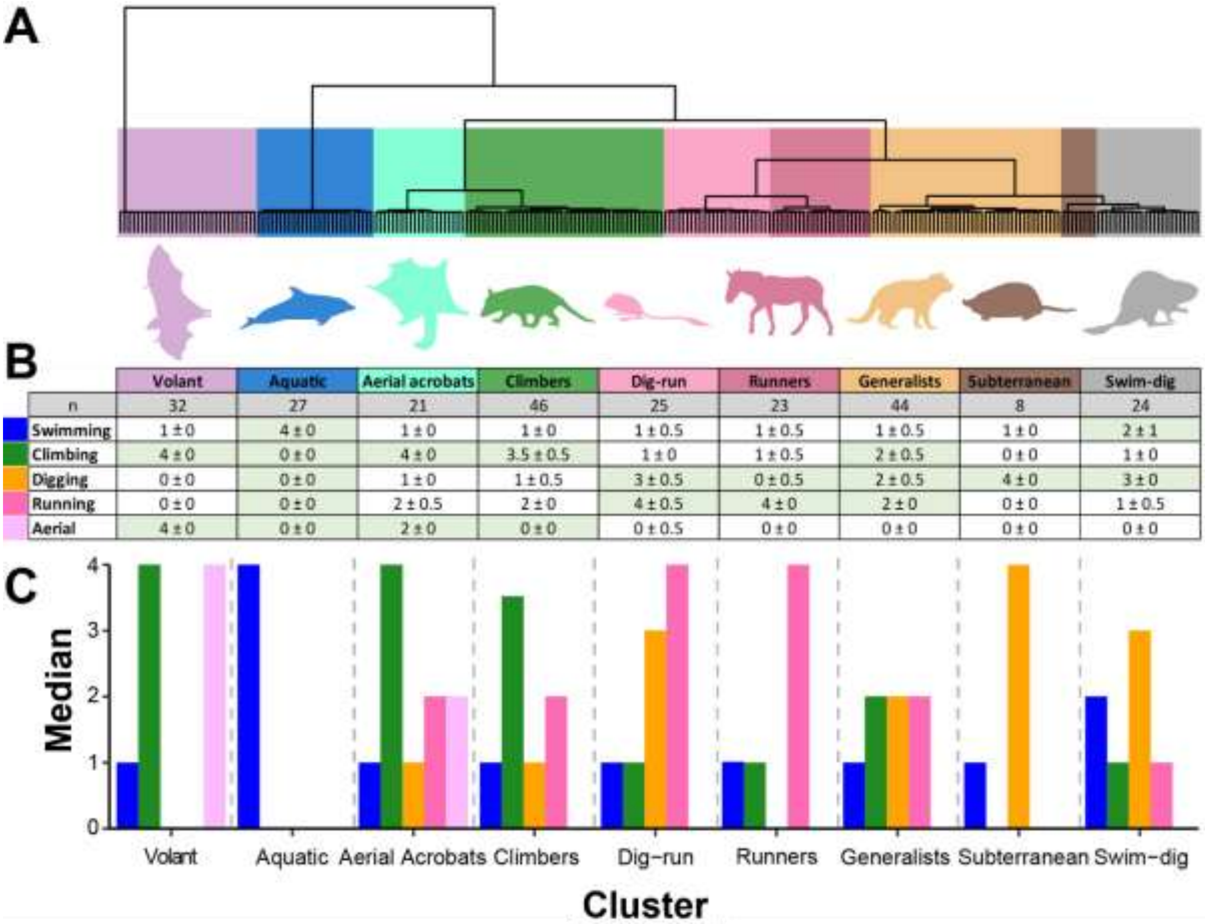
	PC1	**PC2**	**PC3**	**PC4**	**PC5**
Swimming	0.88	0.98	0.00	0.10	-0.02
Climbing	-2.50	-0.38	0.10	-0.93	-0.10
Digging	1.18	-1.17	-0.73	0.07	-0.05
Running	1.00	-1.46	0.94	0.12	0.00
Aerial	-2.47	0.60	-0.12	-0.03	-0.54



	Volant	Aquatic	Aerial acrobats	Climbers	Dig-run	Runners	Generalists	Subterranean	Swim-dig
n	32	27	21	46	25	23	44	8	24
Swimming	1 ± 0	4 ± 0	1 ± 0	1 ± 0	1 ± 0.5	1 ± 0.5	1 ± 0.5	1 ± 0	2 ± 1
Climbing	4 ± 0	0 ± 0	4 ± 0	3.5 ± 0.5	1 ± 0	1 ± 0.5	2 ± 0.5	0 ± 0	1 ± 0
Digging	0 ± 0	0 ± 0	1 ± 0	1 ± 0.5	3 ± 0.5	0 ± 0.5	2 ± 0.5	4 ± 0	3 ± 0
Running	0 ± 0	0 ± 0	2 ± 0.5	2 ± 0	4 ± 0.5	4 ± 0	2 ± 0	0 ± 0	1 ± 0.5
Aerial	4 ± 0	0 ± 0	2 ± 0	0 ± 0	0 ± 0.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Figure II.3: Summary of final locomotor clusters arising from hierarchical cluster analysis

A) Dendrogram showing the hierarchical relationships of the 250 species based on their locomotor profiles, calculated using Ward's method. The identity of the nine clusters established previously as optimal are visualised and colour-coded here. Species binomials are omitted for legibility. Animal silhouettes are modified from PhyloPic (www.phylopic.org); species as follows from left to right: Pteropus medius *(Indian flying fox),* Tursiops truncatus *(common bottlenose dolphin),* Petaurus breviceps *(sugar glider),* Didelphis virginiana *(Virginia opossum),* Jaculus jaculus *(lesser Egyptian jerboa),* Equus africanus *(African wild ass),* Sarcophilus harrisii *(Tasmanian devil),* Condylura cristata *(Star-nosed mole), and* Castor canadensis *(North American beaver). B) This table provides median scores and quartile deviations (median ± QD) for each locomotor variable in each cluster, as well as number of species in each cluster (n) is provided. Boxes highlighted in green indicate scores particularly relevant or distinctive for each cluster. C) Bar chart visualising the locomotor profiles of each cluster, represented by median scores for each locomotor variable in each cluster.*

II.3.3. Behavioural space

Figures II.4 and II.5 show how scores in each ability relate to each species' position in the behavioural space by plotting gradients of increasing ability score in the PC1-PC2 and PC3-PC4 behavioural spaces. Variation along PC1 is primarily related to climbing ability and aerial movement, both of which have high negative loadings. Variation on PC2 is primarily related to digging and running (both having negative PC2 loadings) and to swimming ability (with positive PC2 loading). Since those three locomotor abilities have positive PC1 loadings, their gradients occur diagonally (Fig. II.4). On PC3, variation is primarily related to running ability (positive loading) and digging ability (negative loading), while variation on PC4 is primarily related to climbing ability which has a strong negative loading. Neither swimming nor aerial ability have notable loadings in either PC3 or PC4.

In the PC1-PC2 behavioural space (Fig. II.4) the volant and aquatic species are most clearly isolated from the other clusters, at the negative extreme of PC1 and the positive extreme of PC2, respectively. A clear behavioural gradient exists from the climbers around the origin of the behavioural space, through the aerial acrobats with more negative PC1 values, to the volant species with the most negative PC1 values. The remaining clusters overlap to varying extents in the positive half of PC1 and the negative half of PC2.

The PC3-PC4 behavioural space (Fig. II.5) is dominated by the separation of climbers at the negative half of PC4 and the strong run-dig gradient along PC3. In this gradient, subterranean species are isolated at the negative end of PC3, followed by the swim-dig cluster and then the generalists with progressively less negative PC3 values. The generalist cluster partly overlaps with the run-dig cluster around the origin, but then the gradient continues with increasingly positive PC3 values towards runners at the positive extreme. Along PC4, volant species and the aerial acrobats have notably higher scores than climbers but lower than aquatic species, with barely any overlap between those clusters. However, this separation occurs at the region of the PC3-PC4 behavioural space shared by generalists and dig-runners, obscuring any potential interpretation.

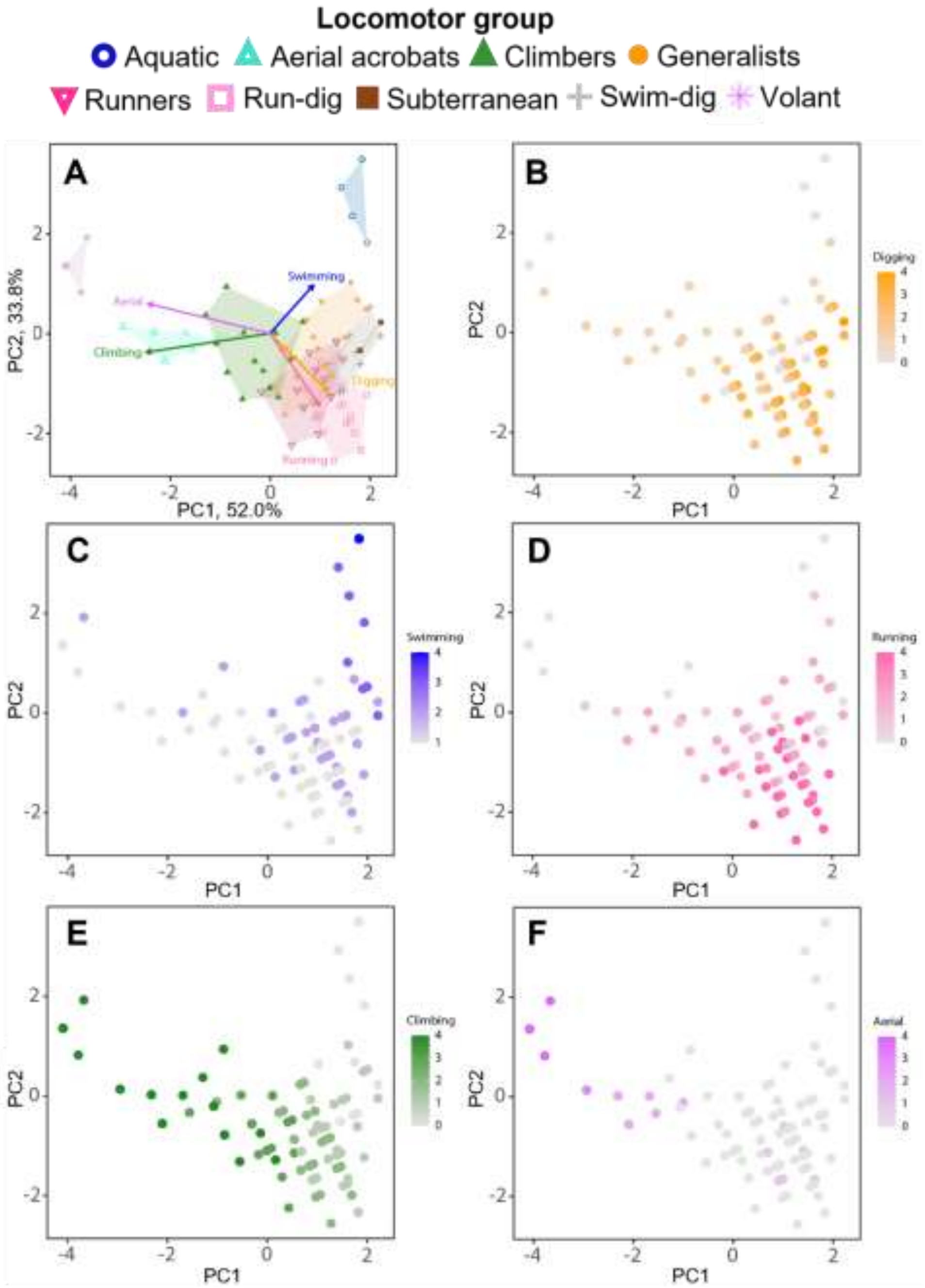


Figure II.4: PC1-PC2 behavioural space occupation by the different locomotor clusters, and behavioural gradients within the behavioural space

Results of the polychoric PCA on the scoring matrix of locomotor ability. A) Species have been colour-coded by their cluster assignment, with convex polygons drawn for each cluster. The coloured arrows represent the loadings of each locomotor variable in PC1 and PC2 (see Table II.2). B)-F) Increasing scores in each of the five locomotor variables are indicated with colour gradients.

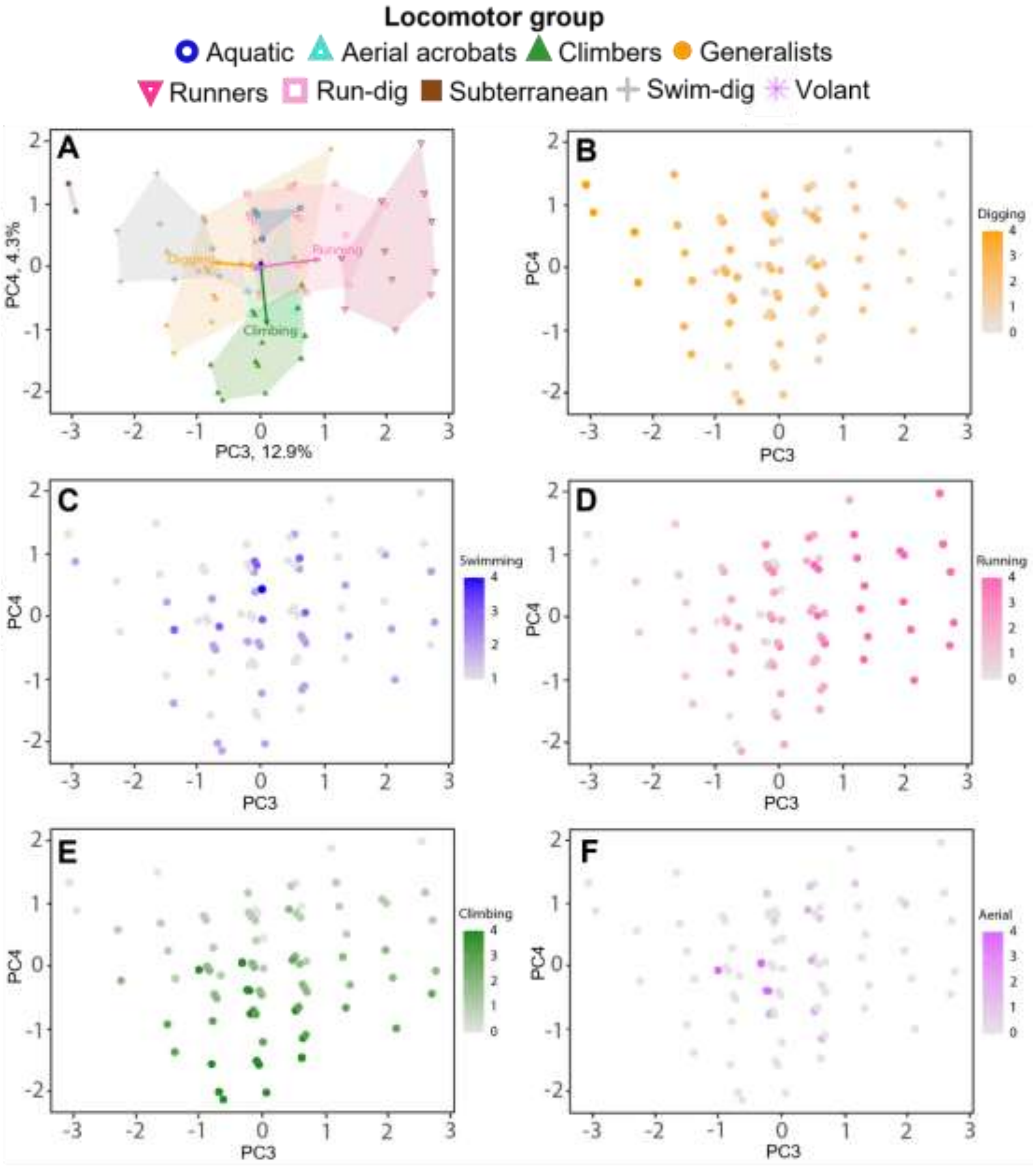


Figure II.5: PC3-PC4 behavioural space occupation by the different locomotor clusters, and behavioural gradients within the behavioural space

Results of the polychoric PCA on the scoring matrix of locomotor ability. A) Species have been colour-coded by their cluster assignment, with convex polygons drawn for each cluster. The coloured arrows represent the loadings of each locomotor variable in PC3 and PC4 (see Table II.2). B)-F) Increasing scores in each of the five locomotor variables are indicated with colour gradients.

II.4. Discussion

This chapter provides a successful proof-of-concept of a novel method for quantifying behaviour on a broad comparative mammal locomotion dataset, facilitating the creation of locomotor variables for use in subsequent chapters. Bringing together concepts of behavioural scoring (Rojas et al. 2011; Kissling et al. 2014; Wisniewski et al. 2023) and hierarchical cluster analysis on behavioural data (Lintulaakso et al. 2022), this method improves upon traditional behavioural categorisation methods in extant mammals by increasing behavioural repertoire information captured, and reducing subjectivity in both the creation of locomotor groups and in the assignment of species to those groups, which themselves provide a more nuanced and representative system of categorisation than the previous systems. The method can be modified for use on any behavioural variable, such as diet or habitat preference, in any taxonomic group, and it is time-efficient enough to be reasonably performed as the initial portion of a larger functional morphology analysis.

In particular, while scoring matrices and cluster analysis have been utilised separately to quantify dietary information previously (Rojas et al. 2011; Kissling et al. 2014; Lintulaakso et al. 2022; Wisniewski et al. 2023), this combined application allows quantification of mammal behaviour with far greater resolution than traditional categorisation. Another advantage is the flexibility provided by this method since, depending on the analysis, the behavioural matrix can be used without reducing its dimensionality (as the polychoric PC scores), or converted into a mathematically derived categorical variable. If a categorical variable is the desired output, all these behavioural scores are then utilised within the cluster analysis to determine the final number of levels (clusters) and their definitions (locomotor profiles) within the categorical variable, reducing the dimensionality in an objective manner. In this case study for mammal locomotion, since each level of the categorical variable will include information on all five modes of locomotion, this novel method greatly increases the quantity of information on behavioural repertoire used to determine locomotor groups. Decisions regarding group number and identity of the groups in the locomotor categorical variable are thus taken out of the hands of the researcher, and instead are determined mathematically, and the scoring process minimises subjectivity using strict scoring criteria and definitions.

II.4.1. Comments on methodology

With some alterations to the criteria, the principle of the scoring matrix can be applied to any taxonomic group or behaviour, and it can be edited to include as much or as little information as is possible to acquire from the literature and/or direct observation.

II.4.1.1. Scoring adaptability

The scoring criteria presented here were designed with all mammals in mind. For this reason, some aspects are generalised. When working with a smaller taxonomic group (e.g. Carnivora), a single behavioural group (e.g. arboreal animals), or non-mammals, the criteria can be edited accordingly to best capture the relevant behavioural repertoires in the study group. Some examples of possible alterations and additions include:

1. Stance/limb posture might be added as an additional column to the scoring criteria which would include predefined scores for plantigrade, digitigrade, etc.
2. Scoring criteria could be edited to specify whether a behaviour is forelimb or hindlimb dominated, akin to Oxnard (1963) in mammals, or Heers & Dial (2015) and Macaulay et al. (2023) in the context of birds and their dinosaur ancestors.
3. Certain behaviours could be further subdivided into separate scores. For example, aerial acrobatics could be divided according to length of between-perch leaps relative to body size; or excavating complex burrows despite feeding overground could represent an intermediate score between simple burrows (Digging 3) and subterranean life (Digging 4) by assigning that behaviour to Digging 3.5.
4. Substrate use could be specified as an independent criterion to be scored, indicating an animal’s proficiency at movement in each substrate. Alternatively, separate variables could be added to denote which substrates (or abilities) are used in different behaviours (e.g. while foraging; while foraging and fleeing; in all circumstances; etc.).

It should be noted that the scoring matrix, as it is presented here, can be used as a ‘first pass’ before more specific criteria are introduced to examine particular taxonomic groups or behavioural groups in greater detail. Modifications such as the ones described above are particularly useful in studies planning on using the full behavioural matrix as data (e.g. as part of a 2B-PLS, as a covariate in multivariate regression, etc.), since in this case the method is more robust to behavioural variables having different ranges and scales. However, it is also important to note that, if the scoring criteria are edited substantially, interobserver repeatability tests should be performed with the new criteria to verify that subjectivity is still low.

II.4.1.2. Clustering

There are a number of reasons underlying the choice of Ward’s method for clustering these data. There are two main types of hierarchical clustering: agglomerative and divisive. Though divisive clustering (e.g. DIANA [Kaufman & Rousseeuw 1990]) has some advantages over agglomerative clustering, notably that it is computationally less complex and demanding, agglomerative clustering has the important advantage that it manages outliers more successfully than divisive clustering; outliers are absorbed into larger clusters as agglomeration occurs, rather than the outliers splintering from the main group of observations early and defining clusters (Murtagh & Legendre 2014). The nature of using mathematics to generate levels for a categorical variable is that biological interpretability of the clusters is not guaranteed, so the contents of each level should be inspected for potential outliers. Nevertheless, this can also be interpreted as a positive – potential behavioural outliers are brought to the researchers’ attention this way (e.g. low locomotor ability species in the generalists cluster). Since this dataset represents a wide variety of locomotor profiles, there was a reasonably high possibility of a locomotor profile being an outlier and causing an inappropriate splinter in the dataset. Therefore, an agglomerative method is most suitable here.

There are several examples of agglomerative hierarchical clustering methods. However, Ward’s method is exceptional among these methods in that, rather than using Euclidean distances as metrics for similarity directly, Ward’s method uses a measure of how much the within-cluster sum of squares will increase if two clusters merge, and determines agglomerations to minimise this growth. By using this metric for determining agglomeration, the function essentially ‘checks’ before merging groups that this merge does not cause a large increase in the sum of squares, which would imply that disparate observations are being placed into a single cluster (Ward 1963). In this study, it was desirable to produce clusters (locomotor groups) which are defined by within-cluster similarity and between-cluster dissimilarity – that all species placed in the same locomotor group exhibit a behavioural repertoire more similar to other members of the cluster than to members of any other cluster. Additionally, the main caveat of other popular clustering methods such as k-means (which is not hierarchical) is the necessity to specify output cluster number prior to running the analysis (MacQueen 1967). In the context of this study, it was advantageous that cluster number did not need to be specified in order to run the analysis, since determining the optimum cluster number *after* the initial cluster was performed minimises subjectivity at this step. Furthermore, this allowed the hierarchical dendrogram to be visualised at all cluster numbers. For these reasons, Ward's method was the best choice for this work. If it were necessary to use a predetermined cluster number as part of any subsequent analyses using the clusters, k-means may be an appropriate substitute.

II.4.2. Insights on mammal locomotor specialisation

The relatively low number of locomotor profiles identified in the dataset (81 across 250 species) is of interest. Of the theoretically possible 3,125 locomotor profiles, several are impossible in extant mammals while others are unlikely based on how scoring criteria are defined, reducing this theoretical limit. For instance, all extant mammals can at least paddle out of water (i.e. no 0 scores in Swimming), removing 625 theoretical profiles.

Locomotor specialisation (scores of 4 in any ability) explains most of the missing hypothetical profiles, as it is associated with morphological specialisation, which often leads to a particular organ or appendage being exceptional in performing one function to the detriment of all other functions (e.g. aquatic and volant animals whose limbs are so morphologically specialised that they are unable to engage in other locomotor behaviours). Thus, specialised animals are unlikely to be very adept in other behaviours. This is particularly evident in clusters which are associated with substrate specialisation, such as the aquatic, volant and aerial acrobat clusters, which in this dataset is reflected as follows:

- Extreme specialisation for swimming (score of 4) in mammals results in the inability to move terrestrially (i.e. all other scores are 0) due to highly modified limbs.
- Specialised aerial behaviours such as gliding and flapping flight (aerial scores of 3 and 4, respectively) require high climbing ability (score of 4), since it is generally the case that a mammal must first climb to a high perch in order to perform aerial behaviours. However, this also seems to limit swimming or running ability (no scores of 3 or 4 for those variables in this subsample) and constrain digging behaviours (no scores over 1 in those species).
- Extreme specialisation for digging (score of 4) seems to limit any potential specialisations into any other locomotor modes, with no scores over 2 were observed in those species
- Specialisation in performing asynchronous gaits (Hildebrand 1977; Hildebrand 1988; Howell 1944; Gambaryan 1972) for extended periods of time (score of 4) seems to limit an animal’s swimming ability (no scores above 2 in these species) and aerial movement beyond extremely high and/or long leaps (maximum scores of 1 in that ability), but is compatible with good climbing and digging abilities.
- Extreme specialisation in climbing (scores of 4) does not seem to conflict with any other locomotor modes beyond the constraints described above.

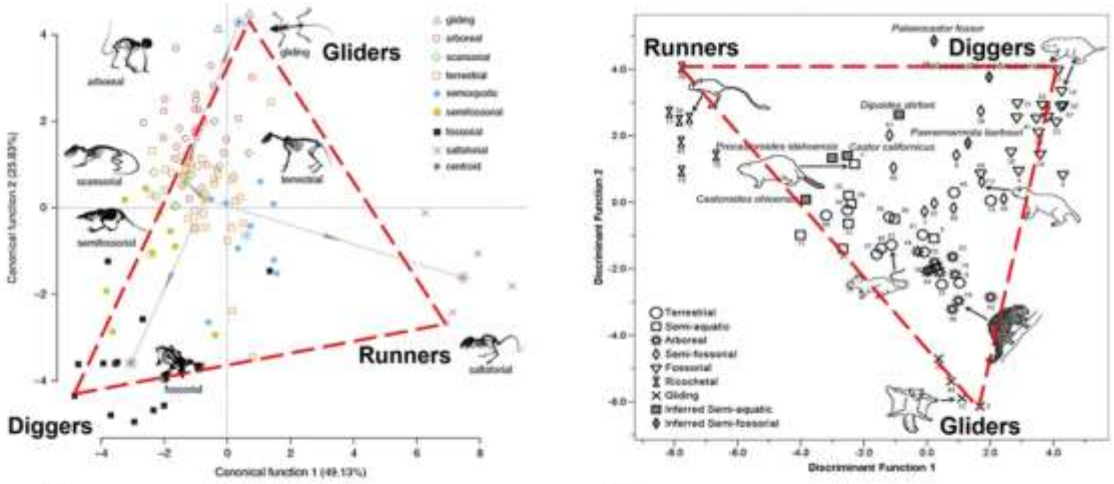
If all these limitations and constraints are calculated simultaneously, the number of theoretical locomotor profiles is reduced to 823, still over a tenfold increase relative to the observed profiles. This may be related to the fact that mammals possess a limited number of appendages with which to specialise – the forelimbs may be specialised for one ability, the hindlimbs another, and potentially the head or tail another still, but this still does not allow a single species to exhibit specialisations in all the locomotor abilities discussed here.

II.4.3. Behavioural vs. morphological spaces

As a final remark, the results of the polychoric PCA highlighted a recurring pattern – points representing the highly specialised groups (‘Aquatic’, ‘Volant’, and ‘Runners’) form a triangle in the PC1-PC2 behavioural space (Fig. II.4A). A similar result has previously been discussed by Grossnickle et al. (2021), who noted the phenomenon of specialisation triangles occurring in PCAs of morphological data (citing [Samuels et al. 2013; Chen & Wilson 2015; Grossnickle 2020]), in which specialised groups occur at vertices (Fig. II.6 A-C), most commonly gliding, cursorial and fossorial species (in datasets which do not include aquatic and volant groups). This same triangle can be observed within the behavioural space produced here (Figs. II.4, II.6D) but the glider vertex expands towards fliers and the fossorial vertex towards aquatic species. While the former extension is easy to understand, the second might seem less intuitive, and yet, several studies have found similar morphological adaptations in both aquatic and fossorial species (e.g. the index of fossorial ability – ratio between olecranon and ulna lengths – is even higher in aquatic species [Samuels et al. 2013; Gálvez-López 2021]). Beyond the matching triangles, this is of interest because both morphological and behavioural data appear to be producing the same result, indicating that these extremes of morphological specialisation exist in association with the extremes of behavioural specialisation, as is the central dogma of functional morphology.

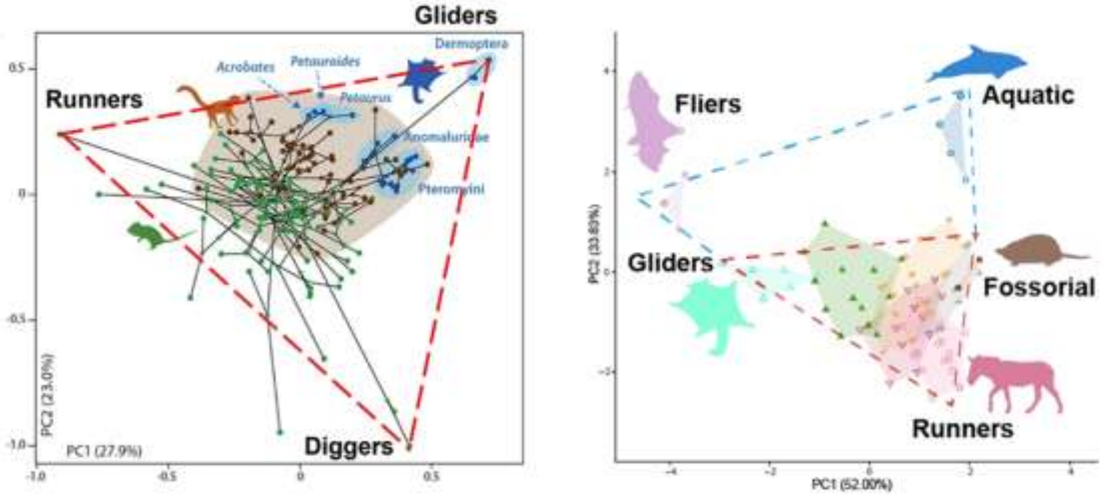
II.5. Conclusions

This novel method for quantifying animal behaviour successfully addresses the issues of traditional behavioural categorisation by increasing behavioural repertoire information captured and decreasing subjectivity in the production of the behavioural variable. The use of this method on mammal locomotion in this chapter provides the basis and justification for its use in subsequent chapters to generate locomotor variables for use in geometric morphometric analyses. Furthermore, the resolution of the data has allowed greater insight into specialisation within mammal locomotion, and how this appears to relate to morphological specialisation, providing a solid basis for investigating the exact nature of this relationship in the scapula moving forward.



A Chen and Wilson 2015

B Samuels and Van Valkenburgh 2008



C Grossnickle *et al.* 2015

D Anderson *et al.* (this study)

Figure II.6: Comparison of locomotor and morphological specialisation extremes
Three examples of locomotor specialisation triangles (in red) from PCAs on morphological data: A) modified from Chen and Wilson (2015, Fig. 4A); B) modified from Samuels and Van Valkenburgh (2008, Fig. 2); and C) modified from Grossnickle et al. (2020, Fig. 3B). Behavioural space D) based on behavioural data (PC1-PC2) from this chapter. The morphological specialisation triangle is highlighted in red, and the expansion described here in blue. Silhouettes as in Figure II.3.

Appendix II.1: Interobserver repeatability

In order to determine whether the scoring criteria definitions satisfactorily reduce subjectivity, and to test whether cluster compositions are affected by any remaining subjectivity, interobserver repeatability was assessed. Though subjectivity cannot be removed entirely since each individual interprets scoring criteria and sources independently, this analysis aims to assess the robusticity of the method to this individual variation.

A subsample of 30 species from the original 250 was selected to include as much taxonomic and locomotor diversity as possible, while including at least two representatives of each of the whole dataset clusters. These species were independently scored by eight individuals without any knowledge of each other’s scores, and Ward’s hierarchical clustering was performed on each set of scores to identify the same number of clusters as in the whole dataset (k = 9). Note that, while a different optimal number of clusters may have been recommended by cluster validation methods for this reduced dataset, the aim is to evaluate how potential changes in scoring affect clustering, not how optimal cluster number changes with sample size. In line with University of York Department of Archaeology ethical guidelines, informed consent was obtained from each participant prior to scoring, and all data are anonymised. Participants are referred to as P1-P8.

The process is considered repeatable if three conditions are met:

1. The same clusters identified in the whole datasets (based on their median scores in each locomotor ability) can be identified among participants.
2. Mean square error (MSE) for participants is lower than one unit.
3. Canonical Variate Analysis (CVA) has low cross-validated classification rates differentiating participants (<25.0%), and high cross-validated classification rates differentiating clusters (>25.0%).

Mean square error (MSE) of each participant was calculated by subtracting their scores from those of each other participant and calculating an averaged sum of those values squared. These pairwise interobserver MSEs were then averaged for each participant to calculate a general mean. CVAs were carried out on a supermatrix combining the polychoric PC scores from all participants, with jackknife cross-validation. The *CVA* function in the R package *Morpho* was used to carry out the CVAs (Schlager 2017).

Results

The selected species and the assigned scores for each participant can be seen in S.II.1.B. With reference to the three conditions of repeatability above, the results are as follows:

1. When Ward's hierarchical cluster analysis was run on the sets of scores provided by the eight participants and examined at k = 9, **all datasets were able to produce at least eight clusters analogous to those produced by the whole set** (i.e. with similar medians in each locomotor ability). The identity of the non-analogous cluster present in six of the participants' results varied across participants, but this would be expected since cluster number was not selected based on any validation method.
2. The **average MSE among participants was 0.43** (range: 0.38-0.48), indicating that differences in any locomotor ability larger than a unit among participants are rare and suggesting that scoring criteria are quite robust but, as expected, still create some subjectivity. These small differences can result in a change to the locomotor profile of a given species, which can lead to the species shifting clusters. For instance, if one participant scores a species 1/1/3/2/0 (Swim/Climb/Dig/Run/Aerial) it may appear in the swim-dig cluster, but if the same species were scored 1/1/3/3/0 by another participant it may appear in the dig-run cluster. In fact, on average, 11.6 species are assigned to different clusters when comparing any two participants (range: 9.1-12.7). Cluster identity appears to remain relatively consistent even in spite of this movement of species between clusters. Slight variations of median scores across participants for a given cluster are likely the result of variation in the number of species having each individual locomotor profile in that cluster.
3. The CVA was **unable to differentiate participants** (correct classification rate = 0.0%), but was moderately **successful at differentiating clusters** (correct classification rate = 47.9%).

While this method has several built-in strategies to reduce subjectivity, some variability between observers still exists. First, there is variability in the ability scores themselves, which arises from each participant's interpretation of the scoring criteria and the sources they used, and from the information that each source contains. Overall, variability in the scores was relatively low, with only 4.6% of them presenting quartile deviations larger than 0.5 (which translates to differences larger than one whole rank between the 25% and 75% quartiles), and 49.3% of the scores having zero quartile deviation.

The second source of variability, cluster assignment, is mathematical and thus largely outside the researcher’s control. While the number of differences in cluster assignments between participants might seem problematic, several factors mitigate this. First, hierarchical clustering has been shown to perform poorly in small sample sizes (Dalmaijer et al. 2022), and the repeatability dataset falls well below recommended sample sizes in clustering analyses (Dolnicar et al. 2013). Second, clusters were evaluated at a specific k value instead of that recommended by validation methods. As we mentioned previously, due to the greedy nature of agglomerative clustering, some k values are better than others. Thus, to reduce this secondary source of variability, it is recommended to use as large a dataset as possible.

Conclusion: the method can be considered sufficiently repeatable.

Chapter III

Shouldering the burden:

Functional morphology of the therian scapula

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Research Degree Thesis Statement of Authorship

Note that where a paper has multiple authors, the statement of authorship can focus on the key contributing/corresponding authors.

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Thesis title	Shoulder to shoulder: Comparative functional morphology of the scapula across therians

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*The description of the candidate and co-authors contribution to the work may be framed in a manner appropriate to the area of research but should always include reference to key elements (e.g. for laboratory-based research this might include formulation of ideas, design of methodology, experimental work, data analysis and presentation, writing). Candidates and co-authors may find it helpful to consider the CRediT (Contributor Roles Taxonomy) approach to recognising individual author contributions.

III.1. Introduction

The mammal scapula (Fig. III.1) presents a particularly interesting, if challenging, opportunity to relate biomechanical function to anatomical form, being both biomechanically complex and highly variable in its morphology (Monteiro & Abe 1999; Böhmer et al. 2020). The scapula forms part of the shoulder (or pectoral) girdle, connecting the forelimb to the body, and is a weight-bearing element in quadrupeds, responsible for maintaining the position of the anterior thorax against gravity (Jenkins 1974). Importantly, the scapula is fundamentally involved in stride production in quadrupedal mammals, contributing the most of any forelimb segment to propulsion during locomotion (Fischer et al. 2002). In fact, scapular rotation was found to account for >60% of stride length in some species (the rock hyrax [Fischer 1994] and the brown lemur [Schmidt et al. 2002]). The 20+ muscle attachments present on the mammal scapula (the functions and attachment loci of which are provided in Fig. III.2 & Table III.1), and the fact that it is connected to the thorax by soft tissue only, allow it to move very freely – tilting, rotating and translating along the body wall, not to mention that the glenohumeral joint connecting the scapula and humerus is a ball-and-socket joint. This high level of mobility results in extremely nuanced movements being possible, but it is also crucial that the scapula and shoulder joint as a whole are stable through these motions. Depending on many factors – like behavioural repertoire, size, and clavicle presence/absence – different species have a different emphasis on mobility versus stability, or may vary in exactly what these qualities mean within the species' circumstances.

Despite this complexity and variation, there are aspects of the general architecture of the scapula that remain constant across extant therian mammals (that is, all mammals except monotremes). The scapula (Fig. III.1) is a plate of bone which lies on the thorax, being attached to the body wall by soft tissue only. The lateral side of the scapula is divided by the scapular spine into two fossae: the infraspinous fossa on the caudal side, which houses the origin of the *m. infraspinatus*; and the supraspinous fossa on the cranial side, which houses the *m. supraspinatus*. The medial side of the scapula blade comprises (almost in its entirety) the subscapular fossa, which provides the origin of the *m. subscapularis*. The spine rises laterally from the blade, approximately perpendicularly. At its distal end, closest to the joint, the spine expands into the acromion, which articulates with the clavicle in claviculate mammals. There are two regions which may be distinguished on the acromion: the hamatus process (which is the articulation for the clavicle), and the suprahamatus process, slightly proximal and generally caudal to the hamatus, which is also known as the metacromion. For the purposes of this chapter, ‘acromion tip’ refers to the hamatus process and ‘metacromion’ refers to the suprahamatus. The blade transitions distally into the glenoid cavity via the scapular neck. The glenoid provides the articulation for the proximal humerus, forming the ‘socket’ in this ball-and-socket joint. Thus, the glenoid is concave and approximately circular, elliptical or ovoid-shaped. At the medio-cranial edge of the glenoid cavity arises the coracoid process. This process varies greatly across therians, from an elongate bone strut which forms a key component of the shoulder joint, to an extremely reduced or barely identifiable tubercle.

Though this anatomy is homologous across therian mammals, the shoulder girdle of monotremes (that is, echidnas and platypus) is not homologous to that of the therians. While earlier tetrapods possessed a shoulder girdle element known as the procoracoid or anterior coracoid, early non-mammalian synapsids developed an adjacent novel element called the true coracoid or, from here onwards, simply the coracoid (Romer & Parsons 1977; Luo 2015). These animals had sprawling limb postures and fixed shoulder girdles, which is also the case in extant monotremes. Monotremes, however, have a much-reduced procoracoid and greatly expanded coracoid which forms an articular portion of the glenoid fossa, as well as providing important muscle attachment sites (Luo 2015). In monotremes, there is no scapular spine homologous to that of therians, and the *m. subscapularis* originates on the lateral side of the blade (alongside the *m. infraspinatus*) while the *m. supraspinatus* originates from the medial side. This is in direct contrast to the origins of these muscles in therians (Regnault et al. 2020) (Fig. I.2, Fig. III.2 & Table III.1). In association with the transition to parasagittal limbs and mobile shoulder girdle in therians, the rearrangement of musculature resulted in the loss of the procoracoid entirely, and complete fusion of the coracoid and scapula into a single element. This is still evidenced by the presence of two separate ossification centres during development for the scapula and coracoid regions in therians (Monteiro & Abe 1999). These differences in function and anatomy mean that it is nigh on impossible to include monotremes in the same study as therians when in the context of scapular functional morphology.

Therian mammals comprise a group of close to 6,500 extant species (Upham et al. 2019) divided into 26 orders (Burgin et al. 2018) which range greatly in body size (from the Etruscan shrew at 1.3g, to the blue whale weighing as much as 190,000kg [Nowak 1999]). They also exploit a wide variety of niches, including powered flight (achieved only by chiropterans), obligately aquatic groups (cetaceans and sirenians), groups which live almost entirely underground (e.g. moles, which are not a single phylogenetic grouping); as well as extremely proficient climbers (such as highly arboreal primates), diggers (such as armadillos and many rodents), and runners (such as rabbits & hares, ungulates, and high-speed runners like cheetahs). Therian global success and diversity in niche occupation makes the group a potential goldmine of information on functional adaptation.

The variation in therian life histories coupled with variation in scapular morphology offers a tantalising opportunity to investigate the links between scapular form and function. Firstly, as it pertains to locomotion behaviour, but additionally how size, evolutionary history, and clavicle presence play their roles in shaping the scapula. Many authors have been drawn to the puzzle of scapular functional morphology in mammals, studying the scapulae of a broad range of therian groups (e.g. small cursors: Seckel & Janis 2008; Carnivora: Taylor 1974, Gálvez-López 2014, Gálvez-López & Casinos 2022; Marsupialia: Warburton 2003, Astúa 2009; Primates: Young 2004, Taylor & Slice 2005, Young 2008, Preuschoft et al. 2010; Xenarthra: Monteiro & Abe 1999; Rodentia: Swiderski 1993, Morgan 2009; Cetacea: Strickler 1978; Sirenia: Domning 1977). These studies repeatedly identify an important role of locomotion behaviour in explaining scapular morphology, though some find that this is superseded by the effects of evolutionary history (Monteiro & Abe 1999; Astúa 2009).

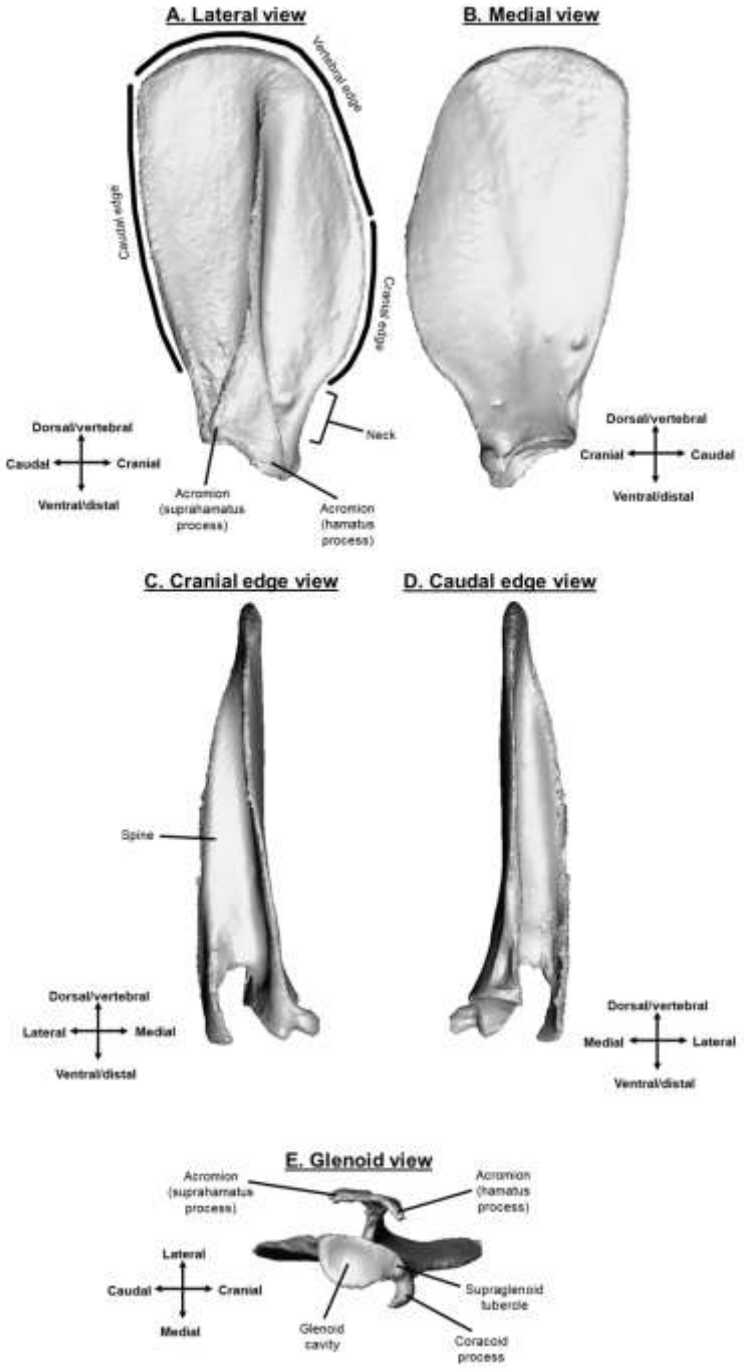


Figure III.1: General scapular anatomy in therians
*These images illustrate the standard orientation and nomenclature used throughout this chapter (following Atlas of Terrestrial Mammal Limbs [Böhmer et al. 2020]). The scapula used in this figure is a specimen of a Virginia opossum (*Didelphis virginiana*) from the Cambridge University Museum of Zoology (accession: UMZC A4 5/2).*

Table III.1: Muscles associated with the scapula in therian mammals
The table provides the muscle nomenclature used throughout this chapter, as well as the function and attachment sites of the muscle on the shoulder, and whether or not the scapular attachment point is a muscle origin (O) or insertion (I). This table is a truncated and adapted version of Table I.2.1. from Atlas of Terrestrial Mammal Limbs *(Böhmer et al. 2020, p15-21) with additional reference to* Miller's Anatomy of the Dog 4th Ed. *(Evans & de Lahunta 2012).*

Muscle (abbreviation)	**Main function(s)**	**Shoulder attachment point(s)**	**Origin or insertion on scapula**
m. clavotrapezius (CT)	Scapula abduction (and protraction indirectly)	Clavicle if present and raphe with *m. clavobrachialis* and *m. cleidomastoideus*	N/A
m. acromiotrapezius (AT)	Scapula abduction and protraction, shoulder stabilisation	Scapular spine and acromion	I
m. spinotrapezius (ST)	Scapular retraction and shoulder stabilisation	Scapular spine	I
m. cleidomastoideus (CM)	Humerus protraction	Clavicle if present and raphe with *m. clavotrapezius* and *m. clavobrachialis*	N/A
m. clavobrachialis (CB)	Humerus protraction	Clavicle if present and raphe with *m. clavotrapezius* and *m. cleidomastoideus*	N/A
m. serratus ventralis (SV)	Scapula adduction, retraction and protraction	Medial dorsal aspect of scapula	I
m. rhomboideus cervicis (RCe)	Scapula adduction and protraction and neck elevation	Cranial portion of dorsomedial border of scapula	I
m. rhomboideus thoracis (RT)	Scapula adduction and retraction	Caudal portion of dorsomedial border of scapula	I
m. rhomboideus capitis (RCa)	Scapula protraction and neck elevation	Lateral to *m. rhomboideus cervicis*	I
m. rhomboideus profundus (RP)	Scapula protraction and neck elevation	Lateral to *m. rhomboideus capitis*	I
m. omotransversarius (OT)	Scapula protraction and neck elevation	Metacromion process	I
m. subclavius (SC)	Shoulder stabilisation	Clavicle	N/A
m. supraspinatus (SS)	Shoulder joint extension and shoulder stabilisation	Supraspinous fossa	O

m. infraspinatus (IS)	Shoulder joint flexion, lateral humerus rotation, and shoulder stabilisation	Infraspinous fossa	O
m. spinodeltoideus (SD)	Shoulder joint flexion and humerus abduction	Scapular spine, superficial to *m. infraspinatus*	O
m. acromiodeltoideus (AD)	Shoulder joint flexion and humerus abduction	Acromion process	O
m. teres minor (TMN)	Shoulder joint flexion and lateral humerus rotation	Caudal border of scapula (near glenoid)	O
m. epitrochlearis (ET)	Humerus retraction and elbow joint extension	Caudal border of scapula (lateroventral to *m. teres major*)	O
m. triceps brachii caput longum (TBLO)	Shoulder joint flexion and elbow extension	Caudal border of scapula (medial to *m. teres minor*)	O
m. subscapularis (Sub)	Humerus adduction and shoulder stabilisation	Subscapular fossa	O
m. teres major (TMJ)	Shoulder joint flexion and humerus retraction	Caudal border of scapula	O
m. coracobrachialis (CO)	Shoulder stabilisation and humerus adduction	Coracoid process	O
m. biceps brachii (BB)	Shoulder joint extension and elbow flexion	Tendon from supraglenoid tubercle of scapula and from coracoid process if second head present	O

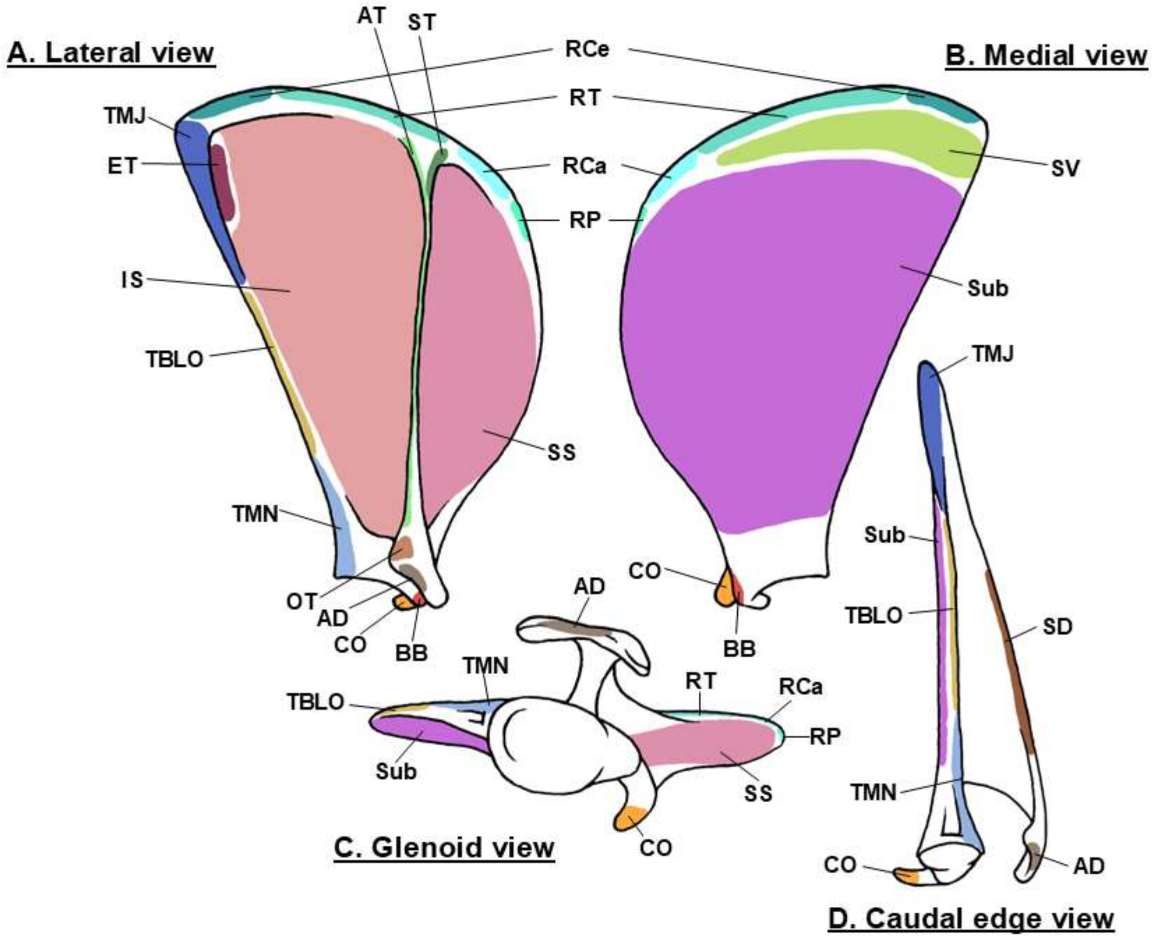


Figure III.2: Muscle attachment sites of the therian scapula
These images illustrate the muscle attachment regions on the scapula (following Atlas of Terrestrial Mammal Limbs *[Böhmer et al. 2020] and* Miller's Anatomy of the Dog 4th Ed. *[Evans & de Lahunta 2012]). The illustration of the scapula is based on the mean shape within this dataset and does not represent any specific species. Muscle attachment areas will vary somewhat across species. Abbreviations follow Table III.1.*

To date, there has not been a class-wide study of 3D scapular morphology in therian mammals. Oxnard's 1968 work is the phylogenetically broadest study of scapular morphology so far, including 194 genera of extant mammals from nine taxonomic groups (many of which, following the current taxonomic classification scheme, align with taxonomic groups represented in this chapter), and it is worth discussing here in greater detail. The primary purpose of Oxnard's paper appears to have been broad validation of his findings in primates (Oxnard 1963; Oxnard 1967a & b), and the focus is on the ability of scapular morphology to distinguish arboreal species from other locomotor modes using Canonical Variate Analysis (CVA). While some research suggests that morphology associated with functional requirements of locomotion are superimposed upon phylogenetically determined base morphology (Monteiro & Abe 1999; Astúa 2009), Oxnard suggested that the opposite may be the case – that phylogenetic variation has arisen over evolutionary time and is superficial to underlying basic patterns of functional adaptation. In essence, he implied that there are universal aspects of scapular morphology associated with locomotion (specifically arboreality) which emerge whenever a taxonomic group adapts towards said locomotion behaviour, and that phylogenetic variation is superimposed upon this. Oxnard found that arboreality is consistently associated with lateral positioning of the shoulder joint (dorsalisation of the scapula), and craniolateral torsion of the scapula (that is, the positioning of the glenoid more cranially and laterally relative to the rest of the blade) associated with resisting tensile forces. Though it constitutes the broadest comparative study of scapular morphology in mammals and contains a very large number of individual specimens, this work is considerably limited. Firstly, it describes shape in terms of ratios and angles, failing to capture a significant proportion of scapular morphology, especially around the glenoid and coracoid. Secondly, the study is heavily primate-centric, using measurements designed for the primate scapula, and with a very considerable proportion of the dataset being primates (557 of a total 1,188 specimens are primates, or 46.9%). Lastly, the study only explores arboreality and does not investigate the various non-arboreal modes of locomotion individually. Why, then, has there not subsequently been a therian-wide study of the relationship between 3D scapular morphology and locomotion behaviour? It is likely that there are, broadly, two reasons for the lack of such work:

- **Complexity:** The complexity of scapular movement in therian mammals makes the scapula enticing to study from a biomechanical standpoint, but also makes it extremely difficult to model, and even to discuss with consistent nomenclature across different phylogenetic groups. For this reason, a certain amount of simplification is necessary, e.g. in this study, a single standardised orientation is used even though scapular orientation varies throughout stride and among different groups. Additionally, modern geometric morphometric methods (GMM) make it possible to utilise a large number of landmarks in 3D, reducing the risk of oversimplifying scapula shape.

- **Scarcity:** The scapula is liable to fragment as it is largely made up of a thin plate of bone. In a palaeontological context, this means that scapulae are rarely recovered, and even more rarely recovered in an approximately complete condition. Thus, long bones which are more likely to preserve are preferentially selected for postcranial work in palaeontology. In museum collections of extant species even, it is often the case that one or both of the scapulae are damaged due to their fragile nature. For these reasons, acquiring complete specimens from across mammals (including those which are very small and particularly fragile) is challenging, and being able to utilise any functional information to address palaeontological questions relies on enough functional information being contained within the less fragile area of the bone (namely, the glenoid and neck region).

With these difficulties in mind, however, this chapter aims to address the primary question, **are there aspects of scapular morphology in therians which can be consistently associated with differences in locomotion behaviour across a broad taxonomic scale?** In order to address this question, though, it is first important to investigate the influences of some other key factors on scapular morphology and variation, especially when they may obfuscate the effects of differences related to locomotion (e.g. Gálvez-López 2021). The additional factors explored here are size and allometry, evolutionary history, and clavicle presence/absence.

III.1.1. Size and allometry

Hypothesis III.1 ($\mathbf{H_{III.1}}$):

Body size will significantly affect scapular morphology. Particularly, large size will be associated with an enlarged vertebral border.

As previously mentioned, the scapula is a weight-bearing component of the forelimb, so differences in body size are likely to change the functional demands which the scapula must meet. In quadrupedal mammals, the thorax is suspended from the shoulder girdle by muscles such as the *mm. rhomboidei, m. serratus ventralis* and *m. trapezius*, the former two of which originate on or near the vertebral border of the scapula, and the latter of which inserts onto the acromion and scapular spine (respectively). In particular, it is important to note the role of the scapula and its musculature in moving the thorax through the shoulder girdle during stride. This is facilitated by muscles which have a thorax (axial) attachment point caudal to their forelimb (appendicular) attachment, such as the *m. pectoralis, m latissimus dorsi, m. serratus ventralis* and *m. trapezius* (the latter two of which attach directly to the scapula, while the former attach to the humerus) (Jenkins 1974). Thus, the areas of the scapula most expected to be associated with weight-bearing are the vertebral border and the vertebral end of the spine. This was identified as the case in didelphid marsupials by Astúa (2009).

It is also crucial to understand the differing limb posture in small versus large mammals. While the largest terrestrial mammals such as elephants have columnar limbs in which the skeletal elements are essentially stacked vertically, small mammals have a characteristic ‘zigzag’ limb posture which acts as shock absorption when traversing uneven terrain (Fischer 1994). This difference in orientation of the limb influences its biomechanics, such as changing muscle lines of action. For this reason, it is likely that differences in limb posture may be associated with differences in morphology across the whole blade. It is also important to note the interplay of body size and locomotion. Some types of locomotion, such as flapping flight, are likely constrained to small body sizes. Meanwhile, aquatic lifestyles free the animal from the effects of gravity and may facilitate growth to larger sizes (Goldbogen 2018), perhaps without associated adaptations in the scapula. Differential scaling in scapular morphology has also been identified in didelphid marsupials (Astúa 2009) and carnivorans (Gálvez-López 2014), with large and small species presenting different allometric slopes.

III.1.2. Evolutionary history

Hypothesis III.2 ($H_{III.2}$):

There will be a significant effect of evolutionary history on scapular morphology, potentially greater than that of the other factors.

Evolutionary history (a broad term which, in this context, is associated with taxonomy and phylogeny) is almost certain to play a role in influencing scapular morphology for several reasons. First, shared evolutionary history has previously been found to be highly influential on scapular morphology in multiple taxonomic groups (xenarthrans

[Monteiro & Abe 1999]; didelphid marsupials [Astúa 2009]; carnivorans [Gálvez-López 2014]). In fact, in xenarthrans (Monteiro & Abe 1999) and in didelphid marsupials (Astúa 2009) evolutionary history has been found to have a greater influence on scapular morphology than locomotion. These findings contradict Oxnard's (1968) hypotheses with regards to arboreality specifically. Secondly, it is important to consider the role of evolutionary history in clavicle loss and how this affects its role in scapular morphology as a whole. Since the clavicle is generally present or absent consistently across individual orders (Fig. III.3), these orders are likely to exhibit internally consistent shared characteristics associated with clavicle presence/absence. For example, all carnivorans are aclaviculate and are expected to exhibit scapular morphology associated with being aclaviculate. Finally, several taxonomic groups are constrained in their locomotion behaviour – all chiropterans fly and they are the only mammals to do so, while ungulates have never ventured into a subterranean niche, for example.

III.1.3. Clavicle presence

Hypothesis III.3 ($H_{III.3}$):

Scapular morphology will significantly distinguish between claviculate and aclaviculate species, particularly in the size of the acromion process.

The clavicle is a relatively understudied bone, but its anatomical articulation with the scapula makes it extremely important in this context. It is believed that the ancestral state for therian mammals is to be claviculate, and that clavicle loss has occurred multiple times independently, most notably in Ferungulata (Hildebrand 1995; de Souza Junior et al. 2020) (Fig. III.3). For the purposes of this study, species are considered claviculate if an ossified clavicle articulates with the acromion and manubrium, and aclaviculate if these articulations are not present, though it should be noted that in reality there is a degree of nuance in clavicular presence in mammals, with some exhibiting cartilaginous struts in place of an ossified clavicle (de Souza Junior et al. 2020). In claviculate mammals, the scapula is connected to the axial skeleton by the clavicle (which articulates with the manubrium of the sternum). However, in aclaviculate mammals, the scapula is not articulated with the axial skeleton by any osseous elements, being connected to the body primarily by musculature. The clavicle is important in providing stability and power to the shoulder (Jenkins 1974), especially when the shoulder is in extension (Rockwood et al. 2009), a posture common in climbing behaviours. Pathological loss of the clavicle in humans is associated with increased protraction and retraction of the shoulder, but significant weakness when bearing loads above the head (Rockwood et al. 2009). The clavicle acts as both a spoke (maintaining a constant distance between the acromion and manubrium) and as a strut (preventing medial collapse of the shoulder during the propulsive phase of stride). In rats which have had their clavicle surgically removed, the absence of this strut effect is particularly clear, as the shoulder is inclined to collapse medially (Jenkins 1974). Clavicle loss has been interpreted as an adaptation towards increased efficiency in shoulder flexion and extension in cursorial movement where the limbs are held in line with the midline of the body (parasagittal), at the expense of power and stability in movements deviating from this plane (Hildebrand 1995; de Souza Junior et al. 2020). This is also associated with a reorientation of the scapula so that is lies lateral to a tall (dorso-ventrally expanded) and slim (medio-laterally compressed) thorax, rather than lying dorsally on a shorter and wider thorax (Hildebrand 1995). In this position, the shoulder moves in the sagittal plane, increasing stride length (Eaton 1944; Jenkins 1974; Hildebrand 1995).

There is some controversy regarding the association of the acromion and coracoid processes, which may be relevant here given the expectation that clavicle presence/absence will affect the acromion process. From an evolutionary perspective, the coracoid is particularly independent from the rest of the scapula, as has been discussed in the context of monotreme anatomy. In a developmental context, the coracoid arises from an independent growth plate compared to other regions of the scapula (Luo 2015; Young et al. 2019), but developmental genetic studies have indicated that the coraco-gleno-acromial region encompassing the whole shoulder joint of the scapula has unified gene patterning which differs from that of the blade and dorsal spine (Timmons et al. 1994; Pellegrini et al. 2001). There is also evidence that the coracoid may be morphologically integrated with the glenoid, but not with the acromion (Young 2004; Sears et al. 2013). Functionally, the relative length of the coracoid is associated with the size of the *m. coracobrachialis* involved in adduction of the humerus (Argot 2001; Sargis 2002; Salton & Sargis 2008), which is specifically associated with arboreality (Taylor 1974; Argot 2001; Sargis 2002). Given that it is anticipated that climbing animals are more likely to be claviculate and have an enlarged acromion, it is likely that they will exhibit enlargement of the coracoid in addition, but this does not necessarily indicate a relationship between acromion and coracoid prominence.

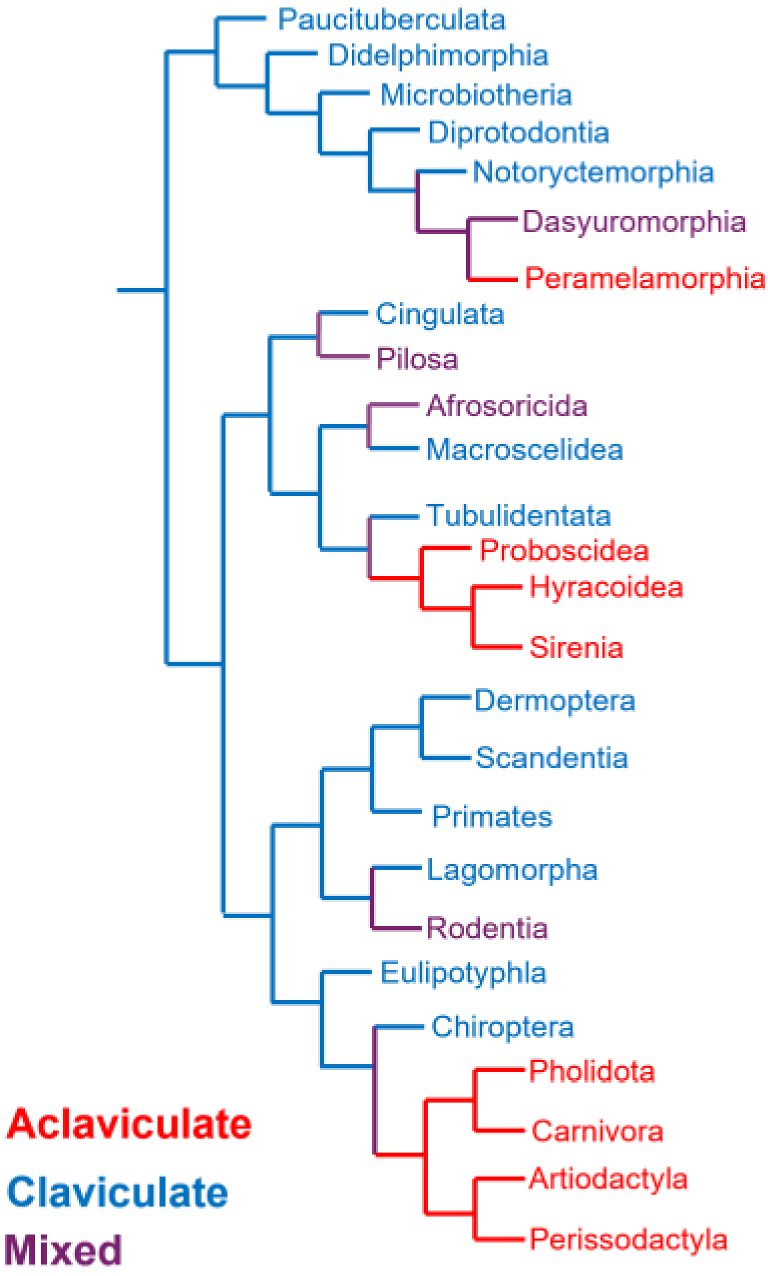


Figure III.3: Extant therian mammal orders and their clavicle condition
A diagrammatic representation of extant therian mammal phylogeny at order level, with colours indicating which groups are entirely claviculate (blue), entirely aclaviculate (red), or a combination (purple). Information from Jenkins (1974), Kingdon (2015), de Souza Junior et al. (2020), and references therein.

III.1.4. Locomotion behaviour

Hypothesis III.4 ($H_{III.4}$):

There will be significant morphological distinctions between functionally different locomotor groups.

Locomotion is a broad concept which is challenging to quantify, as has been thoroughly discussed in Chapter II. Previous studies have found numerous aspects of morphology functionally associated with locomotion behaviours (Maynard Smith & Savage 1956; Taylor 1974; Monteiro & Abe 1999; Argot 2001; Warburton 2003; Sears 2004; Cooper et al. 2007; Astúa 2009; Morgan 2009; Preuschoft et al. 2010; Gálvez-López 2014), and this is to be anticipated given the scapula's involvement in weight-bearing and stride production (Jenkins 1974; Fischer 1994; Schmidt et al. 2002). Different locomotion behaviours have very different functional requirements, placing different demands on the forelimb skeleton which may be reflected evolutionarily in skeletal morphology. For example, climbing is associated with the need to move the forelimb above the head within a complex 3D canopy environment, and to resist the tensile forces of raising the body upwards through the pectoral girdle (Oxnard 1968; Gálvez-López 2014). Digging, but especially truly subterranean movement, prioritises stability of the forelimb joints and powerful flexion of the shoulder joint in order to facilitate dragging large quantities of substrate backwards (Warburton 2003). Aquatic locomotion may take the form of pectoral oscillation in which the forelimbs must generate thrust through the water, or pelvic oscillation in which the caudal spine and hindlimbs generate thrust and the forelimbs must be both mobile and powerful to facilitate directional control against drag (Sanchez & Berta 2009; Pierce et al. 2011).

It is apparent that the scale of variation in the therian mammal scapula reflects the complex biomechanical demands which it must accommodate as a highly mobile functional element of the forelimb. Just how the numerous factors influencing scapular morphology act and interact and, therefore, how much of scapular morphology can be directly associated with locomotion behaviour, is explored in this chapter. The 201 species of extant therian mammals included have a wide diversity of locomotion profiles and body sizes, and are drawn from across the whole of extant therian mammal phylogeny. The 3D landmark configuration captures the shape of the scapula in high resolution, while the locomotion scoring matrix developed in Chapter II captures locomotor function in higher resolution than has previously been possible in functional morphology studies. Multivariate statistical methods, such as Principal Components Analysis (PCA) and phylogenetic regressions are utilised throughout this chapter in order to address the challenges of this complex dataset and begin to shed light on universal commonalities within the therian scapula. The results from this chapter provide the most comprehensive look to date at the various factors influencing mammalian scapula morphology, and what this implies about the possibility of inferring behaviour in extinct mammals from scapular remains.

III.2. Materials & methods

III.2.1. Data acquisition

III.2.1.1. Specimen acquisition

Specimens of 201 extant therian mammal species are included in this chapter (one specimen per species), representing 74% of all extant therian mammal families and subfamilies (where such taxonomic divisions exist). Details of each specimen are available in S.III.1.A. It should be noted that the thylacine (*Thylacinus cynocephalus*) is included despite having become extinct within the last 100 years. These species were selected entirely on the basis of availability and completeness of the scapulae, and were acquired from a variety of sources, predominantly MorphoSource (www.morphosource.org; accessed 2021-2024), Primate Research Institute (Kyoto University; KUPRI), Natural History Museum (London), University of Cambridge Museum of Zoology, and Muséum National d'Histoire Naturelle (Paris). From MorphoSource and KUPRI, several specimens were available to download as scapula surface files, but the majority were downloaded as CT data files (TIFF files) which were segmented in Avizo v. 9 (Thermo Fisher Scientific, Waltham, MA, USA) to extract a scapula surface file. Many specimens from the Natural History Museum (London) and the University of Cambridge Zoology Museum were scanned as surface files in-person using either an Artec Space Spider or Artec Leo structured light scanner (Artec 3D, Luxembourg), while all other specimens from these collections were CT scanned upon request in-house at the Natural History Museum and at the University of Cambridge. Specimens from the Muséum National d'Histoire Naturelle (Paris) were CT scanned at the University of Montpellier, courtesy of Dr Pierre-Henri Fabre and Dr Lionel Hautier. Scan resolution ranged from 1-120µm with a variable range of current intensity (up to 2000µA) and power (up to 450W) based on specimen size and preservation status.

Though it would have been preferable to control for body side by selecting only the right or left scapula for every specimen, this was not possible due to incompleteness and damage to specimens. For this reason, the right scapula was chosen where possible, but in all other cases the most complete scapula was used. Additionally, it was not possible to select specimens of only one sex due to lack of availability and due to this information often not being known for specimens. It is possible that there are effects of sexual dimorphism in some species which could not be taken into account. However, since only one specimen was included per species, intraspecific shape variation such as lateral asymmetry and sexual dimorphism should not affect these results and their ability to inform clade-wide morphological trends.

III.2.1.2. Scapula morphology

Geometric morphometrics is a methodology for quantifying and studying biological shape in Euclidean space using a Cartesian coordinate system. The principal workflow of GMM is as follows: the biological form is quantified using the coordinates of pre-defined loci (landmarks) on each specimen, the sets of coordinates are standardised against one another for comparison of shape only via Procrustes superimposition, multivariate analyses are performed to address the relevant research questions/hypotheses, and the results are interpreted accordingly (Bookstein, 1991).

III.2.1.2.1. Landmarking

All specimens were landmarked in 3D in Avizo v. 9. The landmark configuration comprises 19 true landmarks and seven curves which contain 52 semilandmarks, meaning a total of 71 landmarks were used in this study (Fig. III.4 & Table III.2). The choice of landmarks (a modified version of the configuration used in Gálvez-López 2014) was based on anatomical significance and overall shape representation, as well as repeatability. Information on repeatability testing carried out for this study can be found in Appendix III.1.

III.2.1.2.2. Procrustes superimposition

The goal of Procrustes superimposition is to ensure that only variation in shape is being assessed in further analyses. Once all specimens in the dataset are represented as landmark configurations, they still cannot be compared directly due to variation in scale, translation in Euclidean space and rotation. The most commonly accepted method for accomplishing this (and the one used here) is Generalised Procrustes Analysis (GPA; Gower, 1975), though alternatives have been proposed (e.g. Lele and Richtsmeier, 2001). GPA mathematically aligns the configurations by their centroid (the geometric centre of the shape), then rotates and scales them to minimise variation between configurations. Any variation between configurations still remaining can, therefore, be assumed to represent variation in shape only. GPA was carried out in R Statistical Environment (R Core Team 2025) using the *procSym* function in the package *Morpho* v. 2.12 (Schlager et al. 2017). The output set of coordinates is referred to throughout as the Procrustes coordinates, distinguished from the raw coordinates. Throughout this chapter, wireframes are provided to illustrate shape changes, mean shapes, etc. and these were acquired from MorphoJ v. 1.07a (Klingenberg 2011) following Procrustes superimposition.

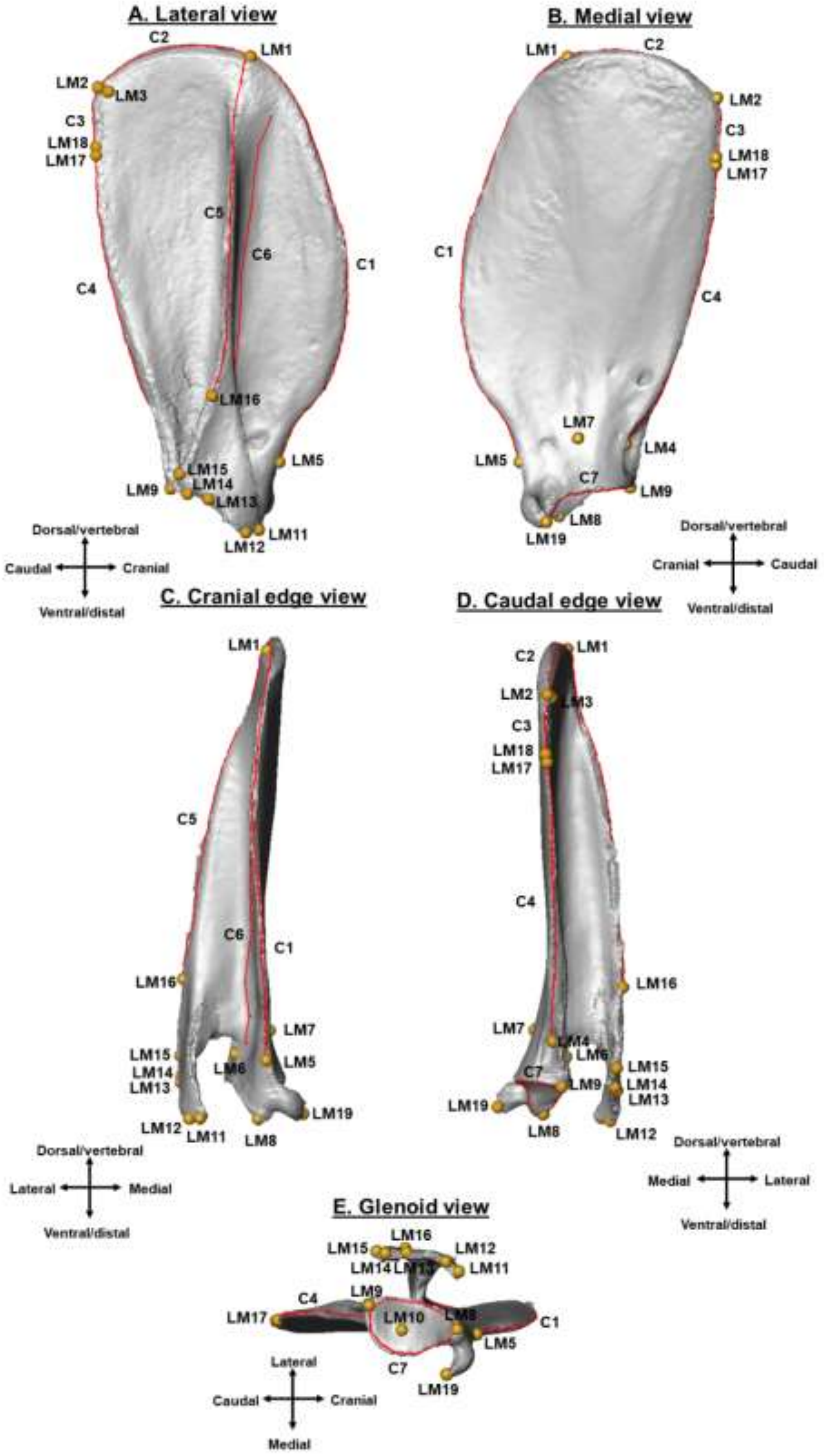


Figure III.4: Landmark configuration
Locations of the 19 true landmarks (shown as gold points) and the seven semilandmark curves (shown as red lines) used in this study. This landmark configuration is modified from Gálvez-López (2014).

Table III.2: Description of landmark placements

Anatomical description of each of the 19 true landmarks and the seven semilandmark curves used in this study. This landmark configuration is modified from Gálvez-López (2014).

Identifier	Type	Description
LM1	True landmark	Intersection between spine and vertebral border.
LM2	True landmark	Extreme of caudal angle.
LM3	True landmark	Caudal extent of infraspinous fossa at the caudal angle.
LM4	True landmark	Point of maximum curvature along caudal neck margin.
LM5	True landmark	Point of maximum curvature along cranial neck margin.
LM6	True landmark	Point of maximum curvature along lateral neck margin.
LM7	True landmark	Point of maximum curvature along medial neck margin.
LM8	True landmark	Cranialmost point of glenoid cavity.
LM9	True landmark	Caudalmost point of glenoid cavity.
LM10	True landmark	Deepest point of glenoid cavity.
LM11	True landmark	Cranialmost point of tip of hamatus process.
LM12	True landmark	Caudalmost point of tip of hamatus process.
LM13	True landmark	Point of maximum curvature between hamatus and suprahamatus processes.
LM14	True landmark	Ventralmost point of tip of suprahamatus process.
LM15	True landmark	Dorsalmost point of tip of suprahamatus process.
LM16	True landmark	Limit between acromion and spine.
LM17	True landmark	Ventralmost end of limit between *m. teres* and *m. subscapularis* origins.
LM18	True landmark	Dorsalmost end of limit between *m. teres* and *m. subscapularis* origins.
LM19	True landmark	Tip of coracoid process.

C1	Semilandmark curve	Curve representing cranial edge and cranial portion of vertebral border. Drawn from LM5 to LM1. Contains landmarks 20-29.
C2	Semilandmark curve	Curve representing caudal portion of vertebral border. Drawn from LM1 to LM2. Contains landmarks 30-34.
C3	Semilandmark curve	Curve representing border of *m. teres major* origin. Drawn from LM2 to LM18. Contains landmarks 35-37.
C4	Semilandmark curve	Curve representing caudal edge. Drawn from LM17 to LM4. Contains landmarks 38-44.
C5	Semilandmark curve	Curve representing lateral edge of spine. Drawn from LM16 to LM1. Contains landmarks 45-54.
C6	Semilandmark curve	Curve representing base of the spine. Drawn from glenoid end of spine where spine is distinguished laterally from the blade, to vertebral end of spine (when spine is no longer distinguished from blade). Contains landmarks 55-64.
C7	Semilandmark curve	Curve representing glenoid circumference. Drawn from LM8 to LM9 along the lateral border of the glenoid, then from LM9 to LM8 along the medial border. Contains landmarks 65-71.

III.2.1.3. Scapula centroid size

Size of the scapula was measured using centroid size, as is common practice in the literature. Values for centroid size (CS) are extracted during the GPA process for each specimen. These values reflect the true absolute sizes of the scapulae prior to scaling. Values for centroid size were transformed using natural log to obtain values of log centroid size (logCS). Both CS and logCS are used in some regressions to address the possibility of differential scaling, see Section III.2.2.1.1., but logCS is otherwise used.

III.2.1.4. Evolutionary history

The phylogeny used for this work was obtained from VertLife.org (Upham et al. 2019). Phylogenetic signal in scapular morphology (Bloomberg's K) and phylogenetic signal in the residuals (Pagel's lambda, λ) were assessed using the *physignal.*z function in the *geomorph* package in R. Throughout, a categorical variable representing taxonomic group is used. This divides the species into nine monophyletic clades: Afrotheria (n = 12), Xenarthra (n = 6), Euarchonta (n = 21), Glires (n = 38), Eulipotyphla (n = 6), Chiroptera (n = 26), Ferae (n = 34), Euungulata (n = 33), and Marsupialia (n = 25). This system of categorisation was chosen to avoid single-species groups (such as the order Macroscelidea), while retaining biologically informative phylogenetic divisions (for example, the superorder Euarchontaglires is divided into its composite grandorders, Euarchonta and Glires to avoid loss of information by combining so many species into one group).

III.2.1.5. Clavicle presence

For the purposes of this work, the clavicle is considered to be present if there is an osseous structure articulating with the acromion and manubrium, and absent if this is not the case. Within this dataset, 117 species are claviculate and 84 species are aclaviculate. This information was obtained from literature review (Trotter 1885; Jenkins 1974; Kingdon 2015; de Souza Junior et al. 2020).

III.2.1.6. Locomotion behaviour

The method for quantifying locomotion established in Chapter II was used here to obtain a scoring matrix and categorical variable specific to these 201 species. A full description of the process is provided in Appendix III.2. Following these results, eight clusters are used in this chapter: Aerial acrobats (n = 17), Aquatic (n = 23), Climbers (n = 38), Generalists (n = 50), Runners (n = 37), Subterranean (n = 7), Volant (n = 26; all chiropterans), and Other (n = 3 outliers).

III.2.2. Multivariate analyses

III.2.2.1. Phylogenetic linear regression models on Procrustes coordinates

Phylogenetic linear regressions on the Procrustes coordinates (described in Section I.4.3.), were used to interpret the relative significance and contribution to overall variation of several variables within a phylogenetic context. Eight variables are available for inclusion in the these models:

locom: locomotor group, a categorical variable with 8 levels.
clav: clavicle presence, a categorical variable with 2 levels.
logCS: log centroid size, a continuous variable.
swim, climb, dig, run & aerial: locomotion ability scores, continuous.

The locomotor ability variables (raw, not from the polychoric PC scores matrix) are treated as continuous variables for the purposes of these models, despite technically being ordinal in nature. This is justified following the method of Williams (2022) for determining if an ordinal variable is more appropriately treated as continuous or categorical in this context. In order to test this, a model was constructed for each ability scoring variable either as categorical or continuous, and the two models per ability were compared using AIC (Akaike’s Information Criterion) with the function *model.comparison* in the R package *RRPP* v. 2.1.0 (Collyer & Adams 2018; Adams & Collyer 2025). For all five scoring variables, the superior model is the one in which they are treated as continuous variables.

The locom categorical variable could not be included alongside the locomotor ability scoring variables because this would be circular and essentially include the same information twice (as the ability scores were used in order to construct the categorical variable). Therefore, two different models were produced, one containing locomotor group (**model1**) and one containing all the locomotor ability scores (**model2**). A model containing two-way interactions was also produced (**model3**). Many variables are correlated, such as climbing and aerial ability. Interactions could only be included for variables which are not correlated and for which an interaction in biologically interpretable. Therefore, the interactions of clavicle presence with logCS and ability scores which are not claviculate or aclaviculate specific are included (e.g. the interaction of aerial ability and clavicle presence is not investigated because all high scorers in aerial ability are claviculate).

III.2.2.1.1. Differential scaling

In order to assess potential differential scaling, phylogenetic linear models on the Procrustes coordinates were used including centroid size (CS) and log centroid size (logCS) as terms. Differential scaling refers to cases in which the allometric effect is different at different sizes, for example there may be a greater allometric effect in larger animals than smaller animals. This is interpreted by examining the effect size (Z) of both parameters in their regressions (modified from Gálvez-López 2014). Where the effect size is larger for the logCS term than CS, it demonstrates that log-scaling fits the data better than linear scaling, which implies that the allometric effect is greater in smaller animals, and vice versa.

III.2.2.2. Principal Components Analysis (PCA)

Overall shape variation in the dataset was investigated using Principal Components Analysis (PCA; described in Section I.6.2.). The resulting morphospace was visualised according to locomotor group, locomotor ability score gradients, taxonomic group, clavicle presence, and size (logCS) gradient.

III.2.2.2.1. Phylogenetic allometric regressions on PCs

The relationship between the PCs and size (represented by logCS), was investigated using phylogenetic generalised least squares (PGLS) regressions (described in Section I.6.2.). This makes it possible to interpret scapular shape changes associated with changes in size, while additionally interpreting the influence of phylogeny on these relationships via the output values of Pagel’s lambda (λ; Pagel 1999).

III.3. Results

III.3.1. Variation in scapular morphology

A broken-stick model showed that the first 11 principal components (PCs) are interpretable. PC1 and PC2 combined account for 55.5% of total shape variation in the sample (37.5% and 18.0%, respectively), while PC3 and PC4 only account for 8.8% and 7.6% of variation respectively. Furthermore, examination of the latter two PCs indicates that they do not show informative shape changes associated with any of the variables investigated in this chapter (locomotor group, taxonomic group, and clavicle presence). For these reasons, only shape change in PC1 and PC2 are discussed throughout the main text, while PC3 and PC4 are described in Appendix III.3.

Shape change on PC1 (37.5%; Fig. III.5) is mainly related to cranio-caudal width of the blade, and the relative sizes of the supraspinous and infraspinous fossae. At the **negative extreme of PC1**, we see a thin, elongate scapular shape, with significantly reduced infraspinous fossa relative to supraspinous fossa. The caudal edge is curved such that the border projects laterally in the plane of the spine, exposing the medial side of the scapula at this edge. The acromion is prominent and extends caudally and beyond the glenoid, and the spine is raised laterally out from the blade along its entire length. The neck is cranio-caudally thinner than the glenoid. The coracoid is short and extends medio-caudally inwards towards the joint. Meanwhile, at the **positive extreme of PC1**, the scapular blade is greatly expanded cranio-caudally. The infraspinous fossa is considerably larger than the supraspinous. While the acromion is clear and defined, it does not extend beyond the glenoid. Rather, it projects over the cranial edge. The spine is raised laterally out from the blade only from approximately the middle of its length at the glenoid end. The neck is cranio-caudally thicker than the glenoid. The coracoid extends medio-cranially away from the joint.

Shape change on PC2 (18.0%; Fig. III.5) appears to be primarily related to the relative prominence of the acromion and coracoid, the relative prominence and position of the caudal angle, the morphology of the vertebral border, and the dorso-ventral length of the scapula. At the **negative extreme of PC2**, the infraspinous fossa is enlarged relative to the supraspinous, with the caudal border being greatly elongated relative to the cranial, resulting in a prominent caudal angle. The acromion is very prominent, extending cranio-ventrally considerably beyond the glenoid. The spine is only slightly raised laterally out from the blade for much of its length at the vertebral end, only extending further out as it approaches the glenoid. The neck is cranio-caudally thicker than the glenoid. The coracoid is highly elongated and projects highly medio-caudally inwards towards the joint. **At the positive extreme of PC2**, the scapula is dorso-ventrally elongated, the infraspinous fossa is only marginally larger than the supraspinous, with the caudal angle located at approximately half the height of the blade such that the vertebral border is highly convex. While the acromion is clear and defined, it does not extend beyond the glenoid. The relatively distinct metacromion results in an appearance of the acromion projecting slightly caudally. The spine is raised laterally from the blade along its entire length. The neck is cranio-caudally thinner than the glenoid. The coracoid projects cranio-laterally away from the joint.

Overall, blade width and lateral fossa proportions, relative prominence and position of the caudal angle, prominence of the acromion process, and prominence of the coracoid process are the areas of the scapula which present the greatest variability.

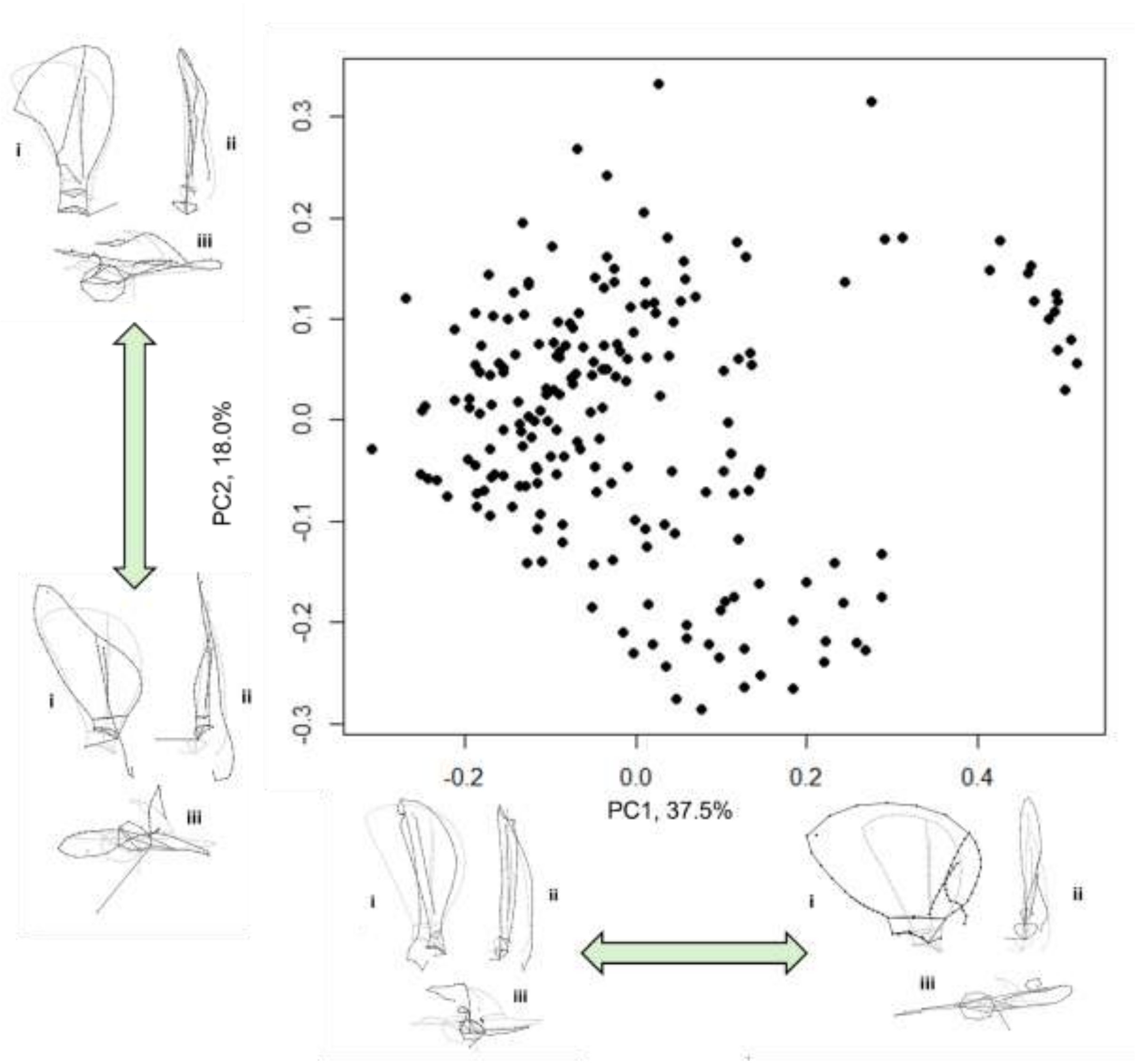


Figure III.5: PC1-PC2 morphospace with shape changes
Visualisation of the PC-PC2 morphospace (representing 55.5% of shape variation) with shape changes on each axis visualised as wireframes, each relative to the mean shape (grey). The wireframes are displayed in three views: i) lateral; ii) caudal; iii) glenoid.

III.3.2. Contributions of factors influencing scapular variation

There is a moderate phylogenetic signal in scapular morphology (Bloomberg's K = 0.46, $p = 0.001$), and a moderate to high signal in the residuals (Pagel's lambda, λ = 0.74). Therefore, the value of λ for each subsequent phylogenetic model on Procrustes coordinates is set to 0.74. A phylogenetic model (**model1**, Table III.3) was constructed including log centroid size of the scapula (logCS, continuous), clavicle presence (binary categorical), and locomotor group (8 level categorical) as predictors. The results show that all three variables significantly influence scapular morphology and, based on effect size (Z), locomotor group is the most influential, followed by clavicle presence, then logCS.

Table III.3: Results of the phylogenetic regression model1
This phylogenetic model of n = 201 species assesses the influence on Procrustes coordinates of three predictors: logCS (continuous), clavicle presence (binary categorical), locomotor group (8-level categorical). The table provides df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in ***bold italics*** *in green boxes.*

model1	df	SS	MS	R^2	F	Z	p-value
logCS	1	0.0014	0.0014	0.0142	3.209	2.928	***0.003***
Clavicle	1	0.0019	0.0019	0.0191	4.322	3.791	***0.001***
Locomotor group	7	0.0103	0.0015	0.1036	3.357	6.329	***0.001***
Residuals	191	0.0839	0.0004	0.8424			
Total	200	0.0996					

The results of **model1** show that scapular morphology significantly differs between locomotor groups, but this does not allow interpretation of contributions of locomotor abilities. In order to assess the influence of each locomotor ability, a new model was constructed which includes the ability scores (five continuous variables) and not the categorical locomotor group terms (**model2**, Table III.4). The results show that all locomotor abilities except swimming significantly influence scapular morphology, aerial ability most, followed by running, then climbing, then digging.

Table III.4: Results of the phylogenetic regression model2
This phylogenetic model of n = 201 species assesses the influence on Procrustes coordinates of seven predictors: logCS (continuous), clavicle presence (binary categorical), and five locomotor ability score variables (continuous). The table provides df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in ***bold italics*** *in green boxes.*

model2	df	SS	MS	R^2	F	Z	p-value
logCS	1	0.0011	0.0011	0.0111	2.482	2.443	***0.006***
Clavicle	1	0.0022	0.0022	0.0218	4.856	4.004	***0.001***
Swim	1	0.0003	0.0003	0.0033	0.741	-0.579	0.722
Climb	1	0.0010	0.0010	0.0105	2.341	2.228	***0.012***
Dig	1	0.0009	0.0009	0.0086	1.910	1.766	***0.04***
Run	1	0.0015	0.0015	0.0151	3.360	2.796	***0.002***
Aerial	1	0.0016	0.0016	0.0165	3.679	3.354	***0.001***
Residuals	193	0.0861	0.0004	0.8649			
Total	200	0.0996					

Finally, a phylogenetic model was constructed as **model2**, with the addition of four interaction terms: Clavicle*logCS, Clavicle*Climb, Clavicle*Dig, Clavicle*Run. These interactions were included on the basis of biological interpretability, as no other predictor interactions can be considered biologically or statistically interpretable. The results of this model (**model3**, Table III.5) show that all interaction terms except Clavicle*Climb significantly influence scapular morphology. Specifically, this shows that claviculate and aclaviculate species have different allometric trajectories, and different morphologies associated with digging and running behaviour. With the inclusion of these interactions, the main effect Dig is no longer significant as it was in **model2**. This means that the interaction term Clavicle*Dig is explaining variance previously attributed to Dig only, so digging ability does significantly influence scapular morphology but this effect differs in claviculate and aclaviculate taxa. Running ability is still a significant main effect, as well as having a significant interaction with clavicle presence. This means that running ability significantly influences scapular morphology generally, and this effect also differs between claviculate and aclaviculate taxa. Lastly, climbing ability is a non-significant main effect, though it was significant in **model2**, and also has a non-significant interaction with clavicle presence. The non-significance of the interaction is likely due to the taxonomic composition of the dataset – all but one of the aclaviculate climbers (scoring 3 or 4) are members of the group Ferae.

Therefore, this term cannot inform general conclusions about the influence of climbing ability on scapular morphology in claviculate versus aclaviculate taxa. This likely means that climbing ability as a main effect only appears significant in **model2** due to a combination of clavicle presence and phylogenetic influences.

Within this model, main effects of running and aerial ability have the highest effect sizes, followed by the interaction of clavicle presence and running ability, then the main effect logCS, then the interaction of clavicle presence and logCS. Other terms, even when significant, have low effect sizes (Z < 2.0), which indicates their effect is statistically identifiable but biologically small.

Table III.5: Results of the phylogenetic regression model3

This phylogenetic model of n = 201 species assesses the influence on Procrustes coordinates of seven main effect predictors: logCS (continuous), clavicle presence (binary categorical), and five locomotor ability score variables (continuous). Additionally, four interaction terms are included: the interactions of clavicle presence with logCS, climbing, digging, and running abilities. The table provides df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in ***bold italics*** *in green boxes.*

model3	df	SS	MS	R2	F	Z	p
logCS	1	0.0010	0.0010	0.0101	2.303	2.114	***0.017***
Clavicle	1	0.0009	0.0009	0.0091	2.068	1.970	***0.031***
Swim	1	0.0003	0.0003	0.0027	0.604	-1.092	0.865
Climb	1	0.0005	0.0005	0.0051	1.172	0.643	0.268
Dig	1	0.0007	0.0007	0.0067	1.534	1.243	0.109
Run	1	0.0020	0.0020	0.0197	4.495	3.492	***0.001***
Aerial	1	0.0017	0.0017	0.0170	3.882	3.366	***0.001***
Clavicle*logCS	1	0.0010	0.0010	0.0096	2.186	2.041	***0.016***
Clavicle*Climb	1	0.0006	0.0006	0.0057	1.305	0.869	0.201
Clavicle*Dig	1	0.0008	0.0008	0.0084	1.904	1.788	***0.039***
Clavicle*Run	1	0.0011	0.0011	0.0113	2.586	2.533	***0.004***
Residuals	189	0.0825	0.0004	0.8286			
Total	200	0.0996					

III.3.3. Size and allometry

According to the results of the phylogenetic models **model1-3**, logCS significantly influences scapular morphology across therians. Modelling the influence of logCS as the only predictor variable (**model4**, Table III.6) supports the significant influence of logCS on scapular morphology (*p = 0.001*, Z = 4.03). Visualising the shape change associated with logCS is achieved by extracting the regression scores from this model (Drake & Klingenberg 2007), and this shows that cetaceans and chiropterans are outliers in this allometric context (Fig. III.6A). Excluding these groups from the model (**model4b**, Table III.6) produces a higher effect size, indicating that inclusion of these groups within the model partially obscures the degree to which logCS influences scapular morphology in other groups. Comparison of effect size (Z) in **model4b** (log centroid size, logCS) and **model4c** (raw centroid size, CS), which both exclude cetaceans and chiropterans, indicates differential scaling in which the allometric effect is greater in smaller taxa (Z is higher in the logCS model).

Table III.6: Results of the phylogenetic regression model4
*These phylogenetic models assess the influence on Procrustes coordinates of: **model4**, logCS across all species (n = 201); **model4b**, logCS excluding cetaceans and chiropterans (n = 160); **modelc**, raw centroid size (CS) excluding cetaceans and chiropterans. The tables provide df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in **bold italics** in green boxes.*

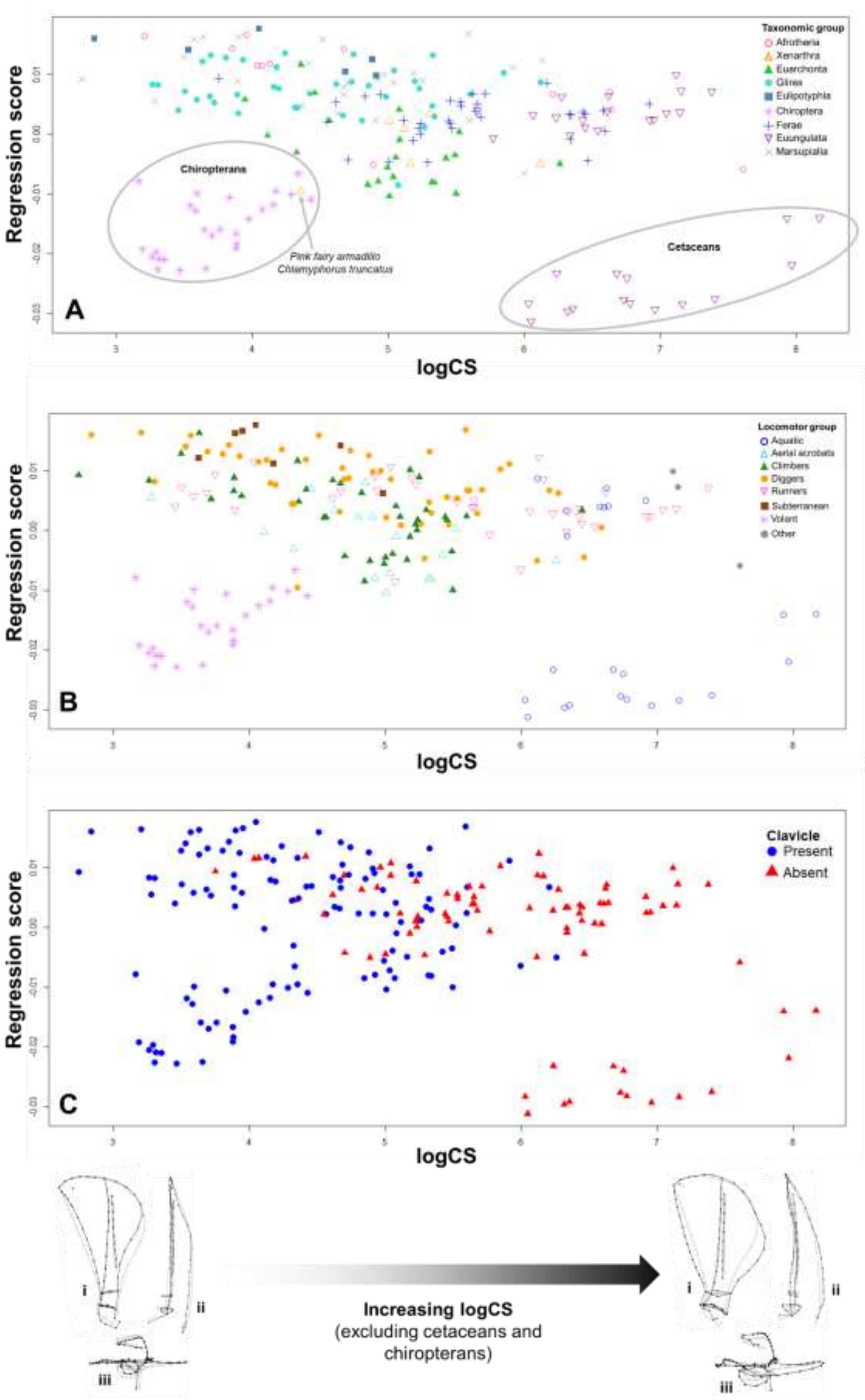
model4	df	SS	MS	R^2	F	Z	p
logCS	1	0.0027	0.0027	0.0272	5.562	4.034	***0.001***
Residuals	199	0.0969	0.0005	0.9728			
Total	200	0.0996					

model4b	df	SS	MS	R^2	F	Z	p
logCS	1	0.0027	0.0027	0.0379	6.219	4.422	***0.001***
Residuals	158	0.0685	0.0004	0.9621			
Total	159	0.0711					

model4c	df	SS	MS	R^2	F	Z	p
CS	1	0.0019	0.0019	0.0265	4.294	3.703	***0.001***
Residuals	158	0.0693	0.0004	0.9736			
Total	159	0.0711					

Returning to Fig. III.6, it can be seen that, excluding cetaceans and chiropterans, increased scapular size is generally associated with increased blade width, elongation of the vertebral border, enlargement of the glenoid fossa, acromion reduction, coracoid reduction and cranialisation, and increased infraspinous dominance. It is worth noting that the greatest shape variation (variation in regression score) occurs around mean scapular size (logCS = 5.0-6.0). This is also related to differences in taxonomic group – euarchontans around the mean size generally have the lowest regression scores (wider blade etc.), while terrestrial ungulates (the largest terrestrial taxa) have lower regression scores than many euarchontans. These differences in allometry between taxonomic, locomotor, and clavicle presence groups is explored further using pairwise comparisons with the *pairwise* function in the *RRPP* v.2.1.2 *package* in R.

Figure III.6: Shape change associated with increased logCS
Visualisation of regression score against log centroid size (logCS). Visualised by A) taxonomic group, B) locomotor group, and C) clavicle presence. Cetaceans and chiropterans are highlighted in A). Shape changes on each axis are visualised as wireframes, each relative to the mean shape (grey). The wireframes represent shape change in the dataset excluding cetaceans and chiropterans. They are displayed in three views: i) lateral; ii) caudal; iii) glenoid.


A
Regression score
logCS
0.01
0.00
-0.01
-0.02
-0.03
3
4
5
6
7
8
Taxonomic group
Afrotheria
Xenarthra
Euarchonta
Glires
Eulipotyphla
Chiroptera
Ferae
Euungulata
Marsupialia
Chiropterans
Cetaceans
Pink fairy armadillo
Chlamyphorus truncatus
B
Locomotor group
Aquatic
Aerial acrobats
Climbers
Diggers
Runners
Subterranean
Volant
Other
C
Clavicle
Present
Absent
i
ii
iii
Increasing logCS
(excluding cetaceans and chiropterans)

It can be seen in Fig. III.7 that logCS has a significant role in the arrangement of the PC1-PC2 morphospace. Investigating the relationships between principal components (PCs) and size using PGLS linear regressions (with the function *pgls* in the *caper* v.1.0.4 package in R) (Table III.7) makes it possible to interpret how the dominant shape variations in the scapula are related to size variation. LogCS is used here since, at such a broad size range, log transformation allows for more interpretable trends. PC1 and PC2 are explored in the main text, but results for PC3 and PC4 can be found Appendix III.2. These results, along with the visualisation of logCS gradients in the PC1-PC2 morphospace (Fig. III.7) indicate that much of scapular variation is attributable to influences of size. Results excluding cetaceans and chiropterans are also provided as it is apparent in Fig. III.6 that these two groups have different allometric trends from the rest of the dataset, and may influence relationships of these two PCs with logCS in ways which affect interpretation. These results within the PC1-PC2 morphospace support the findings established from Fig.III.6 – that increased scapula size (excluding cetaceans and chiropterans) is associated with increased blade width, elongation of the vertebral border, enlargement of the glenoid fossa, acromion reduction, coracoid reduction and cranialisation, and increased infraspinous dominance.

Table III.7: Results of the allometric PGLS regressions on PC1 and PC2

*Results of linear PGLS regressions of the first two PCs against log centroid size (logCS). Results are provided including all specimens, excluding cetaceans, excluding chiropterans, and excluding both cetaceans and chiropterans. The tables provide number of specimens (n), p-values, effect sizes (R^2), and Pagel's lambda (λ). Significant p-values are indicated in **bold italics**.*

	n	R^2	Pagel's lambda (λ)	p-value
a. PC1, all species	201	0.005	0.98	0.200
b. PC1, excl. cetaceans	186	0.048	0.98	***0.002***
c. PC1, excl. chiropterans	175	0.024	0.97	***0.020***
d. PC1, excl. cetaceans and chiropterans	160	0.110	0.91	***<0.001***
e. PC2, all species	201	0.065	0.96	***<0.001***
f. PC2, excl. cetaceans	186	0.051	0.97	***0.001***
g. PC2, excl. chiropterans	175	0.043	0.93	***0.003***
h. PC2, excl. cetaceans and chiropterans	160	0.030	0.94	***0.020***

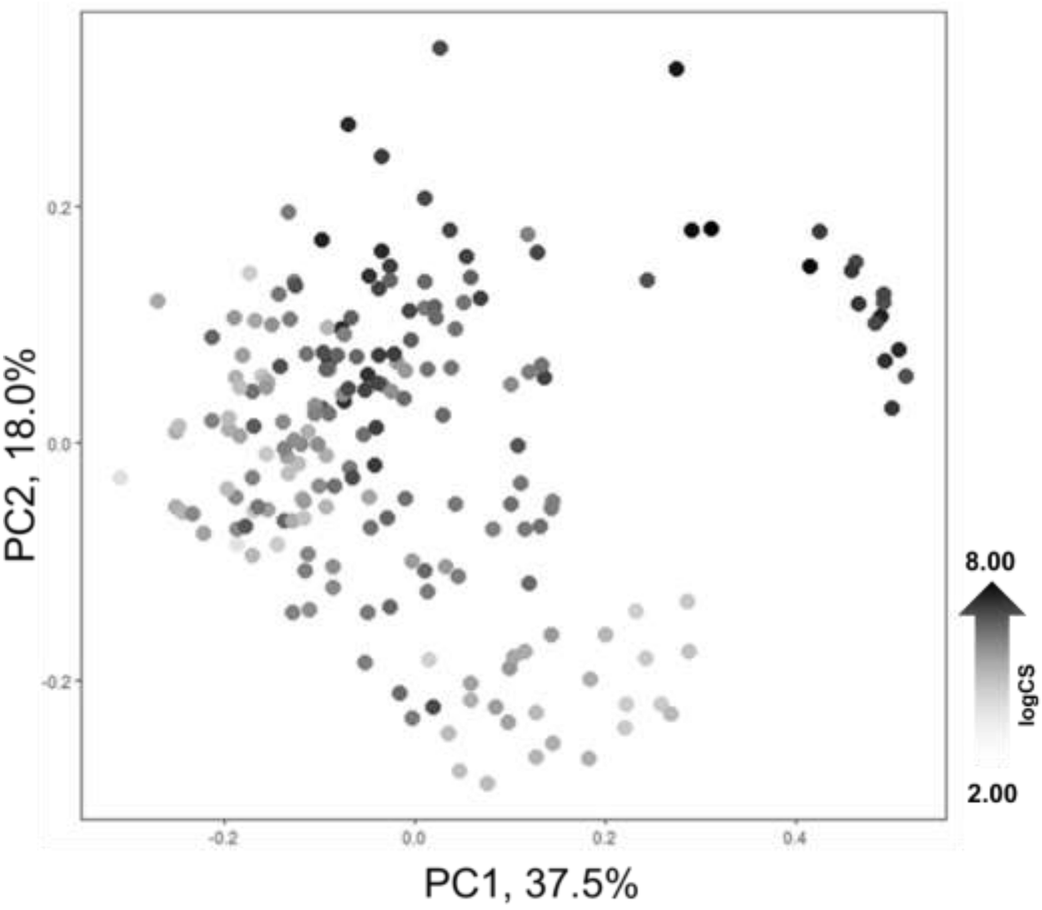


Figure III.7: Size gradient in the PC1-PC2 morphospace
Visualisation of the PC1-PC2 morphospace, coloured in a gradient according to the value of log centroid size (logCS).

Phylogenetic regression on the Procrustes coordinates was carried out with models investigating the interactions of logCS with locomotor group (**model5** and **model5b** in S.III.2.A) and clavicle presence group (**model6** and **model6b** in S.III.2.B). This was followed by pairwise comparisons of the regression slopes for the categories in each group (full results can be found in S.III.2), testing for significant differences in magnitude of the allometric scaling and significant differences in slope angle. Whether cetaceans are included within the aquatic category or separated into their own category, shape variation is significantly related to logCS, locomotor group and the interaction of the locomotor group with logCS, with consistently higher effect sizes (Z) when cetaceans are treated separately from other aquatic taxa. When cetaceans are included in the aquatic category, the **aquatic** trend is significantly different in the magnitude of the allometric scaling from those of **climbers** (*$p = 0.029$*), **generalists** (*p = 0.038*), and the outliers category, **other** (*p = 0.025*). None of these groups have a significantly different orientation from the aquatic group. When **cetaceans** are separated into their own category, it becomes clear that they were driving the results of the aquatic group – it is **cetaceans** specifically which exhibit a trend with significantly different magnitudes of allometric shape change from those of **climbers** (*p = 0.004*), **aerial acrobats** (*p = 0.031*), **generalists** (*p = 0.003*), and **other** (*p = 0.034*), as well as **runners** (*p = 0.023*). **Cetaceans** also have a significantly different allometric orientation from **generalists** (*p = 0.043*). However, the **non-cetacean aquatic** group is only significantly different in magnitude from **other** (*p = 0.031*), but is different in trajectory orientation from **climbers** (*p = 0.011*) and **generalists** (*p = 0.047*). The outlier group, **other**, is significantly different in magnitude from **runners**, **subterranean**, and **volant** groups, as well as having a significantly different orientation from **volant** taxa. However, this is a very small group (n = 3) which does not reflect a distinct locomotion repertoire, so these results are not biologically interpretable. Regarding clavicle presence, the interaction of clavicle presence and logCS has a significant influence on scapular morphology, but **claviculate** and **aclaviculate** taxa do not exhibit significantly different magnitudes of allometric change or orientation. This is the case whether cetaceans and chiropterans are included or not. This most likely indicates a difference in allometry between **claviculate** and **aclaviculate** taxa which was not explicitly measured here, such as intercept or position in shape space.

In order to compare allometry in different taxonomic groups, it was necessary to perform a regression on the Procrustes coordinates outwith a phylogenetic framework, using *procD.lm* functions (S.III.2.C). Cetaceans were separated from the terrestrial ungulates for these analyses. The results show that the majority of pairwise taxonomic group comparisons of allometric change magnitude are significant, but relatively few comparisons of orientation are significant (specifically, Afrotheria vs. Cetaceans *p = 0.007*; Afrotheria vs. Chiroptera *p = 0.001*; Euarchonta vs. Cetaceans *p = 0.01*; Cetaceans vs. Marsupialia *p = 0.026*). Notably, cetaceans are the most consistently different from other taxonomic groups.

III.3.4. Evolutionary history

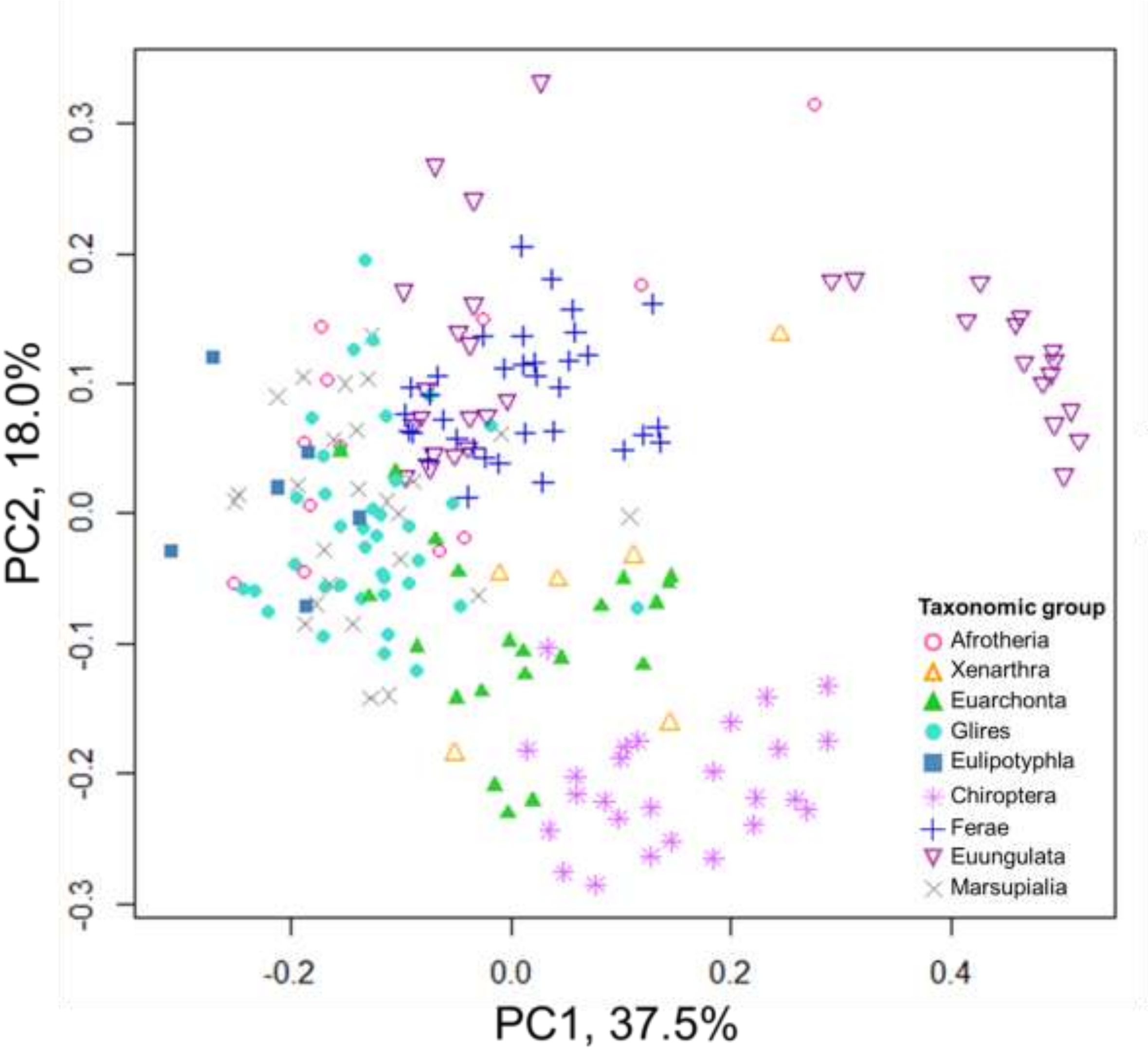


Figure III.8: PC1-PC2 morphospace visualised by taxonomic group
PC1-PC2 morphospace visualisation with points differentiated into the nine taxonomic groups.

The phylogenetic signal in scapular morphology was found to be moderately strong (Bloomberg's K = 0.46, Z = 19.82), in line with the prediction of **$H_{III.2}$**. Fig. III.8 shows the PC1-PC2 morphospace with taxa assigned to the nine monophyletic taxonomic groups outlined above, showing that several taxonomic groups are constrained to specific areas of the morphospace, though there is considerable overlap. **Ferae** are notably constrained to the upper part of the centre of the morphospace, being aclaviculate but otherwise morphologically close to the mean shape. **Euungulata** (also aclaviculate) are all located in the upper portion of PC2, but are divided into an aquatic component (cetaceans) which are almost entirely isolated at the high end of PC1, and a terrestrial component (terrestrial Artiodactyla and Perissodactyla) slightly below the centre of PC1. While the terrestrial ungulates' position just below the centre of PC1 indicates that their scapular blade is approximately average in width or slightly thinner than the mean shape, the variation of position in the upper half of PC2 indicates that there is considerable variation in the morphology of the vertebral border.

Reflecting their vast disparity in body shapes, the **Afrotheria** are distributed relatively widely around the morphospace, though they are constrained to the upper two thirds of PC2. The majority of afrotherians have a highly constrained position at approximately -0.2 on PC1 with considerable spread around the centre of PC2, representing slim scapulae with variable vertebral border morphology. These afrotherians, however, are not unusual in this morphology as many marsupials, Glires, and eulipotyphlans are also found in this region. There are some notable afrotherian outliers, though. The most obvious is the African elephant (*Loxodonta africana*) which is high on both PC1 and PC2, existing alone in this region of the morphospace, which represents a wide scapular blade which is dominated by the infraspinous fossa, and in which the caudal angle is highly ventral so that the highest point of the blade is where the scapular spine meets the vertebral border. Its next closest afrotherian is the tree hyrax (*Dendrohyrax dorsalis*), both phylogenetically and in the morphospace. The hyrax is found associated with the Ferae, relatively high on PC1 thanks to its wide scapular blade (which is infraspinous dominated) but, unlike the elephant, the caudal angle represents the highest point of the blade (though this is subtle). Also associated with the Ferae, as well as the terrestrial Euungulata, is the dugong (*Dugong dugon*) which is much higher on PC2 than its fellow sirenian, the manatee (*Trichechus manatus*). This represents a difference in vertebral border morphology: the dugong has a longer and more curved vertebral border in which the caudal angle is lower than the vertebral end of the scapular spine, whereas the manatee has a shorter vertebral border in which the caudal angle is the highest point. Closely associated with the manatee is the aardvark (*Orycteropus afer*). Lastly, one species with the lowest values on PC1 is the golden mole (*Amblysomus hottentotus*) which is closely associated with other subterranean species thanks to its very slim scapular blade. **Eulipotyphla** are also all located in this region low on PC1, and around the centre of PC2, representing slim scapular blades and some variation in vertebral border morphology but centred closely around the mean shape.

The **Xenarthra** are mostly located around the centre of PC1 and just below the centre of PC2. This represents claviculate scapulae close to the mean shape. However, there are some noticeable outliers: the giant anteater (*Myrmecophaga tridactyla*) which is closest of any species to the cetacean region of the morphospace, and the two armadillos (*Cabassous chacoensis* and *Chlamyphorus truncatus*) which are closely associated with the Chiroptera.

The **Euarchonta**, which are all claviculate, are found from low on PC1 and central on PC2, to central on PC1 and low on PC2. Many have scapulae very similar to the mean claviculate shape (Fig. III.9), but there are some key outliers. Firstly, the chimpanzee (*Pan troglodytes*), common squirrel monkey (*Saimiri sciureus*) and white-fronted capuchin (*Cebus albifrons*), which are associated with the morphospace of the Chiroptera. Secondly, the highest euarchontan on PC2 is the large treeshrew (*Tupaia tana*), one of only two euarchontans in the dataset which are not primates (the other being the Philippine flying lemur [*Cynocephalus volans*]).

Marsupialia and **Glires** overlap almost entirely within the morphospace, being found in a large region in the negative half of PC1. This broadly represents slim scapular blades with considerable variation in vertebral border morphology and variation in clavicle presence (though the majority are claviculate). There are, however, two interesting outliers – the marsupial red kangaroo (*Macropus rufus*) and the springhare (*Pedetes capensis*) within Glires, which will be discussed further below with regards to their unusual locomotion behaviour.

The **Chiroptera** are also noteworthy, being located lower on PC2 than the other groups (in part due to all being claviculate), and in the upper portion of PC1. This represents a relatively wide scapula with infraspinous dominance to varying degrees, and importantly, with a caudal angle that is very prominent relative to the rest of the vertebral border.

III.3.5. Clavice presence

It is clear from **model1-3** that clavicle presence has a significant influence on scapular morphology, having the largest effect size in **model2** when no interactions are included. It can be seen in **model8** (Table III.8) that, in isolation from other predictors, clavicle presence significantly affects scapular morphology, supporting the influence of this main effect. It was also clear in **model3**, which included several interaction terms with clavicle presence, that the significant influence of clavicle presence on scapular morphology is related to differences in morphologies associated with allometry and locomotion abilities between claviculate and aclaviculate taxa.

Table III.8: Results of the phylogenetic regression model8
This phylogenetic model of n = 201 species assesses the influence on Procrustes coordinates of clavicle presence, a binary categorical variable (claviculate n = 117, aclaviculate n = 84). The table provides df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in ***bold italics*** *in green boxes.*

model8	df	SS	MS	R2	F	Z	p-value
Clavicle	1	0.0040	0.0040	0.0397	8.236	4.804	***0.001***
Residuals	199	0.0956	0.0005	0.9603			
Total	200	0.0996					

The arrangement of the PC1-PC2 morphospace is greatly influenced by presence or absence of the clavicle. In fact, the distinction between claviculate (n = 117) and aclaviculate taxa (n = 84) on PC2 is quite striking (Fig. III.9), with claviculate species in the lower half and aclaviculate species in the upper half (though it is important to note an area of overlap between -0.02 and 0.14 on PC2, the densest and most taxonomically varied area of the morphospace). Based on this, there appear to be some key features of the morphology which generally distinguish claviculate and aclaviculate taxa:

i) In the claviculate condition, the acromion is prominent and enlarged, extending beyond the glenoid, while it is reduced and may be essentially absent in the aclaviculate condition.

ii) The morphology of the vertebral border differs between claviculate and aclaviculate taxa. Specifically, in claviculate taxa the caudal angle tends to be the (dorsally) highest point of the scapula, with the cranial portion of the vertebral border sloping down considerably. Meanwhile, in the aclaviculate taxa, the highest point of the blade tends to be approximately at the point where the scapular spine meets the border, and both the caudal and cranial portions of the border slope down.

Beyond these specific aspects, there appears to be substantial variation in morphology within the claviculate and aclaviculate groups which is not explained by the presence or absence of the clavicle.

Clearly, the presence or absence of the clavicle has an impact on scapular morphology and, fully in line with **$H_{III.3}$**, this differentiation is primarily related to differences in acromion process prominence. It was also anticipated that enlargement/reduction of the acromion may be associated with equivalent changes to the coracoid, especially in climbers. This appears to be the case specifically in claviculate species with high climbing ability only (climbers, aerial acrobats and volant species) which have an enlarged coracoid that is directed caudally towards the joint. There does not appear to be an overall association between the acromion and coracoid processes, however, as other claviculate groups exhibit mean coracoid size or reduced coracoids which tend to be directed cranially.

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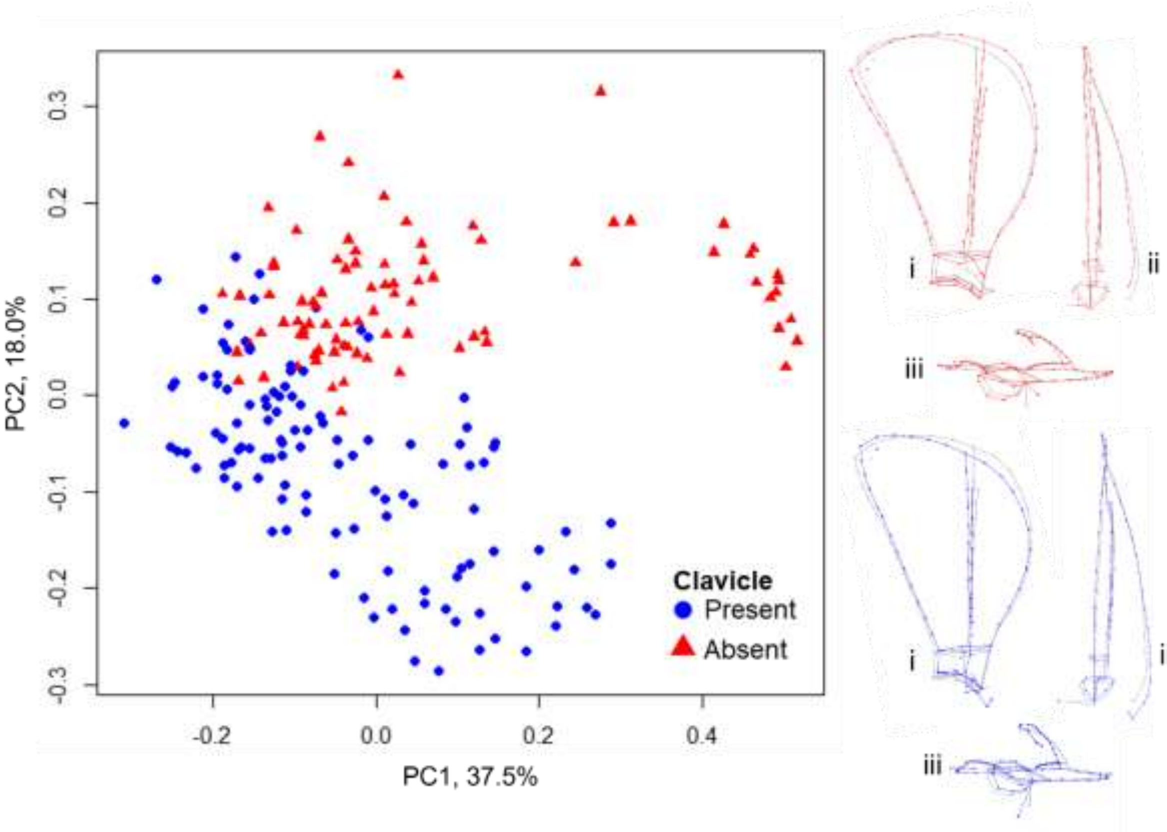


Figure III.9: PC1-PC2 morphospace visualised by clavicle presence
PC1-PC2 morphospace visualisation with points differentiated into claviculate (blue circles) and aclaviculate (red triangles) species. On the right are the mean shapes for claviculate (blue, below) and aclaviculate (red, above) taxa, relative to the overall mean shape in the dataset (grey). The wireframes are displayed in three views: i) lateral; ii) caudal; iii) glenoid.

III.3.6. Locomotion behaviour

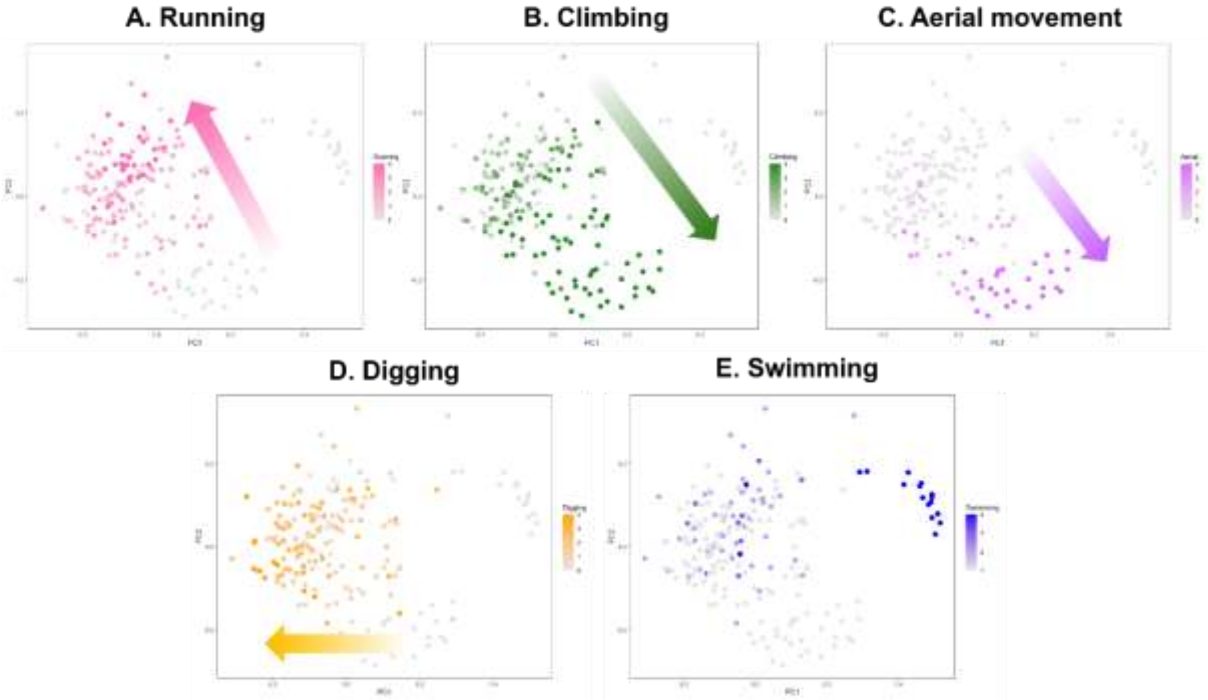


Figure III.10: PC1-PC2 morphospace visualised with locomotor ability gradients
Visualisation of the PC1-PC2 morphospace with points coloured in gradients according to the species' locomotor ability score in each scoring category. Arrows loosely indicate ability gradients.

Finally, in order to address the principal question of this chapter, we now consider how locomotion behaviour influences scapular morphology. In **model1** it was found that different locomotor groups exhibit significantly different scapular morphologies (*p = 0.001*), with this term having a stronger effect (Z) than logCS or clavicle presence. In **model2** the scores for the five locomotor abilities are included as separate terms, and climbing, digging, running and aerial behaviour are significantly related to scapular morphology (*p = 0.012, 0.040, 0.002, 0.001* respectively), though swimming is not (p = 0.722). Aerial ability has the largest effect size in the model apart from clavicle presence, while digging has a relatively low effect size. In single-term models (**model9-13**, Table III.9), all five locomotor abilities are significantly related to scapular morphology, with aerial movement having the largest effect size, followed by digging, then climbing, running, and swimming with the lowest. This indicates that, particularly swimming ability, does not have an independent influence on scapular morphology because it is highly related to other predictors in **model2**. Similarly, digging ability significantly influences scapular morphology but the effect is linked to other predictors.

Table III.9: Results of the phylogenetic regression model9-13
These phylogenetic models of n = 201 species assesses the influence on Procrustes coordinates of each of the five locomotor ability scores as single terms. The tables provide df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in ***bold italics*** *in green boxes.*

model9	df	SS	MS	R^2	F	Z	p
Swimming	1	0.0010	0.0011	0.0110	2.215	1.996	***0.024***
Residuals	199	0.0985	0.0005	0.9890			
Total	200	0.0996					

model10	df	SS	MS	R^2	F	Z	p
Climbing	1	0.0026	0.0026	0.0263	5.376	3.854	***0.001***
Residuals	199	0.0970	0.0005	0.9737			
Total	200	0.0996					

model11	df	SS	MS	R^2	F	Z	p
Digging	1	0.0031	0.0031	0.0310	6.366	4.223	***0.001***
Residuals	199	0.0965	0.0005	0.9690			
Total	200	0.0996					

model12	df	SS	MS	R^2	F	Z	p
Running	1	0.0024	0.0024	0.0240	4.894	3.647	***0.001***
Residuals	199	0.0972	0.0005	0.9760			
Total	200	0.0996					

model13	df	SS	MS	R^2	F	Z	p
Aerial	1	0.0038	0.0038	0.0384	7.947	4.539	***0.001***
Residuals	199	0.0958	0.0005	0.9616			
Total	200	0.0996					

Locomotor behaviour also influences the arrangement of the PC1-PC2 morphospace. There are some identifiable behavioural gradients within the morphospace (Fig. III.10). In particular, there is a relatively clear gradient of **climbing ability** associated with decreasing PC2 and increasing PC1; that is, increasing climbing ability is associated with increasing blade width (though not to the extreme of cetaceans), increasing infraspinous fossa dominance, and increasing prominence of the caudal angle, as well as increased prominence of the acromion and coracoid processes. This gradient is also closely associated with the **aerial movement ability** gradient due to the close behavioural association between climbing and aerial behaviour. There is also evidence of a gradient of **running ability** in the opposite direction to that of climbing ability. This indicates that increased running ability is associated with small decreases in scapular width and infraspinous dominance, and decreasing prominence of the caudal angle such that the highest point of the blade (dorsally) is approximately where the scapular spine meets the vertebral border. **Digging ability**, meanwhile, appears to loosely increase as PC1 decreases, indicating some association between increased digging ability and decreasing blade width with increasing supraspinous dominance. Finally, there is no obvious **swimming ability** gradient in the PC1-PC2 morphospace, due to the cetaceans exhibiting notably different morphologies from the other aquatic taxa, as will be discussed further.

When the morphospace is visualised with the eight different locomotor groups produced from the scoring matrix (Fig. III.11), some groups are constrained to certain areas of the morphospace, but there is considerable overlap in most cases. It is important to note that, as was highlighted previously, the fact that some locomotor groups are entirely claviculate (e.g. volant) or aclaviculate (e.g. aquatic) affects their position in the morphospace, and in cases where a locomotor group contains claviculate and aclaviculate taxa, the aclaviculate taxa still tend to be higher on PC2.

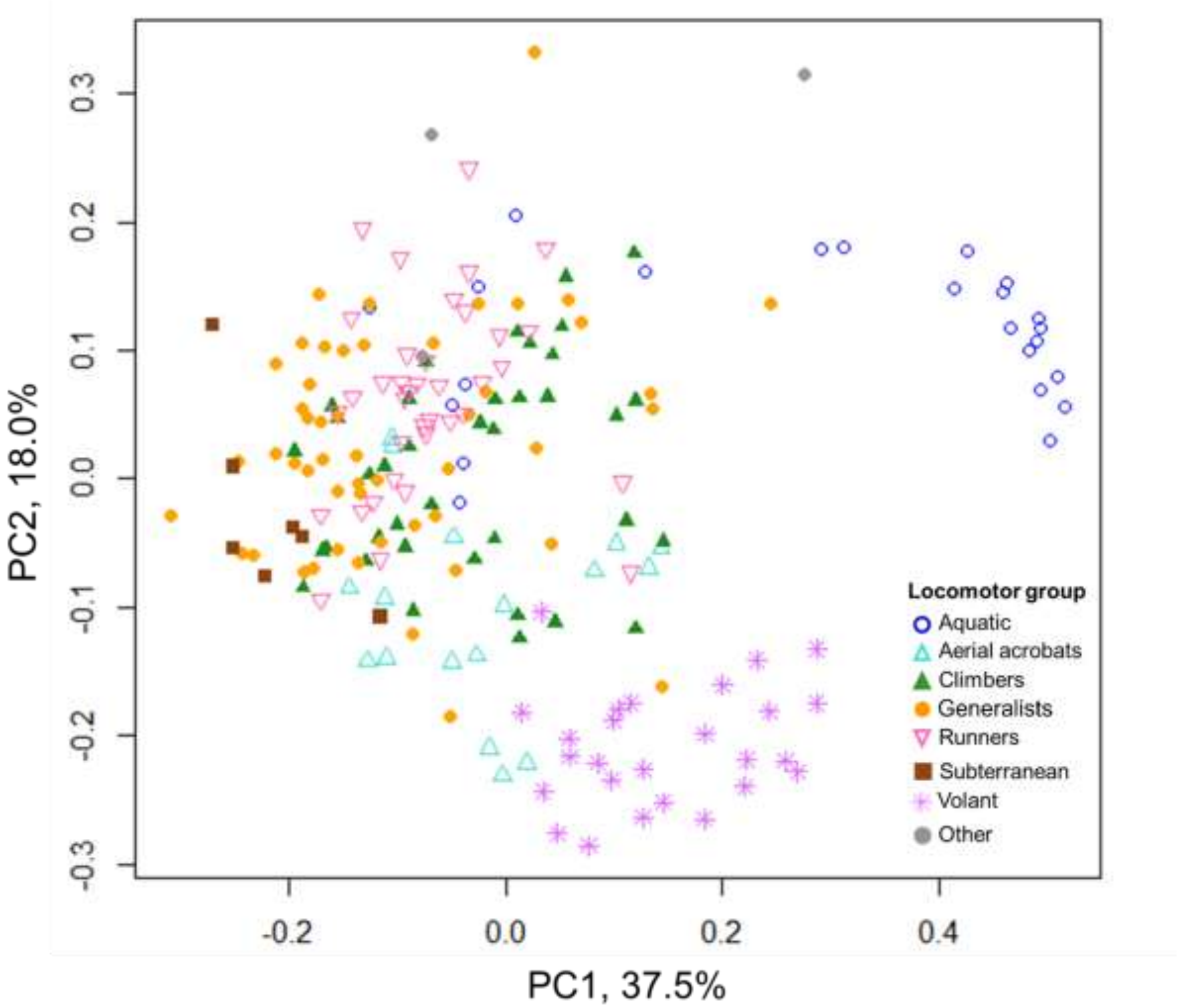


Figure III.11: PC1-PC2 morphospace visualised by locomotor group
PC1-PC2 morphospace visualisation with points differentiated into the eight locomotor groups generated by cluster analysis.

The **aquatic** group is noteworthy in that it is separated into two areas of the morphospace, both in the upper portion of PC2 due to being aclaviculate: aquatic ungulates (cetaceans) are located high on PC1 and almost isolated from the rest of the dataset, while all the other aquatic species are located mostly around the centre of PC1. The cetaceans are at the highest end of PC1 due to their particularly wide scapular blade which is dominated by the infraspinous fossa, while the other aquatic species have slimmer scapular blades which are generally not dominated by the infraspinous fossa and may have a larger supraspinous instead (the exception being the two phocids, *Leptonychotes weddellii* and *Erignathus barbatus*, which are the highest on PC1 of the non-cetacean aquatic species, having larger infraspinous fossae). The variation in position of the non-cetacean aquatic species in the upper portion of PC2 indicates considerable variation in vertebral border morphology. While all the aquatic species in the dataset are aclaviculate, a key difference between cetaceans and other aquatic species is that cetaceans exhibit a prominent, cranially-oriented acromion, while the other aquatic species have reduced acromion processes.

The **volant** group is represented entirely by Chiroptera, whose position in the morphospace has been discussed above. Three euarchontan **aerial acrobats** are located adjacent to the volant species: the chimpanzee (*Pan troglodytes*), the common squirrel monkey (*Saimiri sciureus*) and the white-fronted capuchin (*Cebus albifrons*). The rest of the aerial acrobats are distributed around the centre of PC1 and across the lower portion of PC2 due to all being claviculate. Aerial acrobats overlap considerably with **climbers**, which share a morphospace region with the majority of the other species. However, when climbers, aerial acrobats and volant species are considered in isolation from the other species, evidence of a morphological gradient from climbers through aerial acrobats to volant species emerges, which would reflect an anticipated behavioural gradient. Specifically, this morphological gradient has three main features: as aerial ability increases from climbers to volant, i) the coracoid process becomes longer and is directed more caudally, ii) the acromion process becomes more cranial, and iii) the caudal angle becomes more prominent.

Runners are relatively constrained on PC1, almost all lying between 0.0 and -0.2, but are spread across the upper two thirds of PC2. This reflects an intermediately slim scapular blade with some supraspinous dominance or approximately equal fossae, and considerable variation in the prominence of the caudal angle relative to the rest of the vertebral border. Notably, claviculate runners are located lower on PC2 than their aclaviculate counterparts (which are in the majority) and have generally a more prominent caudal angle. There are two runners which appear to be outliers from the main runners group: the red kangaroo (*Macropus rufus*) and the springhare (*Pedetes capensis*). These two species are located higher on PC1 than the other runners, and deep within the climbing-volant gradient, which is associated with wider scapular blade and increased infraspinous dominance. This is particularly noteworthy because these two species are the most bipedal animals in the dataset, both being ricochetal with their forelimbs largely not involved in locomotion behaviour. Their particular scapular morphology is thus likely associated to the grasping function of their forelimbs, which they share with climbing species.

The relatively few **subterranean** species are all found at the low end of PC1 and mostly distributed just below the centre of PC2. This represents a particularly slim scapular blade in which the supraspinous fossa is noticeably larger than the infraspinous. All the subterranean species within the dataset are claviculate, and this is reflected in the majority lying in the lower portion of PC2, being associated with a particularly enlarged acromion process. However, the star-nosed mole (*Condylura cristata*) is found unexpectedly high on PC2, and this is likely due to the caudal angle being notably lower than the rest of the vertebral border, unlike in most claviculate species included here and certainly unlike the other subterranean species. This may be related to the star-nosed mole's propensity for swimming (Nowak 1999).

Generalists are distributed widely below the centre of PC1, overlapping with many other groups. This reflects the diversity of generalist locomotor profiles as well as the advantage of a mean scapular shape for generalist lifestyles. There are, however, some notable outliers. First, the species highest on PC2 is the Javan warty pig (*Sus verrucosus*), due to the acromion being greatly reduced (though a metacromion is clearly distinguished) and the vertebral border being subtly curved such that the point where the scapular spine meets it is the highest point. The giant anteater (*Myrmecophaga tridactyla*) is the closest of any taxa to the cetaceans, high on PC1. This is due to the anteater possessing a particularly wide scapular blade and highly cranially-directed acromion and coracoid processes. Lowest of all species on PC1 is the cinereus shrew (*Sorex cinereus*), which has the slimmest blade in the dataset. Lastly, the two armadillos (the Chacoan naked-tailed armadillo [*Cabassous chacoensis*] and the pink fairy armadillo [*Chlamyphorus truncatus*]) are located unexpectedly close to the volant group. This is specifically due to the armadillos having greatly elongated acromion processes which almost double the length of the scapula, as well as wide scapular blades and prominent caudal angles.

It is clear that, as predicted in **H$_{\text{III.4}}$**, locomotion behaviour plays a role in influencing scapular variation within this morphospace, but a great deal of the nuance of the morphospace relies on taking the other factors (size, evolutionary history and clavicle presence) into account.

III.4. Discussion

Scapular morphology is influenced by a mosaic of factors, only some of which could be explicitly investigated here. Evolutionary history appears to be notably influential (as was also identified in xenarthrans [Monteiro & Abe 1999] and in didelphid marsupials [Astúa 2009]), largely due to the constraints of the other factors (locomotion behaviour, size, and clavicle presence) along taxonomic lines. However, even outwith the bounds of taxonomic constraint, variation in size and clavicle loss significantly influence scapular morphology in identifiable and biomechanically salient ways. With regards to the primary question of this chapter, differences in locomotion behaviour do fundamentally affect scapular morphology, especially variation in aerial and running abilities, but this is dependent on the influences of evolutionary history, size and clavicle presence. While all of the variables investigated here contribute significantly to scapular variation, with significant terms in phylogenetic models explaining 15.1% of scapular variation at most (**model3**, total R^2 across significant terms is 0.151). This leaves much of the intricacy of scapular morphology in therian mammals yet to be explored.

It certainly cannot be said that the findings of this study support Oxnard's (1968) assertion that the effect of evolutionary history on scapular morphology is second to the effect of locomotion behaviour. However, Oxnard bases this only on the difference between arboreal and non-arboreal taxa, using his linear measurement scheme which was based on primate anatomy, and he does not run a new Canonical Variates Analysis (CVA) for his mammal-wide dataset but instead introduces the non-primates into his primate-trained CVA as novel observations. In contrast, this chapter includes far more information on locomotion behaviour, uses a 3D landmark coordinate configuration explicitly designed to be generalised across therian mammals, and treats all species with equal weight. Therefore, it is likely that the results obtained here better reflect the biological reality than Oxnard's (1968) results.

III.4.1. Overall scapular variation

When looking at scapular variation as a whole across therian mammals, it appears that the majority is related to i) the width of the blade and relative dominance of the two lateral fossae, ii) prominence of the acromion and coracoid processes, and iii) curvature of the vertebral border related to caudal angle prominence. These are all key functional regions of the scapula, which can be directly related to muscle action. Scapular width is important for several reasons: first, the wider the blade the larger the attachment sites can be for the *m. supraspinatus, m. infraspinatus* and *m. subscapularis*; secondly, the relative proportions of the supra- and infraspinous fossae are direct proxies for the relative prominence of the *m. supraspinatus* versus the *m. infraspinatus*, indicating the relative importance of humerus protraction (*m. supraspinatus*) or lateral humerus rotation (*m. infraspinatus*); and finally, increased blade width results in expansion of the vertebral border, providing larger muscles attachment sites for musculature associated with weight-bearing and scapular protraction/retraction (see Fig. III.2 & Table III.1 for specifics of muscle attachment and function). Relative prominence of the acromion and coracoid processes are important because a prominent acromion is associated with the presence of a clavicle, and an elongated coracoid appears to be related to increased climbing ability (which is also usually associated with being claviculate and having a prominent acromion). Lastly, curvature of the vertebral border is influenced by the size and relative importance of the muscles associated with weight-bearing and scapular protraction/retraction, but is also greatly influenced by the way scapular position on the thorax influences the lines of action of these muscles and, similarly, prominence of the caudal angle provides insight into the muscle line of action requirements of the *m. teres major*. Therefore, much of this variation can be tangibly related to functional requirements.

III.4.2. Size and allometry

Hypothesis III.1 ($\mathbf{H_{III.1}}$):

It is expected that body size will significantly affect scapular morphology. Particularly, large size will be associated with an enlarged vertebral border.

In support of $\mathbf{H_{III.1}}$, differences in size (represented by scapular centroid size) appear to play an important role in influencing scapular morphology. In phylogenetic models **model1-3**, logCS is consistently a significant term with relatively high effect sizes, indicating a key relationship between scapular size and morphology. However, this relationship is complex and influenced by the other factors investigated here, especially clavicle presence.

Cetaceans and chiropterans are particularly unusual in their allometric results, though this is easily explained by the specific contexts of their ecology and behaviour. Cetaceans are obligately aquatic and so, despite their large size, the scapula is involved in non-weight-bearing functions described further in Section III.4.5.1., while the intense biomechanical requirements of powered flight in chiropterans obfuscate the influence of the scapula's weight-bearing function. Generally, across the other taxa in the dataset, increased size is associated with increased blade width and curvature of the vertebral border with an increasingly lower caudal angle. The former result is in line with $\mathbf{H_{III.1}}$ and previous research (Astúa 2009) as the increased blade width results in an enlarged vertebral border which can support larger musculature associated with weight-bearing (*mm. rhomboidei, m. serratus ventralis,* and *m. trapezius*). The latter result is most likely associated with differences in limb posture (i.e. crouched vs. straight). Similarly to the differences in scapular position associated with clavicle presence/absence (which are discussed shortly), differences in limb posture determine scapular position relative to the body, which particularly affects the musculature attaching the scapula to the thorax – musculature associated with the vertebral border. Additionally, the caudal angle may be more ventral in large therian mammals with straighter limbs because the extension of the shoulder away from the 'zigzag' posture increases the distance between the origin of the *m. teres major* at the caudal angle and its insertion at the proximal humerus (i.e. its in-lever). The caudal angle being more ventral in large mammals moves the origin of the muscle, minimising the lengthening of this in-lever to avoid loss of functional efficiency. Additionally, increased size is associated with enlargement of the glenoid fossa. Given that the glenoid is the articular surface of the scapula with the humerus, it represents the scapular region most impacted by ground reaction force in quadrupeds (Püschel & Sellers 2016; Arias-Martorell 2018), and evidence has previously been found that increased body mass is related to increased glenoid fossa size (Arias-Martorell 2018 [hominoid primates]; Wölfer et al. 2019 [sciuromorph rodents]).

Evidence of differential scaling (when considered excluding cetaceans) indicates that the allometric effect is greater in smaller species. That is, shape changes associated with changes in size are more pronounced at smaller sizes, in line with results reported in carnivorans (Gálvez-López 2014) but in contradiction to results reported in didelphid marsupials (Astúa 2009). It is evident from pairwise comparisons of trendlines that allometry varies predominantly along phyletic lines, as was previously identified to be the case in carnivorans (Gálvez-López 2014).

III.4.3. Evolutionary history

Hypothesis III.2 ($\mathbf{H_{III.2}}$):

It is expected that there will be a significant effect of evolutionary history on scapular morphology, potentially greater than that of the other factors.

Evolutionary history is a broad term which is used here to refer to information relating to phylogeny and taxonomy. There is a moderate phylogenetic signal in scapular morphology (Bloomberg's K = 0.46), and a moderate to high signal in the residuals (Pagel's λ = 0.74), indicating a deviation from strict Brownian motion which could be explained by functional adaptations. The arrangement of the PC1-PC2 morphospace is evidently influenced by taxonomic group affiliation, arguably more so than it is by locomotor group affiliation or size. Some taxonomic groups are better distinguished from others (the cetaceans and chiropterans being the most clearly differentiated), but there is a key region of the morphospace at the centre of PC2 and in the negative half of PC1 where there is considerable overlap in taxonomic groups. This region of the morphospace is diverse in its make-up, not just taxonomically but in relation to locomotor group, clavicle presence, and size. Therefore, the region may represent positive selection towards a generalised scapula shape rather than representing taxonomically-defined morphological constraints. Further work is necessary to better understand this.

In line with $\mathbf{H_{III.2}}$, evolutionary history appears to play a large role in influencing scapular morphology in therians. However, this is strongly linked to taxonomic constraints on clavicle presence, size and locomotion. For example, Ferae are all aclaviculate despite exhibiting a great variety of locomotion profiles, so their scapular morphology reflects adaptations for different locomotion abilities in association with morphologies related to clavicle loss. Climbers within the aclaviculate Ferae differ substantially in their morphology from euarchontan climbers, which are claviculate. Similarly, all chiropterans are volant and they are the only taxonomic group capable of this feat, so their scapular morphology is a culmination of these factors.

Previous research has identified lower scapular variation in marsupials than in placentals (Sears 2004), associated with a very specific developmental constraint upon their scapula: the necessity of precocial forelimbs so that neonatal marsupials are able to climb into the pouch when born. While this was not explicitly tested here, the reduced morphospace occupation of marsupials relative to placentals supports these findings. However, it is not well supported in comparison to individual placental clades – the marsupials are distributed very similarly to Glires, and are more widely distributed than Ferae. Thus, despite this developmental constraint, marsupials still present more variable scapulae than some placental clades.

III.4.4. Clavicle presence

Hypothesis III.3 ($\mathbf{H_{III.3}}$):

Scapular morphology will significantly distinguish between claviculate and aclaviculate species, particularly in the size of the acromion process.

Across phylogenetic models, clavicle presence consistently significantly influences scapular morphology with relatively high effect sizes. Additionally, **model3** shows clear interactions between clavicle presence and logCS, digging and running which significantly influence scapular morphology. Clavicle presence or absence appears to have a striking effect on the scapula which allows a single principal component (PC2) to almost entirely separate claviculate from aclaviculate taxa. There are two features of the overall scapula morphology which appear to differentiate claviculate and aclaviculate taxa: i) in claviculate taxa, the acromion is prominent and extends beyond the glenoid, whereas in aclaviculate taxa it is noticeably reduced, and ii) the dorsally highest point of the scapula in claviculate taxa is the caudal angle, whereas in aclaviculate taxa it is the point where the scapular spine meets the border. These results are clearly in line with $\mathbf{H_{III.3}}$ as it is evident that aspects of scapular morphology can distinguish claviculate and aclaviculate taxa, and the clearest aspect is the size of the acromion. This is because the clavicle articulates directly with the acromion process, so in the absence of an ossified clavicle the acromion becomes reduced. While this is intuitively predictable, it has not previously been quantified and demonstrated across therian mammals. The difference in vertebral border morphology between claviculate and aclaviculate taxa is particularly notable, since this region is at the furthest point on the scapula from the location of the clavicle when present. It is likely that this difference reflects the difference in scapula position on the ribcage – claviculate taxa tend to have more dorsally positioned scapulae, while aclaviculate taxa tend to have more laterally positioned scapulae (Voisin 2006). Clear examples of this are apes, such as humans, which have clavicles and highly dorsal scapulae, versus horses which have no clavicle and highly lateral scapulae. The difference in position on the body affects the relationship of the scapula to surrounding structures, particularly the vertebral column, and this is likely why it is the vertebral border most affected. In particular, since the musculature connecting the scapula to the body is primarily attached at the vertebral border, differences in the relative position of the vertebral border and torso result in differences in lines of action of these muscles, which may necessitate morphological differences in the border itself.

III.4.5. Locomotion behaviour

Hypothesis III.4 ($H_{III.4}$):

It is expected that there will be significant morphological distinctions between functionally different locomotor groups.

As predicted in **$H_{III.4}$**, variation in locomotion behaviour does appear to be linked to scapular variation in therian mammals. In **model1**, locomotor group is the most influential term based on effect size (Z), and ability scores are consistently significantly related to scapular morphology across models (**model2, model3, model9-13**). Notably, digging and running ability interact with clavicle presence in such a way to significantly influence scapular morphology (**model3**). The arrangement of the PC1-PC2 morphospace is also influenced by locomotor group affiliation and gradients of locomotor abilities, though to a somewhat lesser extent than it is influenced by taxonomic group affiliation or clavicle presence. While the effects of locomotion behaviour may be somewhat obscured by the influences of the other factors investigated here, there are some important functionally-relevant points to note in several groups which distinguish them from others.

III.4.5.1. Aquatic

Swimming ability does not consistently significantly influence scapular morphology in phylogenetic models, perhaps due to the striking morphological differences between cetaceans and other aquatic taxa. Moving through water presents a different set of functional challenges from moving terrestrially or through air. While gravity has little to no effect on animals less dense than water, the density of water dramatically increases drag (Biewener 2003). There are multiple ways in which animals can generate forward motion underwater, but mammals utilise either pelvic or pectoral oscillation. The majority of specialised aquatic mammals swim by pelvic oscillation (cetaceans, sirenians, and phocids), generating thrust via undulation of the spine and hindlimbs (when present) and using the forelimbs for directional control (Fish et al. 1988, Pierce et al. 2011). In order to facilitate this, the forelimbs must be mobile, but stable and powerful in opposition to the force of drag. All of the aquatic species in the dataset are aclaviculate, and generally reflect this in having a reduced acromion process.

Cetaceans, which are pelvic oscillators, have a unique but relatively well-studied scapular morphology such that they are more similar to each other than to other species in the dataset, even differing considerably from the other aquatic species. The cetacean scapula is very wide, often with a greatly enlarged infraspinous fossa and extremely reduced supraspinous fossa (Cooper et al. 2007). This enlarging of the blade has been associated with increasing the origin area for the *m. subscapularis,* which is divided into multiple independent segments, to increase control of the flipper for accurate steering (Sanchez & Berta 2009). Forelimb musculature is concentrated proximally in cetaceans, with the distal forelimb having an extremely reduced range of motion. This means that the muscles of the scapula are particularly large in cetaceans, and this muscle enlargement has also been suggested to increase control of forelimb movement (Sanchez & Berta 2009). The acromion and coracoid are prominent and very similar in morphology to one another, both extending cranially near-parallel to the blade. Both are medio-laterally flat, and relatively dorso-ventrally wide. The spine is barely distinguished from the blade. The coracoid provides the origin for the *m. coracobrachialis*, which acts to flex the shoulder and adduct the humerus, and the positioning of the large coracoid highly cranially may function to increase the size and moment arm of this muscle. The association of the acromion and coracoid is, in fact, likely due to the position of the *m. supraspinatus*, which arises in the greatly reduced supraspinous fossa and passes between the coracoid and acromion where it essentially fills this space (Sanchez & Berta 2009). Thus, this channel between the two processes may be important in providing structural support and direction for the *m. supraspinatus*.

The other aquatic taxa arise from several taxonomic groups and vary in their ability to move on land, from the capybara (*Hydrochoerus hydrochaeris*) which is a mobile generalist with a large aquatic component to its behavioural profile, to the sirenians (*Dugong dugon* and *Trichechus manatus*) which are obligately aquatic. There is considerable variation in the biomechanical demands placed on the forelimbs in this group, and considerable variation in their scapular morphology (particularly relative to shape change on PC2, but less so relative to PC1). Despite the functional requirements of swimming, the non-cetacean aquatic mammals are more morphologically similar to the other non-aquatic taxa than they are to cetaceans. Given the small sample sizes for each subgroup, it is not within the scope of this chapter to make realistic generalisations about how the subtleties of different aquatic lifestyles influence scapular morphology. The scapula in pectoral and pelvic oscillating pinnipeds has been explored previously (Maynard Smith & Savage 1956; Pierce et al. 2011; Gálvez-López 2014) and, despite differences in behaviour, many of the functional requirements placed on the forelimb ultimately result in several commonalities across aquatic carnivorans. The scapula has a characteristic crescent shape in which the caudal border is concave with a protruding caudal angle, the glenoid is caudally-oriented, and the cranial border is convex. This general shape is also found in sirenians (Nganvongpanit et al. 2017). The vertebral border is expanded in association with this shape, which has been linked with enlargement of the *m. serratus ventralis* (*m. levator scapulae* and *m. serratus anterior* in aquatic carnivorans) and *m. deltoideus* (which is a single mass in aquatic carnivorans, arising from the caudal portion of the vertebral border), providing powerful forelimb protraction and retraction, and humerus abduction. The prominent caudal angle and caudally-oriented glenoid result in an increased moment arm of the *m. teres major*, which is associated with powerful humerus adduction (English 1977). These motions are heavily involved in propulsion in pectoral oscillators, as well as both directional control while swimming and limited terrestrial movement in pelvic oscillators (Pierce et al. 2011; Gálvez-López 2014). Of note, the capybara scapula has a somewhat crescent shape, with a convex cranial border and caudally-oriented glenoid. The caudal angle is not particularly prominent, however, so the caudal border is not concave. In the pygmy hippo (*Choeropsis liberiensis*), however, the caudal angle is prominent so the caudal border is concave. The glenoid fossa is somewhat caudally-directed, but not to such an extent as is observed in aquatic carnivorans.

III.4.5.2. Climbers, aerial acrobats and volant species

In the largest phylogenetic model (**model3**), aerial ability score is the most influential term ($p = 0.001$, $Z = 3.37$). Though climbing ability was not found to significantly influence scapular morphology in this model, it was significant in **model2** which does not include interactions. This may be due to the taxonomic composition of the dataset, in which all but one aclaviculate climber are members of the single taxonomic group Ferae, so no true signal is identified in the model which cannot be explained by shared evolutionary history.

There exists an inherent behavioural continuum from climbers, through aerial acrobats, to volant species (i.e. chiropterans). This is because of the way that climbing ability is inexorably linked to aerial movement ability in mammals – in order to engage in aerial behaviours, a mammal must generally climb to a suitably high perch first. This is also clear in scapular morphology as represented by the PC1-PC2 morphospace, specifically in claviculate taxa (N.B. while all aerial acrobats and chiropterans are claviculate, some climbers are aclaviculate). All the claviculate species assigned to the climbers, aerial acrobats or volant categories exist within a defined area of the morphospace, delineated by dotted lines in Fig. III.13A. In all these species, the acromion is prominent and extends cranially beyond the glenoid fossa, the coracoid is elongated and caudally-directed, and the caudal angle is the highest point of the blade. Along this behavioural gradient, as aerial movement ability increases, these features become more pronounced (Fig. III.13B). Firstly, the large acromion provides the articulation for the clavicle, facilitating the mobility and stability necessary for manoeuvring with the arms above the head and through the complex 3D canopy. The acromion also provides the scapular attachments for several muscles involved in stabilisation and complex scapular movement (such as the *m. acromiotrapezius* and *m. acromiodeltoideus*). The acromion becomes increasingly cranial as aerial ability increases, being entirely cranial to the glenoid in the chiropterans. This is because the scapula is highly dorsal in chiropterans, with the joint directed laterally, and the acromion is being directed over the top of the joint dorsally to articulate with the clavicle which passes in front of the joint. This ensures that the clavicle is distant from the shoulder joint, minimising its interference with shoulder mobility (particularly during the upstroke in flight), while allowing the clavicle its full range of motion (Vaughan 1970; Vaughan & Bateman 1970; Gaudioso et al. 2020). Secondly, it was anticipated based on previous research that the coracoid would be enlarged in climbers, as it provides the origin for the *m. coracobrachialis* which is involved in humerus adduction (Taylor 1974; Argot 2001; Sargis 2002; Salton & Sargis 2008). The coracoid is directed caudally around the medial side of the glenoid to provide the appropriate line of action for the *m. coracobrachialis* attaching to the medial side of the humerus. In chiropterans, the coracoid is particularly elongated and caudally-directed, and this is likely to be in order to provide a particularly strong insertion for the *m. pectoralis minor* (which attaches to the coracoid is some taxa like chiropterans, but not ancestrally), stabilising the joint in opposition to the *m. pectoralis major* which is largely responsible for the powerful downstroke necessary to allow powered flight (Biewener 2003; Panyutina et al. 2011). Finally, the caudal angle in climbers, aerial acrobats and chiropterans is prominent, associated with an elongated caudal border and large infraspinous fossa. This prominent caudal angle was previously identified as a key feature of climbers, associated with increased power of the *m. teres major* for shoulder flexion (by lengthening its moment arm), and an enlarged *m. infraspinatus* which is also involved in shoulder flexion and humerus rotation, as well as overall scapula stability (Taylor 1974; Monteiro & Abe 1999; Astúa 2009; Preuschoft et al. 2010). The elongated caudal border has previously been associated with increased use of the forelimbs above the head (particularly in brachiation) in primates (Preuschoft et al. 2010). In all three of these locomotor groups, but particularly in chiropterans, the vertebral border is expanded. This is undoubtedly associated with importance of musculature arising on the vertebral border (especially *mm. rhomboidei* and *m. serratus ventralis*) in elevating the body through the shoulder girdle. These muscles also play important roles in translating the scapula towards the vertebral column (adduction) which is important in facilitating the upstroke in chiropterans (Panyutina et al. 2011).

It is important to consider the aclaviculate climbers independently because clavicle loss would appear to confer a considerable disadvantage in climbing behaviour, which needs to be addressed with different morphologies. The aclaviculate climbers exist in an adjacent and somewhat overlapping morphospace to the claviculate climbers (Fig. III.12A), and with one exception (the tree hyrax [*Dendrohyrax dorsalis*]) all the aclaviculate climbers in this dataset are Ferae, all but one of which are carnivorans (the exception being the African tree pangolin [*Phataginus tricuspis*]). As discussed above, this makes it particularly difficult to make generalisations about aclaviculate climbers without being heavily influenced by taxonomy. Additionally, climbing behaviour and its influences on scapular morphology in carnivorans has previously been explored (Taylor 1974; Gálvez-López 2014).

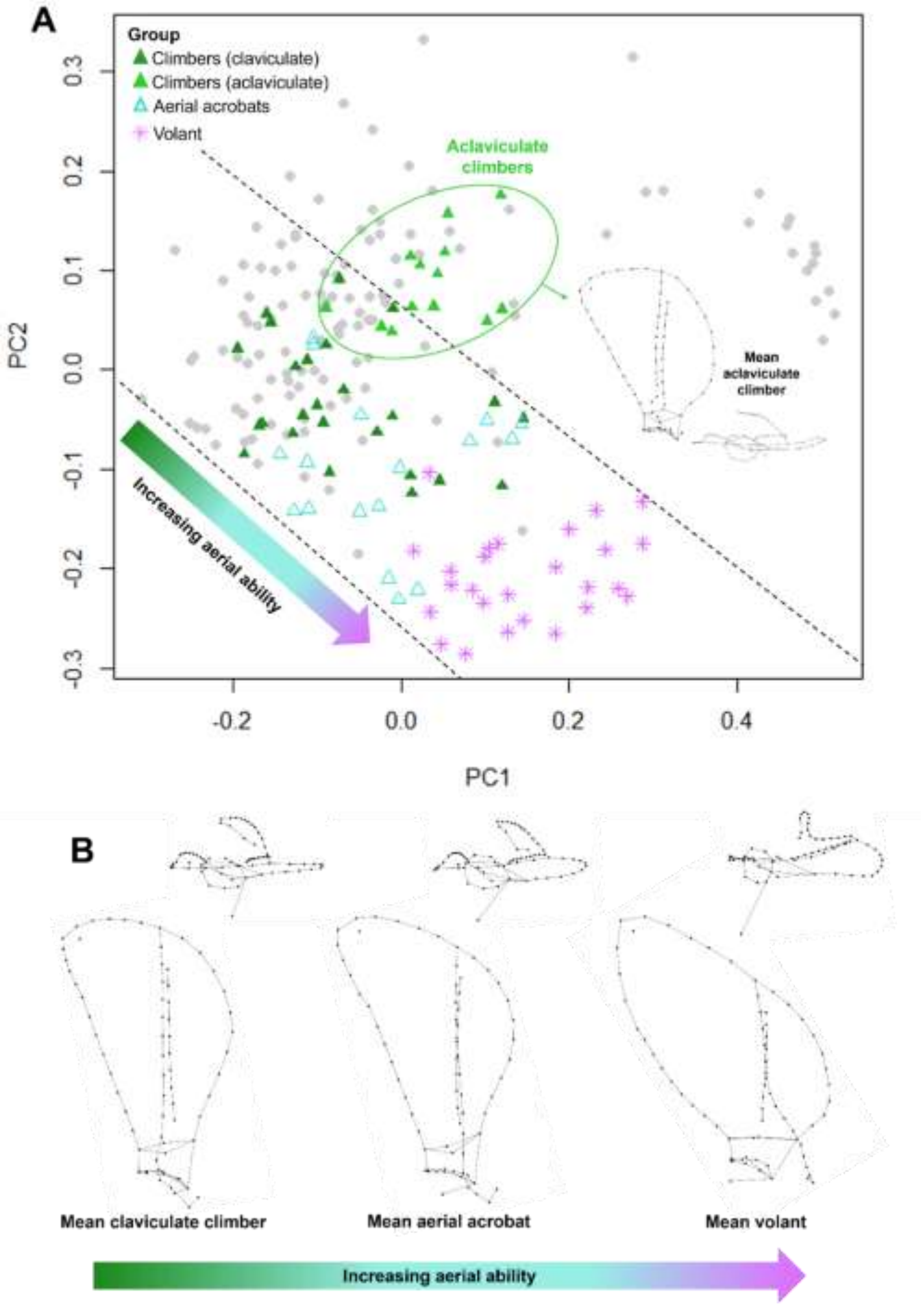


Figure III.12: Climbing and aerial movement in the PC1-PC2 morphospace
A) Scatter plot visualising the first two principal components, highlighting and differentiating aclaviculate climbers, claviculate climbers, aerial acrobats, and volant species. The mean shape for aclaviculate climbers is shown adjacent to their region of the morphospace, in lateral and glenoid view. B) Mean shapes of claviculate climbers, aerial acrobats and volant species, shown in lateral and glenoid views.

III.4.5.3. Subterranean

Subterranean species were found to associate closely in the PC1-PC2 morphospace, sharing many commonalities of scapular morphology. Subterranean life presents unique challenges, particularly due to how mechanically demanding movement through the soil substrate is. Nevertheless, mammals have evolved subterranean lifestyles more than once independently. Subterranean mammals are often given a common name including the term ‘mole’, though the only ‘true moles’ are members of the family Talpidae (within Eulipotyphla). In fact, despite being represented by relatively few species, the subterranean group is one of the most taxonomically diverse in the dataset, with members arising from Chrysochloridae (Afrotheria), Eulipotyphla, Rodentia (Glires), and Marsupialia. It is noteworthy that talpid and chrysochlorid moles were once united taxonomically in the now defunct order Insectivora, and they are found here to share morphological characteristics associated with a shared behaviour. This implies that the morphological adaptations are convergently acquired in response to functional requirements of subterranean life, and this apparent convergence likely gave rise to the erroneous assumption that the chrysochlorids and talpids were closely related (Novacek 1986), which has since been demonstrated to be incorrect with the advent of molecular phylogenetics (Springer et al. 1997; Stanhope et al. 1998). One of the main commonalities across the various ‘moles’ is that they have consistently reverted to a sprawling posture akin to that of early mammal relatives, rather than the parasagittal posture seen in most extant terrestrial mammals (Gambaryan & Kielan-Jaworowska 1997), significantly altering the biomechanics of their forelimb and pectoral girdle. This positions the forelimbs better to perform the ‘breaststroke-like’ digging motion necessary to efficiently displace soil backwards while moving forwards. There are some anatomical commonalities across the subterranean species, the first of which being that they are all claviculate. Secondly, across the subterranean mammals, the scapula is thin and elongated (Warburton 2003). Finally, one of the key features of the subterranean species directly associated with their sprawling posture, is the orientation of the scapula and its position on the body, which differ from that of other extant mammals. The glenoid is consistently highly cranial and resting close to the base of the skull with the scapular blade extending caudally (Reed 1951; Gambaryan & Kielan-Jaworowska 1997; Warburton 2003). In chrysochlorids, the scapular blade is positioned dorsally on the thorax and is approximately parallel to the vertebral column, while it is more laterally positioned but still parallel to the vertebral column in the marsupial mole (*Notoryctes typhlops*), and in Talpidae the caudal border is raised dorsally above the vertebral column (Warburton 2003). There are known to be several anatomical differences between 'moles', which are particularly extreme in Talpidae. For example, the infraspinous fossa is greatly reduced or entirely absent in Talpidae (Reed 1951; Warburton 2003) but is still present in other groups, and the scapular spine is also reduced in Talpidae while it is well-developed in the other groups (Warburton 2003).

The results obtained here appropriately reflect these morphological adaptations. The subterranean species are generally found at the lowest end of PC1 in the PCA morphospace (Fig. III.11), representing very slim scapular blades which are supraspinous-dominated (the talpid star-nosed mole [*Condylura cristata*], being the lowest positioned of the subterranean species on PC1, reflects the extreme reduction of the infraspinous fossa in talpids). With the exception of the star-nosed mole, which is higher on PC2, the subterranean species are relatively closely associated in the PC1-PC2 morphospace, reflecting the commonalities of their adaptations towards subterranean life, namely i) slim blade, ii) enlarged acromion, and iii) prominent caudal angle.

The 'moles' present a particular challenge for large-scale comparative studies like this because of the sprawling posture and unusual position of the scapula on the body, which alter much of the biomechanics of the forelimb. Nevertheless, they are successfully included in the dataset and their position in the morphospace can be appropriately interpreted alongside the other mammals.

III.4.5.4. Runners

Biomechanically speaking, running behaviour requires powerful movement of the forelimb in the parasagittal plane, with minimal lateral movement for directional adjustment and dorso-ventral movement for managing uneven terrain. This is, arguably, the simplest of the locomotion behaviours to model biomechanically, thanks to the majority of motion occurring in a single plane. Perhaps due to the relatively simple biomechanical demands of running, or perhaps in spite of this, running ability significantly influences scapular morphology (**model** & **model3**), and differences in morphology related to running behaviour are different in claviculate and aclaviculate taxa (**model3**) – this is reflected in the PC1-PC2 morphospace. Generally, the runners, claviculate and aclaviculate, are found in a relatively constrained area of the morphospace, almost all being between 0.0 and -0.2 on PC1 but spread widely across PC2 (Fig. III.13). This is because runners generally have slim scapular blades with approximately equal supra- and infraspinous fossae, but the vertebral border varies in its curvature (though never reaching the extremes of aerial acrobats and volant species), partly associated with clavicle presence/absence which also impacts the size of the acromion. The reduction in required range of motion as compared to other locomotion behaviours has been cited as a reason for clavicle loss being associated with running behaviour (Eaton 1944; Rockwood et al. 2009; de Souza Junio et al. 2020). It is, therefore, unsurprising that the majority of the runners in the dataset are aclaviculate (27/37 or 73.0%). However, it should be noted that the interaction of clavicle presence and running ability does not significantly influence scapular variation in all models.

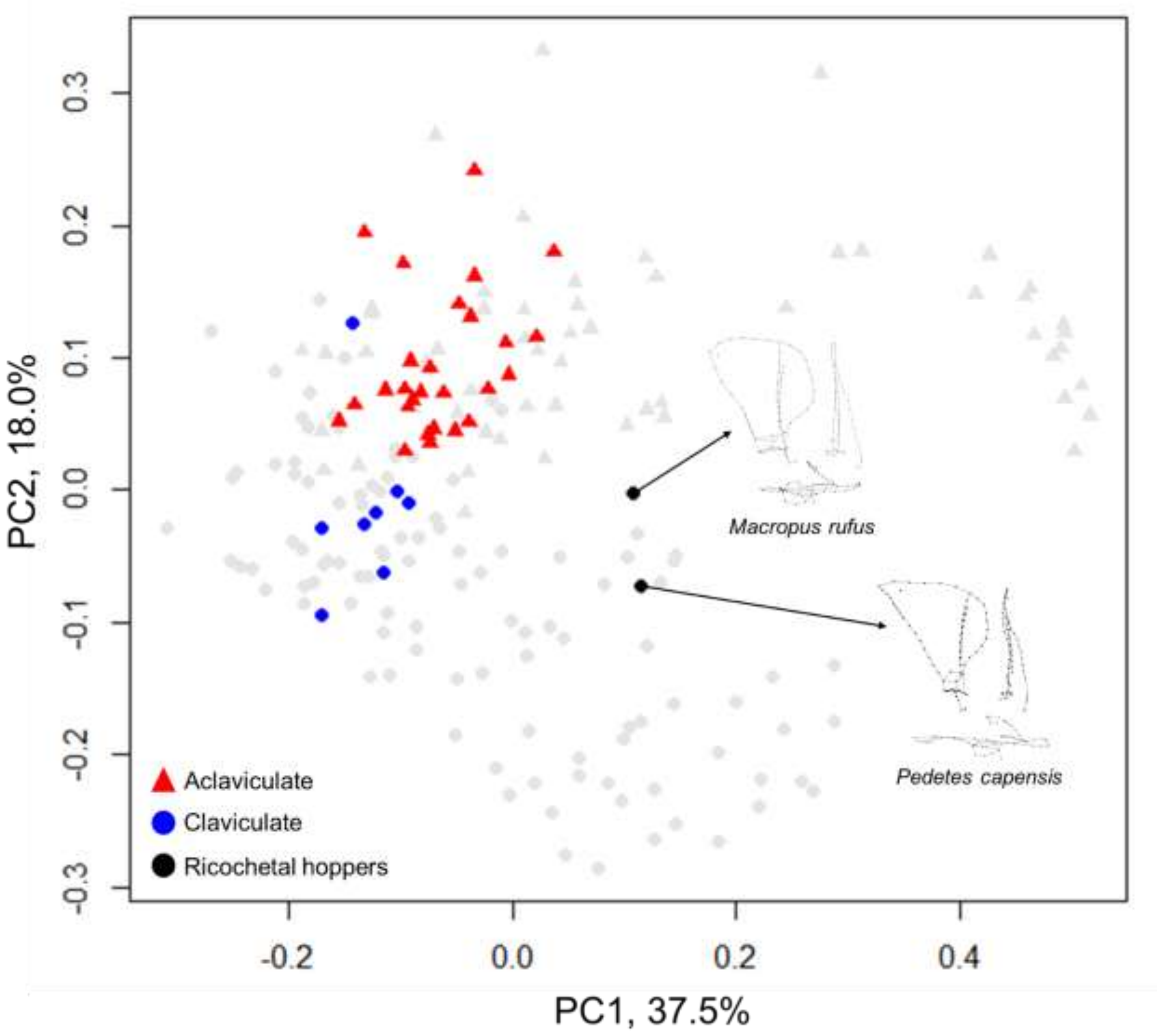
Broadly, the runners can be divided into three morphological groups (Fig. III.13):

- **Aclaviculate + *Elephantulus*** (n = 27): The aclaviculate runners, containing Ferae and terrestrial ungulates, are located in the positive half of PC2 and around the centre of PC1. Despite being claviculate, *Elephantulus rupestris* (elephant shrew) is also found in this region of the morphospace, far more closely associated with the aclaviculate runners than the claviculate runners. This region of the morphospace represents a relatively slim blade which is more supraspinous-dominated, with a reduced acromion and convex vertebral border. The scapula of the elephant shrew has a particularly prominent metacromion. Seckel & Janis (2008) previously found half-bounding in small ‘cursorial’ mammals to be associated with an enlarged metacromion. This process provides the insertions for muscles like the *m. acromiotrapezius* and *m. omotransversarius,* and it has been suggested that the elongated metacromion brings the attachment of these muscles caudal to the centre of rotation of the shoulder joint so that they can take on a greater role in resisting ground reaction force by preventing collapse of the shoulder joint.

- **Claviculate** (n = 7; most Glires, as well as the banded hare-wallaby [*Lagostrophus fasciatus*], and the long-nosed potoroo [*Potorous tridactylus*]): This group is distinct from the aclaviculate runners, being negative on PC2 as well as being low on PC1. This represents a slim scapula with a prominent and high caudal angle. The acromion is prominent and extends directly ventrally. The high caudal angle and prominent acromion may both be associated with the claviculate condition, but the prominence of the caudal angle also likely reflects increased power in shoulder flexion via the *m. teres major*.
- **Ricochetal hoppers** (n = 2; red kangaroo [*Macropus rufus*] and springhare [*Pedetes capensis*]). These two species are very noticeably distinct from the other runners in their morphology, being much higher on PC1 than the other runners due to having wider scapular blades which are distinctly infraspinous-dominated. Both have prominent caudal angles with a large area of origin for the *m. teres major*, and both have prominent acromion processes which are directed ventrally. It is to be expected that these species would differ in their scapular morphology from other runners because their rapid ricochetal locomotion is so hindlimb-dominated, leaving the forelimbs free to perform other behaviours.

It is noteworthy that climbing and running abilities showed opposing morphological gradients in the morphospace (Fig. III.10). These two behaviours arguably represent opposing biomechanical requirements, with climbing requiring high levels of shoulder mobility including laterally from the body, while running requires more adherence to a parasagittal limb position and movement. Indeed, the clavicle is believed to be advantageous in climbing and disadvantageous in running (Jenkins 1974; de Souza Junior et al. 2020). Since running and climbing present such different biomechanical requirements, it appears that specialisation in either may limit specialisation towards the other.

Figure III.13: Running subgroups in the PC1-PC2 morphospace
Visualisation of the PC1-PC2 morphospace highlighting and differentiating claviculate runners, aclaviculate runners, and the two ricochetal hoppers (for which wireframes are provided in lateral, caudal and glenoid views).



III.4.6. Comments on methodology

Undertaking a large-scale comparative study of scapular morphology in therian mammals is fraught with challenges. One such challenge is quantifying something as diverse as locomotion behaviour across therians, but this has been addressed via the quantification method developed in Chapter II. Ideally, such a study would have an extremely large sample size which fully covers all extant families and subfamilies, and with multiple individuals representing each species. Additionally, the specimens would be selected to all represent one sex and one side of the body. However, even with access to several museum collections and online repositories, it was not possible within the time constraints of this project to acquire such an ideal dataset. The dataset used here is the largest and most representative that it was possible to compile, and decisions surrounding sex and body side were made on the basis of availability. With a larger dataset, analyses such as the phylogenetic regression on the Procrustes coordinates would be more robust, particularly in assessing relatively small groups like Xenarthra (n = 6). This is somewhat ameliorated by using continuous variables for locomotion rather than a categorical variable, thereby reducing the possible degrees of freedom in the model. Nevertheless, this study represents the taxonomically broadest study of scapular morphology in therian mammals to date, and all taxonomic and locomotor groups are represented by at least six individuals (with the exception of the ‘other’ locomotor group of behavioural outliers).

A further challenge was accurately capturing scapular morphology at this level of variation. However, this much biological variation in the dataset also means that it is very robust to small-scale variations in landmarking. Ultimately, a landmark configuration based on relatively few anatomically homologous points and several semilandmark curves, which cover much of the blade shape, was successfully applicable across the whole dataset and has appropriately captured variation in scapular morphology across therians.

Additionally, there are ways in which the species’ forelimb biomechanics may differ which are not explored here. Manus posture (plantigrade, digitigrade, unguligrade, etc.) is not included as a variable in this study, but it likely has an influence on scapular morphology. The results of this chapter suggest that differences in position of the scapula on the body and differences in limb posture (extended versus ‘zigzag’) may affect morphology of the vertebral border in particular, and that the unguligrade animals (terrestrial ungulates) represent a relatively consistent and identifiable morphology. One of the reasons this was not included as a variable in this chapter is the difficulty of accurately and representatively categorising species into one posture, since they may adopt different postures while undertaking different types of locomotion. Additionally, some species in the dataset have less common forelimb postures, such as knuckle-walking in the giant anteater and chimpanzee, and species like the Virginia opossum which have a prehensile tail that influences its locomotion.

Of course, in order to compare such a diverse group of animals, simplifications were necessary. Clavicle presence is represented as a binary in this study based on whether or not an osseous clavicle articulates with the acromion and manubrium, when there is, in reality, more nuance in clavicle variation. Some taxa have cartilaginous clavicles (de Souza Junior et al. 2020), or clavicles which do not articulate with both acromion and manubrium (Trotter 1885). These rudimentary clavicles may influence shoulder biomechanics in ways which are not accounted for here when they are coded as absent. It is the case that only osseous elements were considered in the scapula itself, too, when there is usually at least some cartilaginous component of the scapula, especially at the vertebral border. This can be very large relative to the scapula (in horses, for example [Ahrari-Khafi et al. 2017]) and provides muscle attachment sites, essentially meaning that the scapula can be considerably larger than it is represented here but also that the contribution of cartilage to scapula size varies greatly.

Lastly, using the phylogenetic regression to model how multiple factors affect scapula shape was greatly informative in disentangling the interrelationships of variables included here and their influence on scapular variation. It should be noted that the nature of the function used in R (*procD.pgls*) requires that Pagel’s lambda be set at either zero or one, unlike the *pgls* function in which the lambda transformation can be set to maximum likelihood and a value of lambda for each model will then be calculated with the results. For the *procD.pgls* functions in this work, lambda was set to one (which is the default for the model), representing an assumption of maximum phylogenetic influence on the model. While it is likely, based on previous research and the other findings of this work, that there is a strong phylogenetic influence on scapular variation, this assumption must still be recognised.

III.4.7. Future work

There is a great deal left to explore with regards to the functional morphology of the scapula across therian mammals, much of which is not within the scope of this thesis but some of which will be investigated in Chapter IV. Firstly, functional morphology studies in extant animals are crucial in a palaeontological context because they make it possible to infer aspects of ecology or behaviour from skeletal material. Unfortunately, the scapula is not predisposed to preserve well in the fossil record. The only dense area of bone, which is most likely to preserve, is the neck and glenoid region (Behrensmeyer et al. 2000). The results of this study did not indicate that much of scapular variation is associated with the glenoid region, so it is possible that glenoid morphology does not capture sufficient functional information to be useful as a palaeontological tool in isolation. On the other hand, it is possible that, while there are more variable regions of the scapula driving the results obtained here, there is sufficient variation in the glenoid alone to make considerable functional interpretation possible from this region. In order to establish this, it would be necessary to repeat much of the analysis from this chapter on the glenoid region alone, perhaps using a greater number of landmarks to thoroughly represent morphology in this region and avoid losing potentially functional information.

This leads on to another aspect of scapular variation across therian mammals which was not explicitly explored here: modularity and integration. Whether morphology in one region of the scapula is directly associated with morphology in other regions, and whether or not the morphology of one region (such as the glenoid) could be used to infer morphology in other regions are questions which have not been explicitly studied across therian mammals. Young (2004) investigated modularity in hominoid primates, identifying that the blade and spine (including acromion) are integrated as distinct from the coracoid and glenoid which may be integrated with one another or may be independent – both hypotheses were supported. Sears et al. (2013) followed on from Young’s work, looking at scapular modularity in opossums, mice, and bats, and finding that the coracoid and glenoid are consistently distinct regions. In opossums, all other regions investigated were found to be integrated, but in the placentals (bats and mice), the neck and acromion are also distinct, while the scapular spine and lateral fossae are one integrated region. A better understanding of modularity and integration of the scapula across mammals would provide a clearer framework for understanding how changes in one region may influence another. For example, it appears from the results of this chapter that clavicle loss is associated with modifications to both the acromion and vertebral border – is this due to integration, or is it due to functional demands?

There may also be much to be gained from further investigating morphological disparity in the therian scapula. As previously mentioned, Sears (2004) found that the scapula of marsupials is less variable in its morphology than in placentals due to the developmental constraint placed upon marsupials by the necessity of developing strong forelimbs early for the journey up to the pouch once born. While this was not explicitly tested here, it appears from the results that the marsupial scapular morphology is no less variable that that of Glires, and may be even more variable than Ferae within the PC1-PC2 morphospace. Investigating morphological disparity may also provide clearer indications of which locomotor groups are most functionally constrained. For example, it appears that generalists are the most widespread in the PC1-PC2 morphospace and subterranean species are more constrained. If supported by direct evaluation, this would be biologically interpretable as potential convergence in shape associated with a locomotion behaviour relative to generalists.

Given the strong influence of evolutionary history on scapular morphology, and the fact that different taxonomic groups have different morphologies, it is challenging to identify the aspects of scapular shape which may be functionally associated with locomotion, clavicle presence or size. Therefore, it seems prudent to identify a single taxonomic group of therian mammals which can be considered representative of therians as a whole in terms of functional diversity. The best candidate is, therefore, the order Rodentia. Not only are rodents the most speciose of any mammal group with more than 2,500 extant species comprising almost 40% of all mammal species (Burgin et al. 2018), they are also very ecologically diverse. Rodents now have a near worldwide distribution and thrive in almost every habitat, performing nearly all of the types of locomotion described in this chapter (with the exceptions that no rodents are volant or obligately aquatic, and it may be more informative to study a group in which these behaviours are not present since their high functional demands drive a lot of the shape variation observed here). They also vary considerably in size, from the African pygmy mouse which weighs up to 12g to the capybara which weighs up to 66kg (Nowak 1999), and, arguably most importantly, some rodents within the Caviomorpha have lost their clavicle. This means that all the factors investigated in relation to scapular morphology in this chapter can be investigated in rodents independently. Within the results of this chapter, rodents (making up the majority of Glires) are arranged mostly in a region of the morphospace which is highly variable in all the factors included here. Exploring the variation within rodents will illuminate this region more, perhaps indicating if being located in this region is associated with taxonomic shape constraints or positive selection towards a generalist scapular shape associated with functional requirements. If the results obtained within rodents functionally reflect the results obtained across all therian mammals, this would indicate that rodents are an appropriate microcosm of therians for studies of the scapula, and would further support the functional interpretations presented in this chapter. This is the basis for the work carried out in Chapter IV.

III.5. Conclusions

III.5.1. Overall scapular variation

The most variable aspects of the scapula are blade width, ratio of the two lateral fossae, the vertebral border, the acromion process, and the coracoid process.

III.5.2. Size and allometry

Size is highly influential on scapular morphology, with generalisable morphological patterns, thought the exact nature of the allometric variation differs among taxonomic and locomotor groups. Increased size is generally associated with increased blade width and increased convex curvature of the vertebral border. These shifts facilitate larger attachment sites for weight-bearing muscles on the vertebral border and medial side of the scapula blade, and accommodate differences in limb posture in increasingly large mammals.

III.5.3. Evolutionary history

Evolutionary history has a substantial influence on scapular morphology, predominantly as it affects and constrains other factors. Cetaceans and Chiroptera are particularly differentiated from other taxonomic groups in their morphology.

III.5.4. Clavicle presence

Clavicle loss has a distinct fingerprint which takes the form of acromion reduction and a transition from the highest point on the vertebral border being the caudal angle in claviculate taxa, to being where the scapular spine meets the border in aclaviculate taxa. The former adaptation is directly linked with the loss of the articulation, while the latter is likely associated with the lateralisation of the scapula on the thorax in aclaviculate taxa.

III.5.5. Locomotion behaviour

Differences in locomotion behaviours and their respective functional demands clearly influence scapular morphology.

- Increased aerial movement ability (which is tightly linked to high climbing ability) is associated with increased prominence and cranialisation of the acromion process, increased length of the coracoid process, and lengthening of the vertebral border with an increasingly high caudal angle. These features are directly associated with maximising shoulder mobility above the head and in the upstroke position required for powered flight, as well as shoulder stability within a wide range of motion.
- In contrast, increased running ability is associated with slimmer scapular blades and vertebral borders which are generally convex or straight, having a relatively low caudal angle relative to the highest point of the blade. These adaptations facilitate the efficient movement of the forelimb in the sagittal plane, with the scapula more constrained in its motion than is the case in other groups.
- Both running and climbing represent important behavioural niches for mammals, but it appears that substantial adaptation towards one may considerably restrict ability in the other.
- While aquatic taxa are not unified in their scapular morphology, particularly due to the unique morphology of cetaceans, all are aclaviculate. This includes the capybara (*Hydrocherus hydrochaeris*), which is one of the few aclaviculate rodents. Aquatic taxa consistently display scapular morphologies associate with shoulder mobility and strength in resisting the force of drag underwater, such as a prominent caudal angle and caudally-oriented glenoid which increase the moment arm of the *m. teres major*.

- Adaptation towards maximising digging ability in subterranean species consistently results in a strong and rigid shoulder gridle with limited shoulder mobility, associated with a reversion to sprawling postures. The scapula in subterranean species is very slim, with an enlarged acromion and prominent caudal angle.

Appendix III.1: Landmark repeatability testing

It was important to assess the repeatability of the 71 landmark configuration (19 true landmarks and seven semilandmark curves) to determine if each landmark could be placed accurately and consistently across multiple sessions and across multiple diverse specimens. The broad taxonomic scale of the complete dataset, and the highly variable nature of the mammal scapula means that analyses utilising these landmark data are robust to small-scale variations in landmarking. The aim of this chapter is not to differentiate closely related species based on scapula morphology, so it is not necessary for the landmark configuration to be repeatable with this level of precision. It is, however, necessary that the landmark configuration be able to capture large-scale variation in morphology and differentiate between species which have divergent morphologies. Thus, five specimens from diverse taxonomic and locomotor groups were landmarked once per day for three consecutive days. These specimens were: *Condylura cristata* (YPM VZ MAM 014548), *Equus africanus* (uant-bio-fun:EQasi01301), *Globicephala macrorhynchus* (NHMUK ZOO 1992.78), *Loxodonta africana* (MSCC-020), *Pteropus pumilus* (UMMZ 156775), and *Puma concolor* (IMNH 996). The landmark configuration is considered appropriate when 1) the five species are successfully differentiated in the PC1-PC2 morphospace of a PCA, 2) the species are significantly differentiated by a Procrustes ANOVA but the repeats are not significantly different, and 3) the intraclass correlation coefficient is close to 1.00.

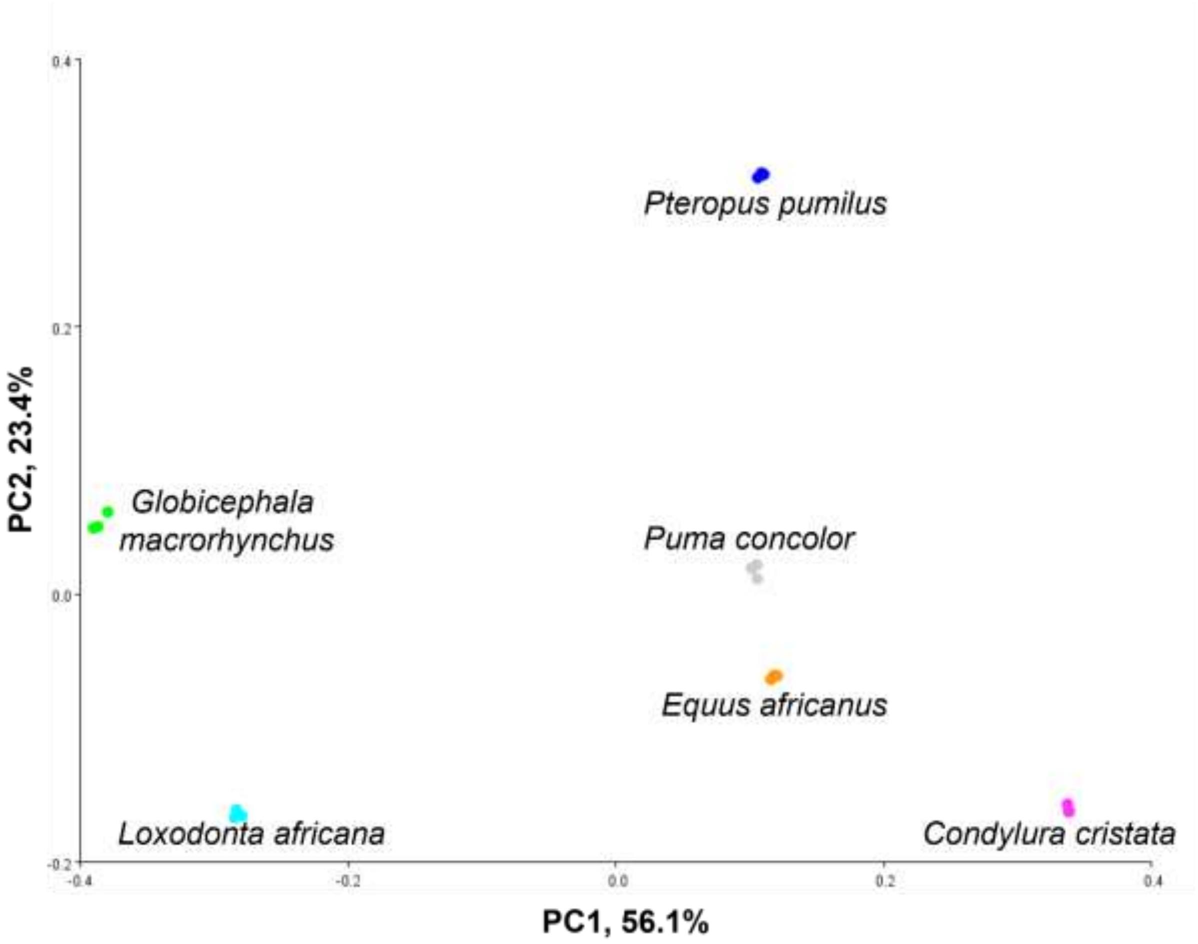
1. In a PCA following Procrustes superimposition, it was expected that each specimen's repeats would cluster together in the PC1-PC2 morphospace, and each specimen would be clearly differentiated. This was found to be the case (App. III.1 Fig. 1), and supports this landmark configuration being appropriately repeatable.

2. A Procrustes ANOVA showed that the specimens are significantly different from one another ($p < 0.0001$), and repeats were not significantly different from one another ($p = 1.00$). This supports this landmark configuration being appropriately repeatable.

3. Intraclass correlation coefficient (ICC) is a metric often used to assess landmarking repeatability, which is calculated as the amount of variation between repeats divided by total variation in the dataset. Therefore, a value close to one indicates lower

variation between repeats relative to total variation (Fruciano 2016). In this dataset, **intraclass correlation coefficient = 0.99**. Measurement error can also be quantified as (1-ICC)*100 (Gálvez-López et al. 2021), and for this dataset **measurement error = 1.00%**. This supports this landmark configuration being appropriately repeatable.

Conclusion: By all metrics, the current landmark configuration is repeatable and appropriate in its current form. Interobserver repeatability was not assessed as all landmarking was carried out by SCA only.



Appendix III.1 Figure 1: PC1-PC2 morphospace
This plot shows the first two PCs of the PCA on the repeatability dataset (five specimens, each landmarked three times with 71 landmarks), with the five species clusters identified.

Appendix III.2: Locomotor quantification

The method laid out in Chapter II was utilised in order to obtain a locomotion scoring matrix (S.III.1.B) and locomotion categorical variable for the specific dataset of 201 species included in Chapter III. The results of the three cluster validation methods (App. III.2 Fig. 1) indicate a consistent optimum at k = 7 and, upon inspection, these clusters are biologically informative. However, the aquatic category produced via clustering includes three terrestrial species (camel *[Camelus bactrianus],* African elephant *[Loxodonta africana]* and black rhino *[Diceros bicornis]*) as outliers. These have low overall scores and have, due to the nature of the cluster analysis, been associated with other low scorers – the aquatic species. Since this is not biologically informative, these three species are considered independently as an eighth group entitled ‘Other’. Unlike the results in Chapter II, which contained a larger dataset, a subterranean group has emerged at lower cluster number, possibly associated with the inclusion of the low scoring terrestrial species in the aquatic group.

The groups are as follows (App. III.2 Fig. 2):

Aerial acrobats (n = 17): This cluster is defined by aerial scores of 2 or 3, and climbing scores of at least 2. This includes gliders and brachiating primates, among others.

Aquatic (n = 23): This cluster contains the obligately aquatic cetaceans and sirenians, the pinnipeds, the pygmy hippo (*Choeropsis liberiensis*), and the capybara (*Hydrochaeris hydrochoerus*). The cluster is defined by high scores in swimming ability associated with low overall scores. The highest scorer is the capybara with a score of 7, which is placed in this cluster thanks to its score of 3 in swimming ability. No other species score above 5 in total.

Climbers (n = 38): This cluster is defined by scores of 3 or 4 in climbing ability, not associated with aerial movement ability. This includes many of the primates, arboreal marsupials such as possums, and arboreal rodents such as squirrels.

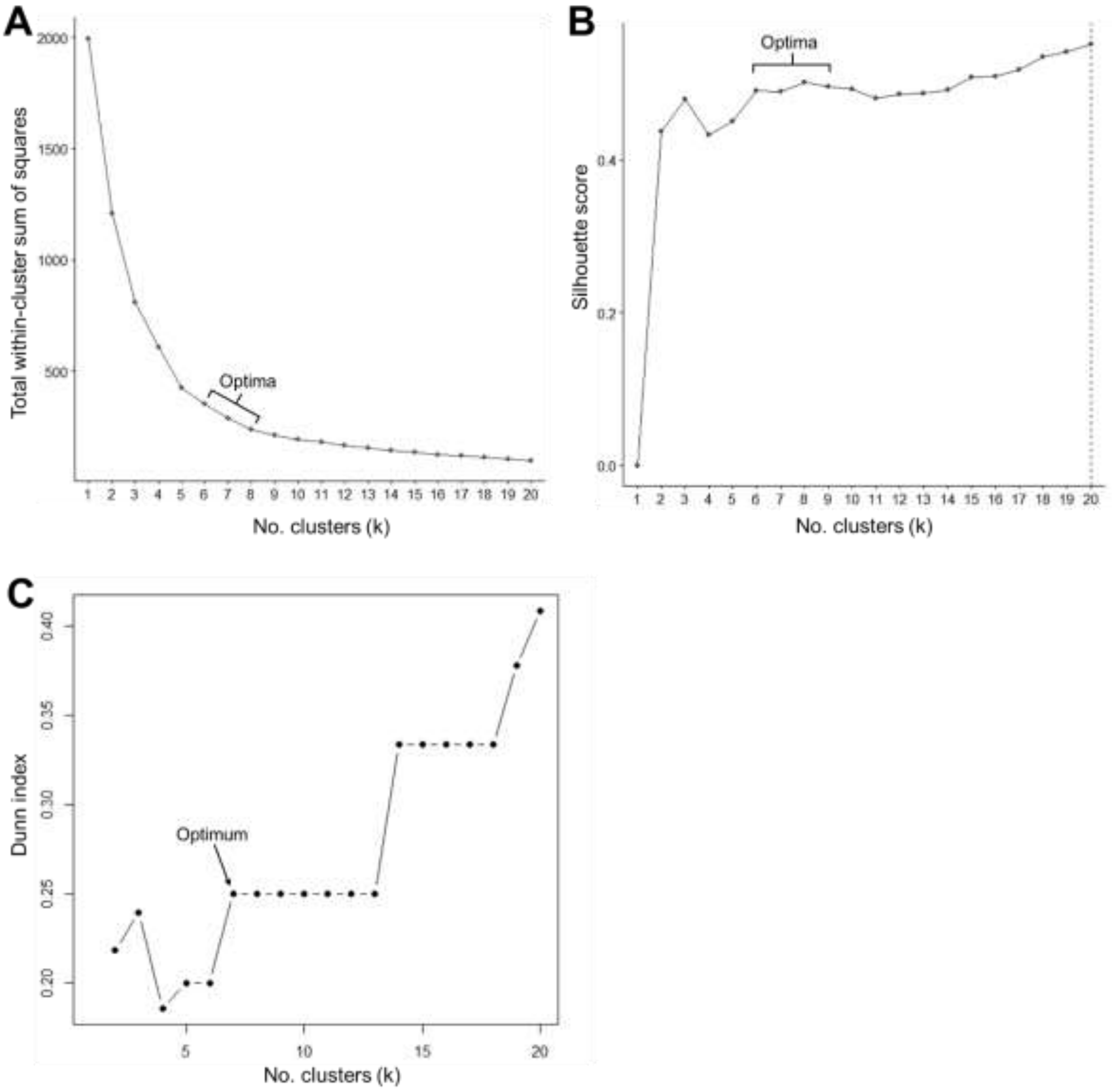
Generalists (n = 50): This cluster has a high mean score in digging ability associated with mean scores >1.00 in all other locomotor modes except aerial movement. This includes generalists with strong digging ability, such as the honey badger (*Mellivora capensis*), as well as generalists scoring 5 or more overall (no species in this cluster have an overall score <5) without a digging focus, such as the brown rat (*Rattus norvegicus*).

Runners (n = 37): This cluster is defined by scores of 3 or 4 in running ability. This includes the ‘cursorial’ animals, such as terrestrial ungulates, saltatorial species (e.g. the small five-toed jerboa (*Allactaga elater*), and some carnivorans.

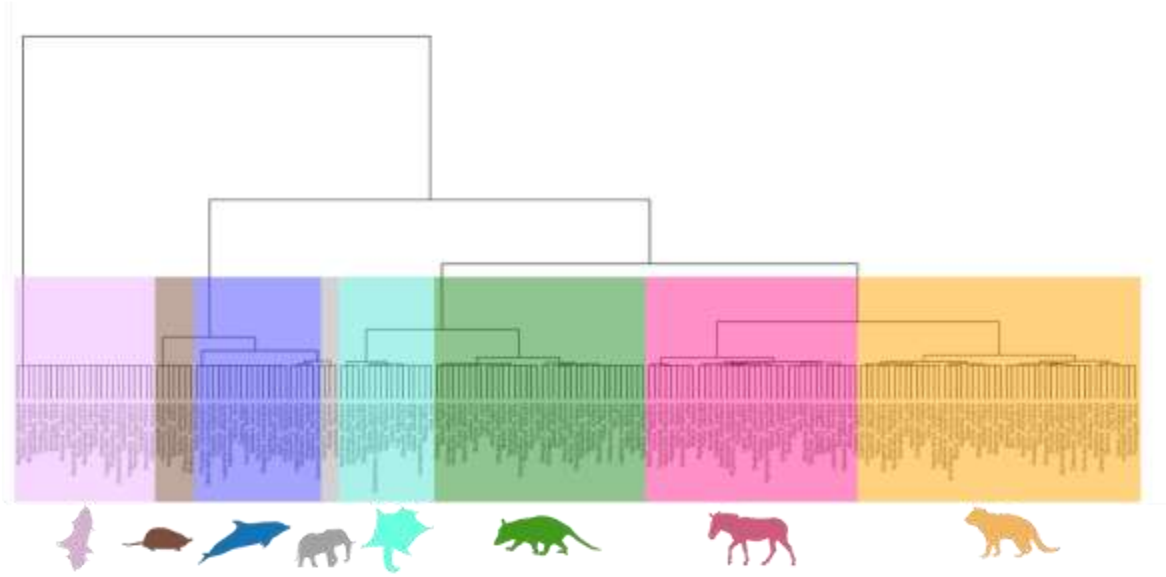
Subterranean (n = 7): This cluster contains the species which score 4 in digging ability associated with scores of 0 in climbing, running and aerial abilities.

Volant (n = 26): This cluster exclusively contains all the chiropterans, being the only taxa capable of powered flight. Species in this cluster are defined by their score of 4 in aerial movement ability, though they also score 4 in climbing ability.

Other (n = 3): Camel *(Camelus bactrianus),* African elephant *(Loxodonta africana)* and black rhino *(Diceros bicornis).* These are species with overall low scores which were placed in the aquatic cluster despite having low scores in swimming ability due to the greedy nature of hierarchical clustering (see Chapter II). For biological interpretability, these species are separated into their own cluster.



Appendix III.2 Figure 1: Results of optimal cluster number tests
Plots showing results of (A) Elbow method: total within-cluster sum of squares against cluster number; (B) Silhouette method: Silhouette scores against cluster number; and (C) Dunn Index values against cluster number. All plots show results for up to 20 clusters (k = 1 to 20) with local optima indicated.



	Volant	Sub*	Aquatic	Other	Aerial acrobats	Climbers	Runners	Generalists
n	25	7	23	3	17	38	37	50
Swimming	1 ± 0	1 ± 0	4 ± 0.25	2 ± 0	1 ± 0	1 ± 0	1 ± 0.5	1 ± 0.5
Climbing	4 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 0	3.5 ± 0.5	1 ± 0.5	2 ± 0.5
Digging	0 ± 0	4 ± 0	0 ± 0	1 ± 0	1 ± 0	1 ± 0.5	2 ± 1.5	3 ± 0.5
Running	0 ± 0	0 ± 0	0 ± 0	2 ± 0	1 ± 0.5	2 ± 0	4 ± 0	2 ± 0.5
Aerial	4 ± 0	0 ± 0	0 ± 0	0 ± 0	2 ± 0	0 ± 0	0 ± 0.5	0 ± 0

*Subterranean

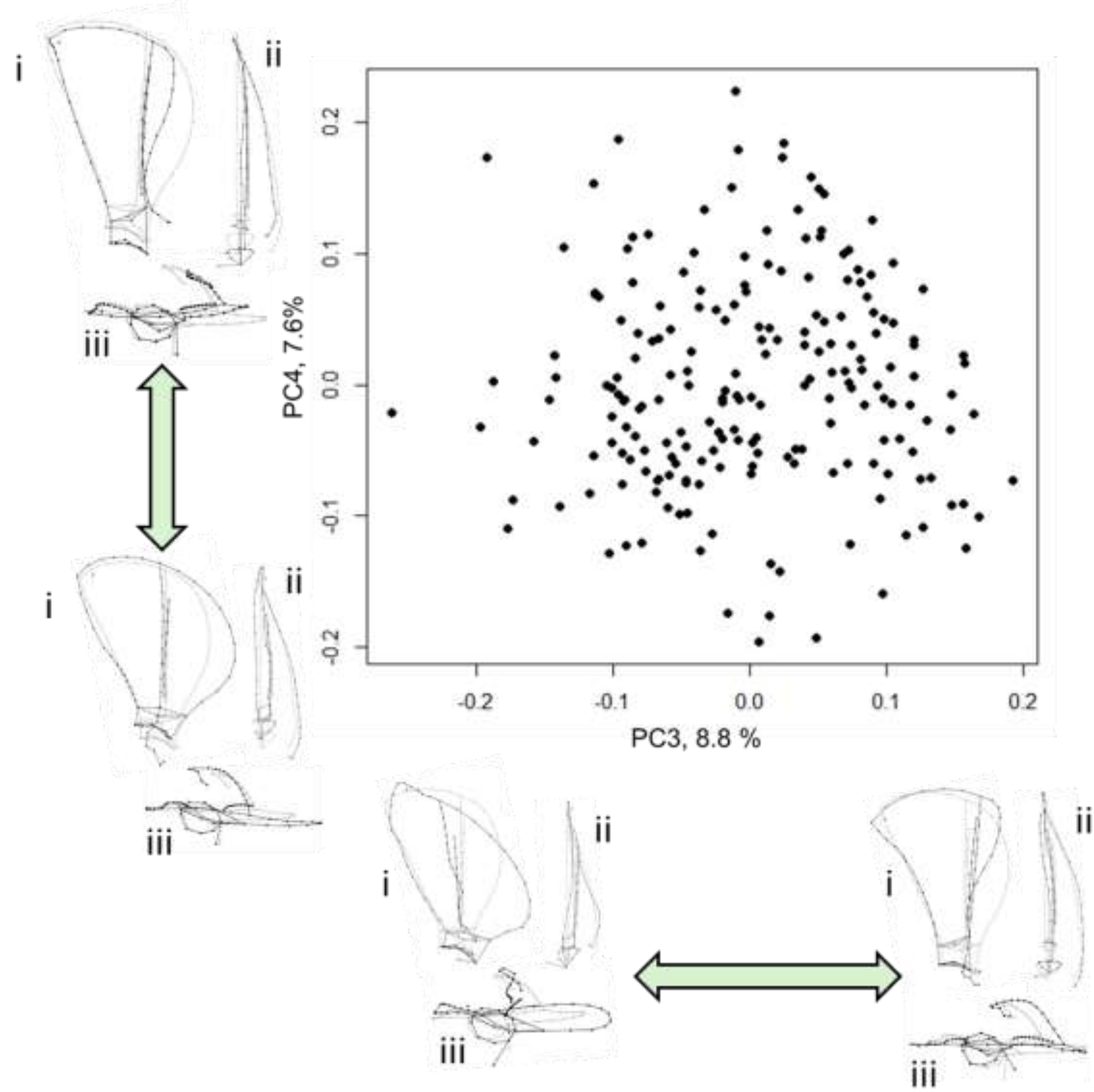
Appendix III.2 Figure 2: Summary of final locomotor clusters arising from hierarchical cluster analysis

(A) Dendrogram showing the hierarchical relationships of the 201 species based on their locomotor profiles, calculated using Ward's method. The identity of the eight clusters established previously as optimal are visualised and colour-coded here. Animal silhouettes are modified from PhyloPic (www.phylopic.org); species as follows from left to right: Pteropus medius *(Indian flying fox),* Condylura cristata *(Star-nosed mole),* Tursiops truncatus *(common bottlenose dolphin),* Loxodonta africana *(African elephant),* Petaurus breviceps *(sugar glider),* Didelphis virginiana *(Virginia opossum),* Equus africanus *(African wild ass), and* Sarcophilus harrisii *(Tasmanian devil).*

(B) The table provides median scores and quartile deviations (QD) for each locomotor variable in each cluster. In addition, the number of species in each cluster (n) is provided.

Appendix III.3: PC3-PC4 results

Shape variation



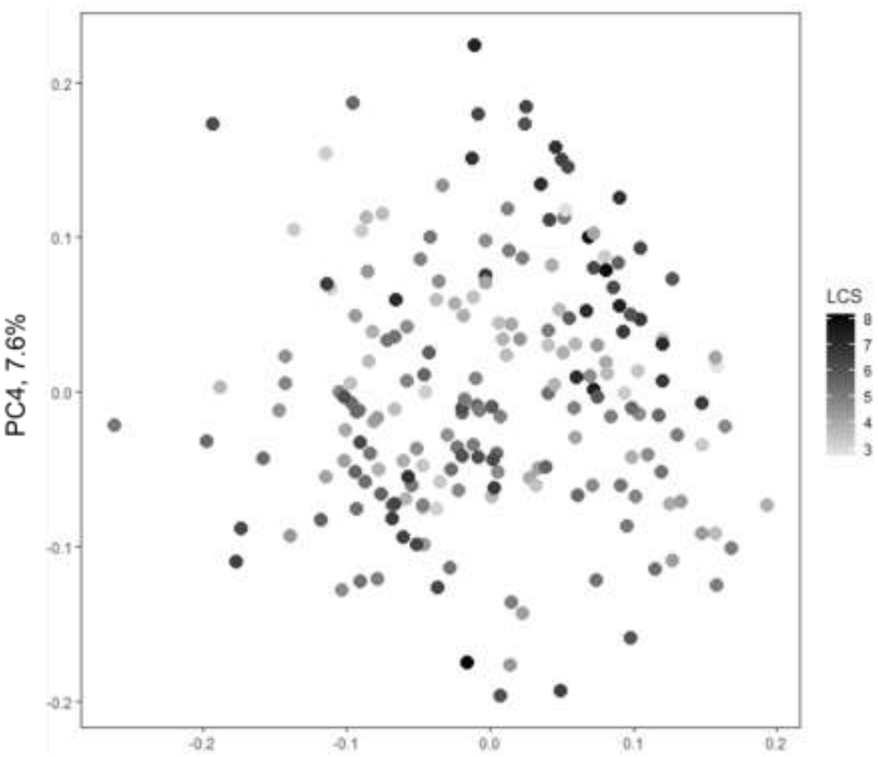
Appendix III.3 Figure 1: PC3-PC4 morphospace with shape changes
Scatter plot visualising the second two principal components (PCs), accounting for a total of 16.4% or total variation in the dataset. Shape changes on each axis are visualised as wireframes relative to the mean shape (grey). The wireframes are displayed in three views: i) lateral; ii) caudal; iii) glenoid.

Shape change on PC3 (8.8%, App. III.3 Figure 1) is primarily related to the size of the supraspinous fossa, the morphology of the vertebral border, and the relative prominence of the acromion and coracoid processes. At the negative end of PC3, the scapula is relatively broad, with the supraspinous fossa larger than the infraspinous.

The supraspinous fossa is widest at the glenoid end of the blade. The highest point of the scapula (dorsally) is the caudal angle, which is prominent. The glenoid is caudally-directed. The acromion process is greatly reduced, not extending beyond the glenoid, but the coracoid process is enlarged relative to the mean shape and caudally directed. The scapular spine is tallest at the glenoid end, and is very short for much of its vertebral end. At the positive end of PC3, the scapula is slimmer, with the supraspinous fossa significantly reduced. The blade has an overall triangular shape. The highest point of the blade is approximately the centre of the vertebral border, caudal to the scapular spine. The scapular neck is long and slim, and the glenoid is ventrally-directed. The acromion is prominent, extending beyond the glenoid cranially, and the coracoid is reduced and cranially-directed. The scapular spine is relatively tall along its entire length.

Shape change on PC4 (7.6%, App. III.3 Fig. 1) is primarily related to the size of the supraspinous fossa, the associated length of the vertebral border, and the direction of the acromion process. At the negative end of PC4, the scapula is wide with the supraspinous fossae being slightly larger than the infraspinous. The supraspinous fossa is widest at approximately half the height of the blade. The highest point of the scapula (dorsally) is the caudal angle. The glenoid is caudally-directed. The acromion is enlarged and extends beyond the glenoid ventrally. The coracoid is approximately unchanged from the mean shape. The scapular spine is relatively tall along its entire length. At the positive end of PC4, the blade is slim and the supraspinous fossa is significantly reduced. The blade has an overall triangular shape. The scapular neck is long and slim and the glenoid is ventrally-directed. The acromion is highly cranially-directed and the coracoid is approximately unchanged from the mean shape. The scapular spine is relatively tall along its entire length.

Size and allometry



Appendix III.3 Figure 2: Visualisations of size gradient (logCS) in the PC3-PC4 morphospace
Scatter plot visualising the second two principal components (PCs), accounting for a total of 16.4% or total variation in the dataset, coloured according to the value of log centroid size (logCS).

Within the PC3-PC4 morphospace (App. III.3 Fig. 2), it is difficult to determine visually how the morphospace may be influenced by variation in size. There are two main hotspots associated with high logCS, in the positive halves of both axes and in the negative halves of both axes. As will be discussed further, these areas represent the Euungulata and the Ferae, respectively.

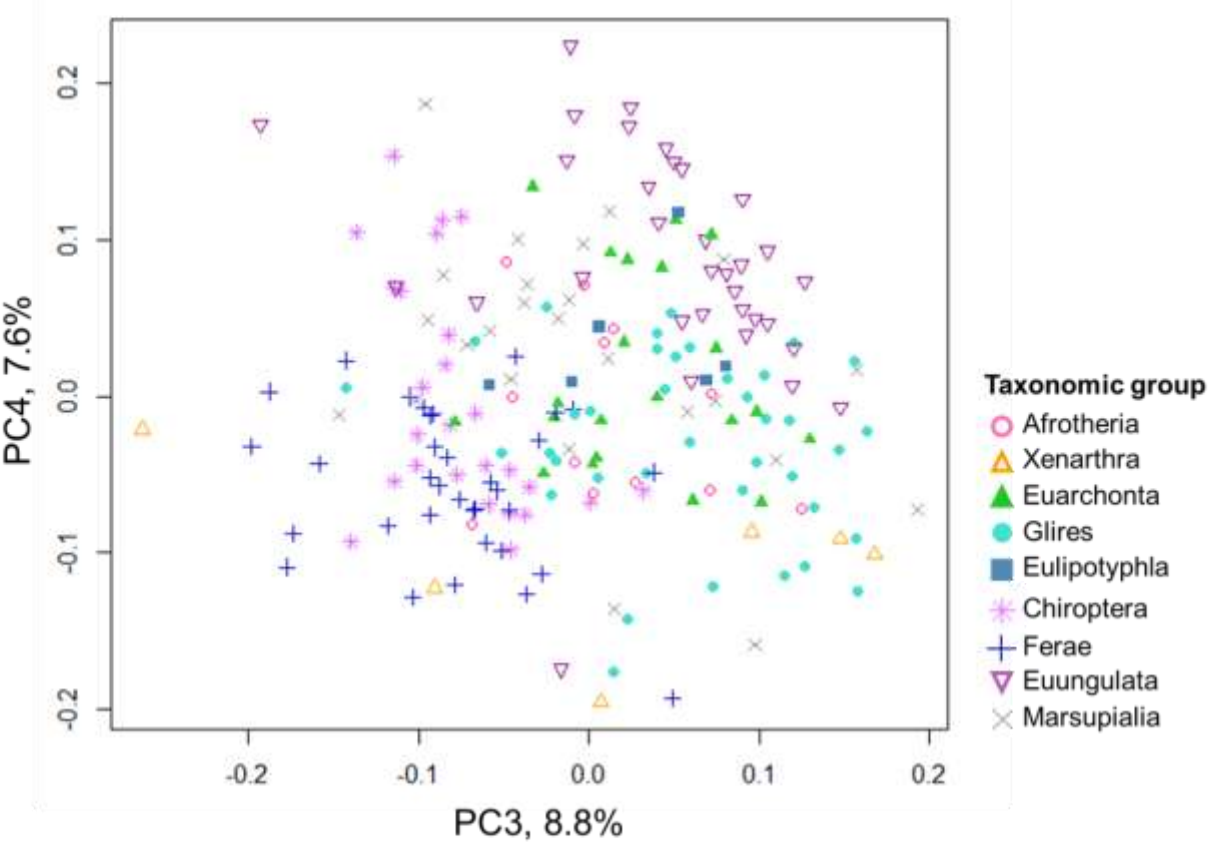
Appendix III.3 Table 1: Results of the allometric PGLS regressions
These tables provide the results of PGLS regressions of A) PC3 against log centroid size (logCS), and B) PC4 against log centroid size (logCS). The regressions are performed on the full dataset, a subset excluding cetaceans, a subset excluding chiropterans, and a subset excluding both. The tables provide p-values, adjusted correlation coefficient (R^2), and Pagel's lambda (λ).

A) PC3, 8.8%	**n**	**R^2**	**Pagel's lambda (λ)**	**p-value**
All species	201	0.012	0.96	0.068
Minus cetaceans	186	0.005	0.95	0.162
Minus chiropterans	175	0.018	0.96	***0.04****
Minus cetaceans & chiropterans	160	0.011	0.95	0.096

B) PC4, 7.6%	**n**	**R^2**	**Pagel's lambda (λ)**	**p-value**
All species	201	0.016	0.85	***0.04****
Minus cetaceans	186	Fails to run		
Minus chiropterans	175	0.014	0.85	0.062
Minus cetaceans & chiropterans	160	0.006	0.91	0.165

As shown in in App. III.3 Table 1, PC3 is only significantly related to logCS when chiropterans are excluded ($p = 0.04$, $R^2 = 0.018$) and this trend is negative. PC4 is only significantly related to logCS when all species are included ($p = 0.04$, $R^2 = 0.016$) and this trend is also negative. Overall, these trends indicate that increased size is generally associated with an enlarged vertebral border and increased supraspinous dominance. The relatively low values of R^2 indicate that these trends are not as strong as significant trends on PC1 and PC2.

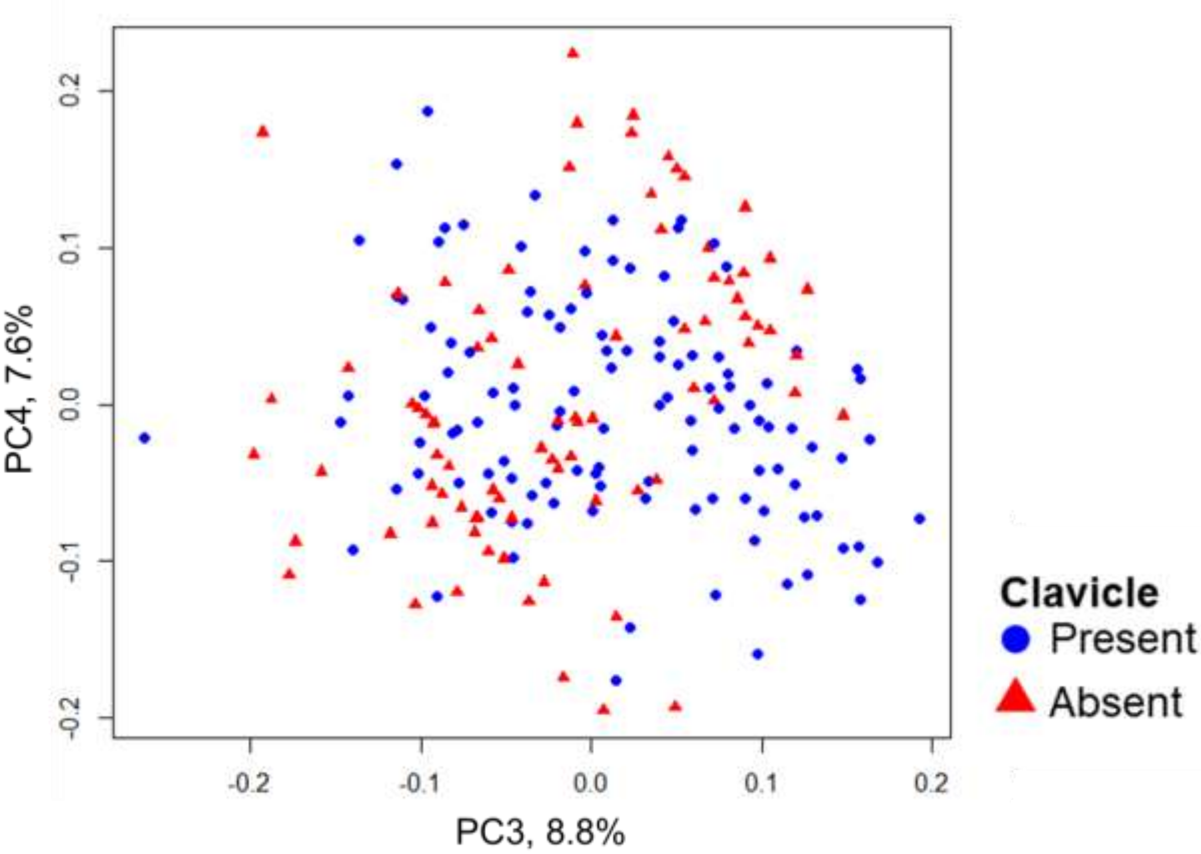
Evolutionary history



Appendix III.3 Figure 3: PC3-PC4 morphospace visualised by taxonomic group
Scatter plot visualising the second two principal components (PCs), accounting for a total of 16.4% or total variation in the dataset. Points are differentiated into the nine taxonomic groups.

There is some clustering of taxonomic groups in the PC3-PC4 morphospace (App. III.3 Fig. 3), which is the clearest relationship of any variables included here to the arrangement of the PC3-PC4 morphospace. Particularly, **Ferae** are clustered in the negative half of both axes, with most species below zero on both, while **Euungulata** (both cetaceans and terrestrial) are located in the positive half of both axes, with most species above zero. There is very little overlap between the Ferae and Euungulata. This indicates that both groups are morphologically differentiated by relative size of the supraspinous fossa (which is larger in Ferae), the length of the vertebral border (which is much longer in Ferae), and the orientation of the glenoid (which is more caudal in Ferae and more ventral in Euungulata). The **Chiroptera** are found in the negative half of PC3 and spread across PC4. **Xenarthra** are all located in the negative half of PC4, spread across PC3. **Marsupials** are generally located in the negative half of PC3 and spread across PC4. **Glires** are mostly located in the positive half of PC3 and the negative half of PC4, while the **Euarchonta** are also found in the positive half of PC3 but extend higher on PC4. **Afrotheria** are widely distributed around the centre of the morphospace.

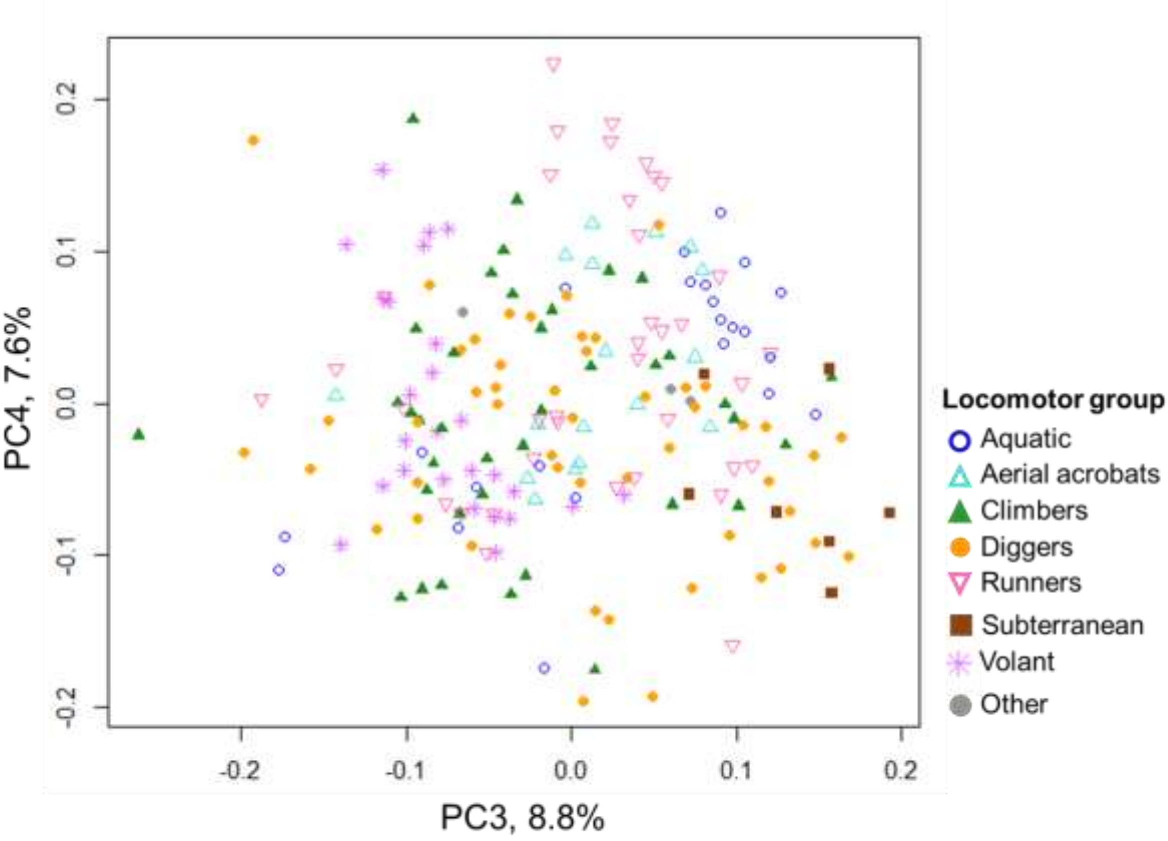
Clavicle presence



Appendix III.3 Figure 4: PC3-PC4 morphospace visualised by clavicle presence
Scatter plot visualising the second two principal components (PCs), accounting for a total of 16.4% of shape variation in the dataset. Points are differentiated into claviculate (blue circles) and aclaviculate (red triangles) species.

There is no evidence of clustering of claviculate versus aclaviculate taxa in the PC3-PC4 morphospace, with both groups distributed approximately equally around the space (App. III.3 Fig. 4).

Locomotion



Appendix III.3 Figure 5: PC3-PC4 morphospace visualised by locomotion group

Scatter plot visualising the second two principal components (PCs), accounting for a total of 16.4% of shape variation in the dataset. Points are differentiated into the eight locomotion groups.

As in the PC1-PC2 morphospace, the **cetaceans** are separated spatially from the **other aquatic** species, primarily on PC3 (App. III.3 Fig. 5). Many of the **runners** are located between 0.0 and 0.1 on PC3, but spread widely across PC4, representing a slim blade which is infraspinous-dominated, but variability in the morphology of the acromion. However, other runners are found in the negative half of PC3 but mostly in the negative half of PC4. **Subterranean** species are all found at the positive end of PC3 and in the negative half of PC4, representing a slim and infraspinous-dominated blade and ventrally-directed acromion. **Climbers, generalists** and **aerial acrobats** are distributed widely around the morphospace and overlap considerably with one another. The **volant** species have already been discussed (as Chiroptera) and are found below 0.0 on PC3 but distributed widely on PC4.

Chapter IV

Of mice and many more:

Functional morphology of the rodent scapula

A manuscript version of this chapter is in preparation for submission to the Zoological Journal of the Linnean Society.

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Research Degree Thesis Statement of Authorship

Note that where a paper has multiple authors, the statement of authorship can focus on the key contributing/corresponding authors.

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Thesis title	Shoulder to shoulder: Comparative functional morphology of the scapula across therians

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Approximate percentage contribution of the candidate to the work (*if possible to describe in this way*)	**N/A**
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Date (DD/MM/YY)	**10/12/2025**

Co-author contributions

By signing this Statement of Authorship, each co-author agrees that:

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Signature of the co-author	
Date (DD/MM/YY)	10/12/2025

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*The description of the candidate and co-authors contribution to the work may be framed in a manner appropriate to the area of research but should always include reference to key elements (e.g. for laboratory-based research this might include formulation of ideas, design of methodology, experimental work, data analysis and presentation, writing). Candidates and co-authors may find it helpful to consider the CRediT (Contributor Roles Taxonomy) approach to recognising individual author contributions.

IV.1. Introduction

Previous research, supported by the results of Chapter III, indicates that scapular morphology in therian mammals is highly complex and influenced by a mosaic of factors both functional and phylogenetic. In the context of locomotion, similar behavioural repertoires have arisen across multiple taxonomic groups (e.g. specialised aquatic behaviour occurs in sirenians, carnivorans, and cetaceans). However, therians from different taxonomic groups which share behaviours do not necessarily share identifiable morphological characteristics of the scapula. In fact, evolutionary history appears to obfuscate some of the functional information which may be contained within scapular morphology. Therefore, in order to delve deeper into this topic it is necessary to narrow the taxonomic breadth of the dataset. The order Rodentia presents the ideal candidate for this purpose due to the size and diversity of the order, the success of rodents across almost every land mass globally, their unprecedented diversity of locomotion behaviour, large size range, and unusually variable clavicle presence within the group.

Rodentia is the most speciose group of extant mammals, containing over 2,500 living species (Burgin et al. 2018) and accounting for almost 40% of all extant therian mammals. Rodents originated within a few million years of the K-Pg boundary (approximately 66 Mya), sharing an earlier common ancestor with Lagomorpha (Huchon et al. 2002; Churakov et al. 2010; Fabre et al. 2012; Wu et al. 2012; Phillips & Fruciano 2018; Iraçabal et al. 2024). Since then, rodents have diversified to occupy every major land mass except Antarctica (Fabre et al. 2012). They are defined by their possession of a single pair of ever-growing incisors on both their maxilla and mandibles which facilitate a herbivorous lifestyle for most species, but opportunistic omnivory is common (Nowak 1999). Rodent success and diversity may be related to their unusually high nucleotide substitution rates, which result in a functionally high rate of evolution and adaptation (Weinreich 2001; Churakov et al. 2010). This also means that the group is ideal for studies of functional morphology because of the inherent potential for diversity facilitated by this rapid evolution, something which has led both Hautier & Cox (2015) and Fabre et al. (2012) to note Rodentia's potential as a model order for the study of factors promoting morphological diversity.

Rodent phylogeny is historically contentious, largely owing to rodents' rapid diversification, but the advent of molecular phylogenetic methods has moved the field towards a consensus in spite of high nucleotide substitution rates confounding molecular clock estimates due to long branch attraction (Churakov et al. 2010). It is now broadly accepted that rodents can be divided into five monophyletic groups: Anomaluromorpha, Castorimorpha, Hystricomorpha, Myomorpha, and Sciuromorpha (Adkins et al. 2003; Montgelard et al. 2008; Blanga-Kanfi et al. 2009; Fabre et al. 2012; D'Elia et al. 2019). However, the root of this phylogeny remains uncertain, with debate surrounding whether Sciuromorpha or Hystricomorpha are the most basal, or whether a trifurcation of Sciuromorpha, Hystricomorpha, and a mouse-related clade (including the three remaining groups) is more accurate (Adkins et al. 2001; Blanga-Kanfi et al. 2009; Fabre et al. 2012; D'Elia et al. 2019). It should be noted that the terms Hystricomorpha, Myomorpha and Sciuromorpha above are being used purely as clade names (following D'Elia et al. 2019) and do not align with the hystricomorphous, myomorphous and sciuromorphous configurations of the jaw-closing muscles (Wood, 1965). While rodent phylogeny has become increasingly well understood, scapular variation across this vast order remains understudied and confined to certain groups (sciuromorphs [Swiderski 1993; Wölfer et al. 2019], caviomorphs [Morgan 2009], echimyids [Carvalhaes et al. 2022] and lab mice [Kimes et al. 1981; Green et al. 2012]). What stands out, though, is the strong influence of phylogeny on scapular morphology in rodents, as will be discussed further.

While the functional morphology of the rodent scapula has been investigated by several authors, their focus on specific rodent groups makes it impossible to draw general conclusions across the whole clade. In fact, many of the previous studies present contradictory results in different rodent groups. Chapter III identified that the most variable aspects of the scapula across therians are blade width and ratio of the lateral fossae, acromion length and orientation, coracoid prominence, and vertebral border morphology. Carvalhaes et al. (2022) found this to be the case in echimyids, but Morgan (2009) found the most variable regions of the caviomorph scapula to be the scapular spine, and the greater scapular notch (the most ventral region where the scapular spine rises laterally from the blade). In agreement with Chapter III and Carvalhaes et al., Kimes et al. (1981) and Green et al. (2012) found that, in response to behavioural constraint, the most variable regions of the scapula in lab mice were blade width and ratio of the lateral fossae. Meanwhile, Swiderski (1993) found that the most variable regions of the sciuromorph scapula were the scapular neck and vertebral border. These findings variably agree with the results of Chapter III, but point to not only scapular diversity in rodents, but also disparity among different locomotor groups.

It is expected that the results of this chapter focusing on rodents will reflect the same functional adaptations of the scapula observed in Chapter III across therians. However, previous research indicates that functional morphology of the rodent scapula may be significantly influenced or, indeed, entirely obfuscated, by phylogenetic inertia. Therefore, the aim of this chapter is to determine, **are there aspects of scapular morphology which can be consistently associated with function in rodents, and do these align with the findings of Chapter III across therians?**

IV.1.1. Size and allometry

Hypothesis IV.1A ($H_{IV.1A}$): Body size will significantly affect scapular morphology.

Hypothesis IV.1B ($H_{IV.1B}$): Large size will be associated with an enlarged vertebral border.

It was found in Chapter III that, in therians generally, large size is significantly associated with increased scapular blade width, elongation of the vertebral border and enlargement of the glenoid fossa. This is in line with functional predictions and previous research, and can be explained as adaptation towards increased attachment areas for musculature involved in weight-bearing, which are located primarily along the vertebral border (Jenkins 1974; Stein 1981; Polly 2007; Fujiwara et al. 2009; Preuschoft et al. 2010), as well as reinforcement of the joint. Rodents vary considerably in size, though to a far lesser extent than therians as a whole. The smallest extant rodent is the Baluchistan pygmy jerboa (*Salpingotulus michaelis*) which weighs approximately 3.2g (though the smallest species in this dataset is the Northern pygmy mouse [*Baiomys taylori*] which weighs approximately 8g), while the largest extant rodent is the capybara (*Hydrochoerus hydrochaeris*) which weighs up to 66kg (Nowak 1999). However, previous studies have not identified a consistent or strong effect of size on scapular morphology in rodents. Morgan (2009) found no significant relationship between scapular morphology and size in caviomorphs, while Carvalhaes et al. (2022) found a significant but low correlation in echimyids. In sciuromorphs, however, significant relationships between scapular morphology and size have been identified, but are dependent on locomotion behaviour (Wölfer et al. 2019). Increased size in arboreal species was associated with enlargement of the supraspinous fossa adjacent to the scapular neck and lengthening of the attachment for the *m. teres major* (the latter of which was also found to be the case in gliders), while increased size in fossorial species is associated with increased blade width.

IV.1.2. Evolutionary history

Hypothesis IV.2 ($H_{IV.2}$): There will be a significant effect of evolutionary history on scapular morphology, potentially greater than that of the other factors.

The results of Chapter III indicate a significant influence of evolutionary history on scapular variation across therians. Additionally, this has also been found in rodents, where the influence of evolutionary history is stronger than any other factor investigated (Morgan 2009; Carvalhaes et al. 2022; de Oliveira et al. 2025). Therefore, it is predicted that the same results will be found across the whole order Rodentia.

IV.1.3. Clavicle presence

Hypothesis IV.3A ($H_{IV.3A}$): Scapular morphology will significantly differentiate claviculate and aclaviculate species.

Hypothesis IV.3B ($H_{IV.3B}$): Aclaviculate species will exhibit a reduced acromion and more curved vertebral border (with a lower caudal angle).

It was found in Chapter III that clavicle presence or absence was clearly differentiated in scapular morphology. Clavicle loss was associated with reduction of the acromion process and a more convex vertebral border with lower caudal angle. While the majority of extant rodents are claviculate, the clavicle is reduced in some Caviomorpha to a degree that can be considered clavicle loss in the context of this thesis, since an osseous clavicle does not articulate with the acromion or manubrium (Rocha-Barbosa et al. 2002). Based on biomechanical predictions and the ecologies of cavioid rodents exhibiting reduced clavicles, Rocha-Barbosa et al. (2002) interpreted clavicle reduction in these rodents as part of an adaptation towards cursoriality, particularly as they did not find any association between body size and clavicle reduction. Five aclaviculate species are included here, all of which were also included in the therian-wide dataset for Chapter III: the capybara (*Hydrochoerus hydrochaeris*), the Patagonian mara (*Dolichotis patagonum*), the red-rumped agouti (*Dasyprocta leporina*), the montane guinea pig (*Cavia tschudii*), and the African crested porcupine (*Hystrix cristata*). While previous research has described differences in myology associated with clavicle reduction in rodents (Rocha-Barbosa et al. 2002), the effects which this reduction may have on scapular morphology have not been explicitly explored.

IV.1.4. Locomotion behaviour

Hypothesis IV.4A ($H_{IV.4A}$): There will be identifiable morphological distinctions between functionally different locomotor groups.

Hypothesis IV.4B ($H_{IV.4B}$): Aerial movement adaptation will be associated with an elongated coracoid.

Hypothesis IV.4C ($H_{IV.4C}$): Climbing/aerial and running specialisations will be associated with opposing morphologies.

Hypothesis IV.4D ($H_{IV.4D}$): Subterranean specialisation will be associated with a very slim scapula blade.

Rodents exhibit a wide range of locomotion behaviours (though none are obligately aquatic or capable of powered flight), and this is largely not taxonomically constrained. Locomotion behaviour was found to have a significant and complex relationship with scapular morphology across therians in Chapter III, influenced considerably by evolutionary history, clavicle presence, and size. Likewise, previous research on rodent scapular morphology indicates a nuanced locomotion-morphology relationship, dependent on evolutionary constraints and influences of size. Morgan (2009) found evidence of differences in scapular morphology associated with differences in locomotion behaviour in caviomorphs, but this was obfuscated by clade-specific behaviour (e.g. members of Erethizontoidea are generally semi-terrestrial climbers, while Cavioidea are mainly generalists and runners). Wölfer et al (2019) found that the three different locomotor groups they investigated in sciuromorphs (arboreal, gliding, and fossorial) exhibited different allometric trends, so the influence of locomotion behaviour on scapular morphology was challenging to disentangle from differences associated with size. However, they also identified that morphology of the acromion region was particularly linked to differences in locomotion, specifically that in the transition from gliding to arboreal to fossorial behaviour, the acromion tip (hamatus process) becomes less prominent and the metacromion becomes more prominent. Under experimental conditions, both Kimes et al. (1981) and Green et al. (2012) found that lab mice which have been behaviourally constrained to vertical climbing exhibit identifiable, but contradictory, morphological changes to their scapulae. Green et al. found that the climbing mice had wider infraspinous fossae than controls, and Kimes et al. found that the climbing mice had overall slimmer blades than controls. Green et al. additionally found that mice constrained to running on a wheel had even more morphologically different scapulae from the controls than the climbing mice did. The running mice had wider scapulae with large attachments for the *m. supraspinatus*, *m. infraspinatus*, *m. teres major* and *m. subscapularis*. Meanwhile, however, Carvalhaes et al. (2022) found no significant influence of locomotion behaviour on scapular morphology in echimyids, but noted that humerus morphology is significantly influenced by locomotion behaviour.

Synthesising previous findings highlights the complexity of rodent scapular morphology and the challenges associated with disentangling functional adaptation from phylogenetic influence and other factors like size and clavicle presence. This is a familiar situation, not dissimilar from the findings of Chapter III across therians. By examining scapular shape across extant rodents in a phylogenetically informed framework, this chapter seeks to clarify the extent to which morphology reflects functional demands – size, clavicle presence and, crucially, locomotion behaviour. Importantly, this chapter will reveal if rodents can be considered a microcosm of therians with regard to scapular functional morphology, closely reflecting the influences of functional demands on the scapula across therians.

IV.2. Materials & methods

The same multivariate analyses are used in this chapter as are used in Chapter III, with any deviation explained within the text.

IV.2.1. Data acquisition

IV.2.1.1. Specimen acquisition

Specimens of 87 extant rodent species are included in this study (one specimen per species), representing 34 of the 36 extant rodent families (Burgin et al. 2018). Specimens representing Petromuridae and Dinomyidae, both monospecific families, could not be obtained for this study. Details of each specimen are available in S.IV.1.A. These species were selected based on availability and completeness of the scapulae, with the goal of including a broad range of taxonomic groups and locomotion profiles. Within this dataset, 37 specimens are carried over from Chapter III, and 50 are cccnew additions to this dataset. Specimens were acquired primarily from MorphoSource (www.morphosource.org; accessed 2021-2025), as well as Natural History Museum (NHM, London), University of Cambridge Museum of Zoology, and Muséum National d'Histoire Naturelle (Paris). As Chapter III, several specimens were available to download as scapula surface files, but the majority were downloaded as CT image data (TIFF files) which were segmented in Avizo v. 9 (Thermo Fisher Scientific, Waltham, MA, USA) to extract a scapula surface file. A small number of specimens from the NHM London and the University of Cambridge Zoology Museum were scanned using an Artec Space Spider surface scanner (Artec 3D, Luxembourg), while many were CT scanned in-house by the museums. Specimens from the Muséum National d'Histoire Naturelle (Paris) were CT scanned at the University of Montpellier, courtesy of Dr Pierre-Henri Fabre and Dr Lionel Hautier. Scan resolution ranged from 1-120μm with a variable range of current intensity (up to 2000μA) and power (up to 450W) based on specimen size and preservation status.

IV.2.1.2. Scapular morphology

The landmark configuration used in Chapter III (Fig. III.4 & Table III.2) was used here without alteration. The 37 rodents included here and in Chapter III were not re-landmarked for this chapter. Landmarking and Procrustes superimposition were carried out as described in Chapter III. Values for centroid size of the scapula were obtained during this process. As in Chapter III, wireframes provided throughout this chapter were obtained from MorphoJ v. 1.07a (Klingenberg 2011) following Procrustes superimposition.

IV.2.1.3. Evolutionary history

The phylogeny used for this chapter was obtained from VertLife.org (Upham et al. 2019). Additionally, the rodents are divided into a categorical variable representing the monophyletic suborders identified by D’Elia et al. (2019): Anomaluromorpha (n = 3), Castorimorpha (n = 5), Hystricomorpha (n = 18), Myomorpha (n = 49), and Sciuromorpha (n = 12).

IV.2.1.4. Clavicle presence

As in Chapter III, for the purposes of this work, the clavicle is considered to be present if there is an osseous structure articulating with the acromion and manubrium, and absent if this is not the case. The vast majority of rodents are claviculate, with some hystricomorphs having become aclaviculate, five of which are included here (see Section IV.1.3.). This information was obtained from literature review (Trotter 1885; Rocha-Barbosa et al. 2002).

IV.2.1.5. Locomotion behaviour

The method for quantifying locomotion established in Chapter II was used here to obtain a scoring matrix and categorical variable specific to these 87 species (S. IV.2). A full description of the process is provided in Appendix IV.1. Following these results, eight clusters are used in this chapter: Climbers (n = 8), Specialised climbers (n = 12), Aerial acrobats (n = 3), Diggers (n = 10), Subterranean (n = 4), Swim-dig (n = 5), Runners (n = 15), and Generalists (n = 30).

IV.3. Results

IV.3.1. Variation in scapular morphology

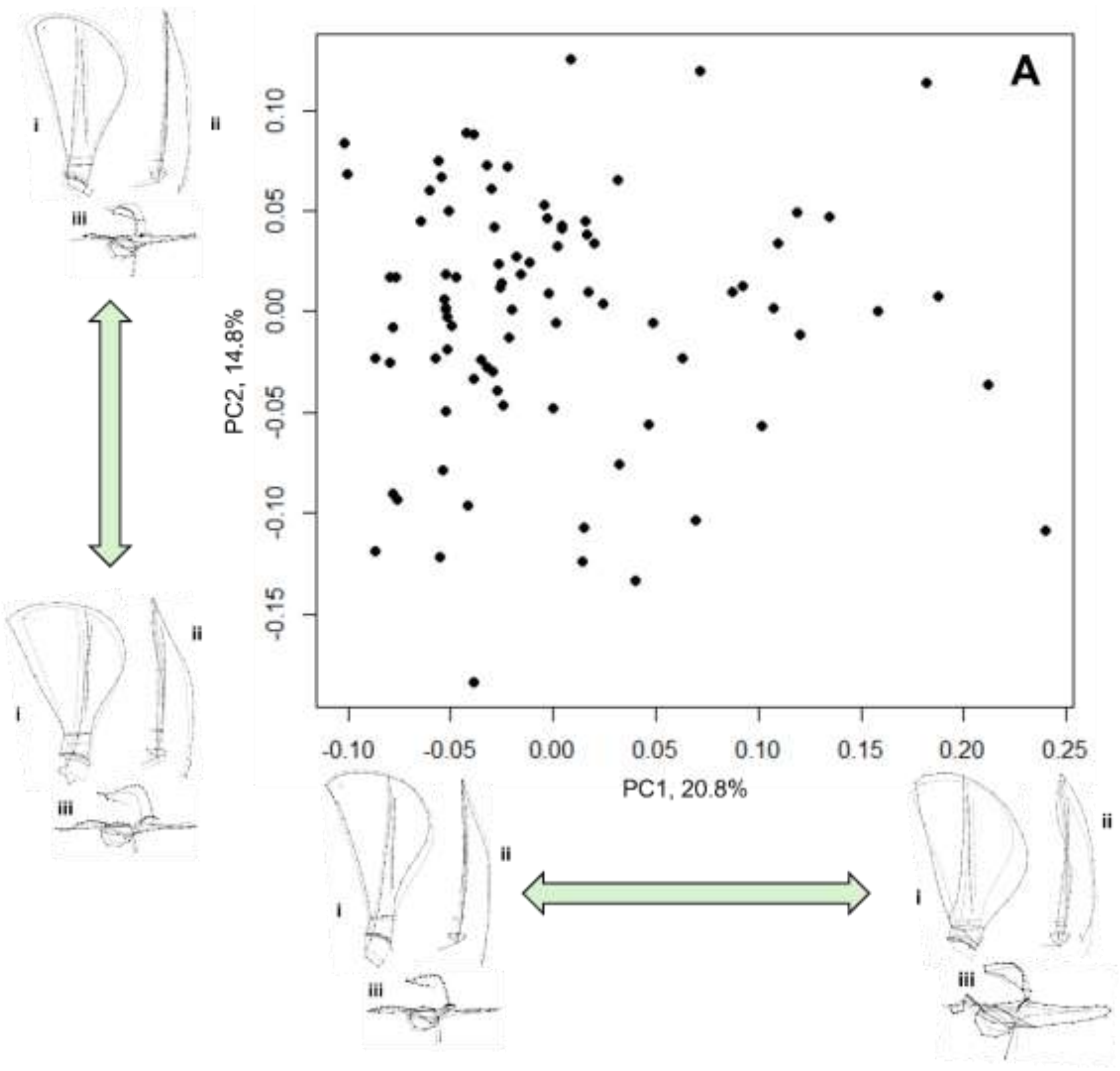
For the most part, the first four PCs are discussed in the main text of this chapter, representing a total of 58.6% of scapular variation. According to a broken stick model, the first six PCs are interpretable. Investigation of PC5 and PC6 can be found in Appendix IV.2, but these PCs are discussed in the main text in the context of size and allometry due to particular relevance. Overall, the most variable areas of the scapula in rodents are blade width, acromion prominence and morphology, vertebral border morphology, and coracoid process prominence.

Shape change on PC1 (Fig. IV.1A) is predominantly related to blade width and relative size of the lateral fossae, the morphology and position of the acromion, and the morphology of the vertebral border and caudal angle. At the **negative extreme of PC1**, the scapula is slim with a slightly larger infraspinous fossa than supraspinous. The caudal angle is prominent and acute, and slightly lower than the vertebral end of the scapular spine. The scapular neck is slim. The acromion is prominent and extends ventrally far beyond the glenoid, more so than it does in the mean shape. The coracoid process is slightly shorter than it is in the mean shape. At the **positive extreme of PC1**, the scapula is wider, particularly the supraspinous fossa which is larger than the infraspinous. The supraspinous fossa is widest close to the middle of the blade height. The scapular neck is wide, and the glenoid is large and somewhat caudally-directed. The caudal angle is not particularly prominent, but is higher dorsally than at the negative end of PC1. The acromion is reduced and does not extend beyond the glenoid. However, both the acromion and metacromion are well-defined, with the acromion tip directed highly cranially. The coracoid process is elongated and directed caudally towards the joint.

Shape change on PC2 (Fig. IV.1A) is predominantly related to width of the scapular blade, the size of the glenoid, and the orientation of the acromion and coracoid processes. At the **negative extreme of PC2**, the scapula is wide, particularly at the vertebral end, with a larger infraspinous fossa than supraspinous. The scapular neck is slim, but the glenoid is somewhat enlarged. The caudal angle is prominent and acute. The acromion is prominent and directed ventrally, with a distinct metacromion directed caudally. The coracoid is slightly reduced and directed a little more cranially than in the mean shape. At the **positive extreme of PC2**, the blade is smaller than the mean shape overall, being slimmer and shorter. The lateral fossae are approximately equal in size. The scapular neck is slim and the glenoid is small. The caudal angle is not well-developed, and is higher than the vertebral end of the scapular spine. The acromion is prominent, extending beyond the glenoid ventrally, with the acromion tip directed highly cranially. The coracoid process is slightly elongated but is oriented in the same direction as the mean shape.

Shape change on PC3 (Fig. IV.1B) is predominantly related to blade width, caudal angle prominence, acromion morphology, and coracoid prominence. The majority of species are located within the range ± 0.08 on PC3. At the **negative extreme of PC3**, the blade is very wide and the infraspinous fossa is slightly larger than the supraspinous. The caudal angle is very prominent and acute. The scapular neck is slim relative to the blade, with the glenoid approximately the same size as in the mean shape. The glenoid is slightly cranially-oriented relative to the mean shape. The acromion process is prominent and, while much of the process is ventrally-directed, the tip is cranially-directed. The coracoid process is reduced and cranially-directed. At the **positive extreme of PC3**, the blade is very slim, being barely wider than the scapular neck throughout its entire height. The lateral fossae are approximately equal in size. The caudal angle is relatively reduced. The glenoid is somewhat caudally-oriented relative to the mean shape. The acromion process is broad and ventrally-directed (barely extending beyond the glenoid), with a somewhat cranially-directed tip, and the metacromion is distinct. The coracoid process is elongated and caudally-directed.

Shape change on PC4 (Fig. IV.1B) is predominantly related to the orientation of the acromion, the length and orientation of the coracoid process, the relative height of the caudal angle, and the relative depth of the attachment area for the *m. teres major*. At the **negative extreme of PC4**, the blade is approximately similar in width to the mean shape, with a slightly larger infraspinous fossa. The caudal angle is high dorsally relative to the end of the scapular spine, and the attachment area of the *m. teres major* is prominent and well-developed. The glenoid is oriented somewhat caudo-laterally relative to the mean shape. The acromion is prominent and cranially-directed. The coracoid process is elongated and caudally-directed. At the **positive extreme of PC4**, the blade is also similar in size to the mean shape, but with a slightly reduced infraspinous fossa. The caudal angle is low relative to the end of the scapular spine. The attachment area for the *m. teres major* is developed but notably less so than at the negative extreme. The scapular neck is slim and elongated relative to the mean shape. The glenoid is somewhat cranially-oriented. The acromion is prominent and caudally-directed with a ventrally-directed tip. The coracoid process is reduced and cranially-directed.



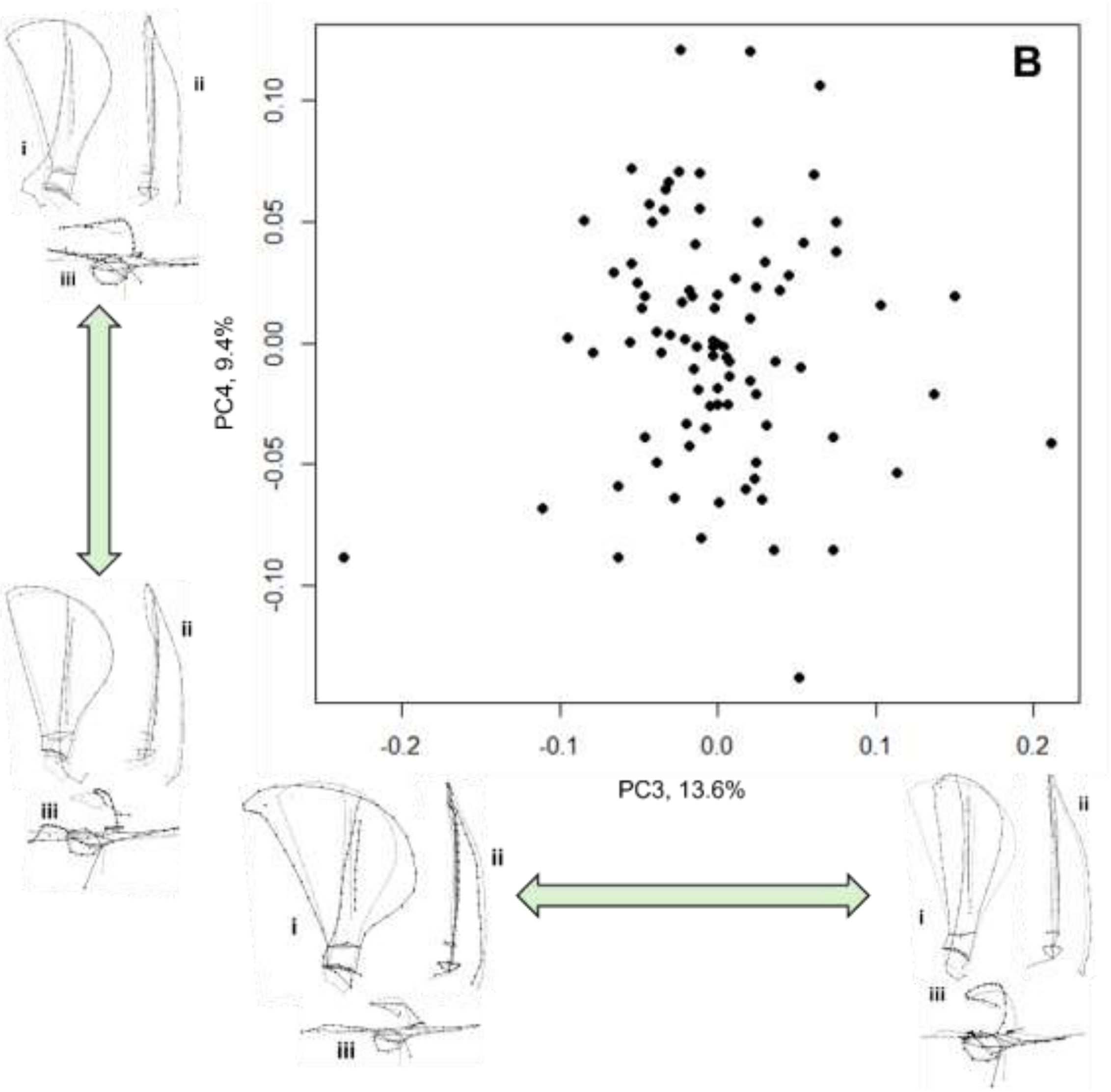


Figure IV.1: PC1-PC4 morphospace with shape changes
Visualisations of the arrangement of species and shape changes associated with A) the PC1-PC2 morphospace, and B) the PC3-PC4 morphospace. Wireframes are displayed in three views: i) lateral; ii) caudal; iii) glenoid.

IV.3.2. Contributions of factors influencing scapular variation

There is a moderate phylogenetic signal in the Procrustes coordinates (Bloomberg's K = 0.55), and in the residuals (Pagel's λ = 0.53). It is important to note that, due to a lower sample size in this dataset (n = 87) with the same landmarking system (producing 213 Procrustes coordinates), Pagel's λ could not be calculated on the Procrustes coordinates, but was calculated on principal components instead to reduce dimensionality of the shape data. A value of λ = 0.53 is used in subsequent *procD.pgls* models in rodents.

A phylogenetic model was constructed including logCS, clavicle presence, and locomotor group (**modelR1a**, Table IV.1). The results show that none of these predictors significantly influence scapular morphology. Likewise, this is the case if each set of locomotor scores (swimming, climbing, digging, running, aerial) is included instead of the locomotor group categorical variable (**modelR2a**, Table IV.1). However, at this lower level of taxonomic variation and with lower sample size than models in Chapter III, real biological influences may be obfuscated by the phylogenetic structure when variance cannot be uniquely attributed to individual variables in the model. Therefore, each model was additionally run outwith a phylogenetic framework using *procD.lm* in order to evaluate relative contributions of functional variables (**modelR1b** & **modelR2b**). The results of these models show significant influences on scapular morphology of logCS, clavicle presence, locomotor group, climbing, running, and aerial movement. Overall, this indicates that functional variables have a real influence on scapular morphology, but are heavily phylogenetically structured.

Table IV.1: Results of the phylogenetic regression modelR1 & modelR2
*These models of n = 87 rodent species assess the influence on Procrustes coordinates of **modelR1**: three predictors - logCS (continuous), clavicle presence (binary categorical), locomotor group (8-level categorical); **modelR2**: seven predictors – logCS, clavicle presence, and five locomotor ability score variables (continuous). **modelR1a** and **modelR2a** are outputs from* procD.pgls *with a phylogenetic framework, while **modelR1b** and **modelR2b** are outputs from* procD.lm *without a phylogenetic framework. The table provides df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in **bold italics** in green boxes.*

procD.pgls	**modelR1a**	df	SS	MS	R^2	F	Z	p
	logCS	1	0.0011	0.0011	0.0119	1.014	0.651	0.271
	Clavicle	1	0.0013	0.0013	0.0152	1.288	0.958	0.189
	Locom. group	7	0.0057	0.0008	0.0645	0.782	-0.324	0.638
	Residuals	77	0.0806	0.0010	0.9068			
	Total	86	0.0889					
procD.lm	**modelR1b**	df	SS	MS	R^2	F	Z	p
	logCS	1	0.0811	0.0811	0.0396	4.174	3.564	***0.002***
	Clavicle	1	0.0875	0.0875	0.0427	4.503	3.452	***0.001***
	Locom. group	7	0.3468	0.0495	0.1691	2.550	4.691	***0.001***
	Residuals	77	1.4959	0.0194	0.7296			
	Total	86	2.0503					

procD.pgls	**modelR2a**	df	SS	MS	R^2	F	Z	p
	logCS	1	0.0011	0.0011	0.0122	1.056	0.714	0.245
	Clavicle	1	0.0012	0.0012	0.0135	1.163	0.843	0.228
	Swim	1	0.0009	0.0009	0.0098	0.845	0.197	0.417
	Climb	1	0.0006	0.0006	0.0065	0.557	-0.297	0.599
	Dig	1	0.0008	0.0008	0.0086	0.742	0.067	0.461
	Run	1	0.0014	0.0014	0.0152	1.312	1.042	0.154
	Aerial	1	0.0013	0.0013	0.0144	1.242	0.899	0.188
	Residuals	79	0.0814	0.0010	0.9153			
	Total	86	0.0889					
procD.lm	**modelR2b**	df	SS	MS	R^2	F	Z	p
	logCS	1	0.0710	0.0710	0.0347	3.593	3.289	***0.001***
	Clavicle	1	0.0713	0.0713	0.0348	3.609	3.103	***0.002***
	Swim	1	0.0079	0.0079	0.0039	0.399	-1.954	0.977
	Climb	1	0.0375	0.0375	0.0183	1.894	1.759	***0.048***
	Dig	1	0.0128	0.0128	0.0063	0.649	-0.766	0.772
	Run	1	0.0780	0.0780	0.0380	3.945	3.273	***0.002***
	Aerial	1	0.0572	0.0572	0.0279	2.892	2.608	***0.004***
	Residuals	79	1.5619	0.0198	0.7618			
	Total	86	2.0503					

IV.3.3. Size and allometry

In **modelR1** and **modelR2**, logCS was not significantly related to scapular morphology within a phylogenetic framework but was in non-phylogenetic modelling. This is also the case when logCS is the only predictor in the model (**modelR3a**, Table IV.2). Therefore, logCS influences scapular morphology, but is not independent of phylogenetic structure. Additionally, comparing effect size (Z) between a model using logCS (**modelR3a** & **modelR3b**) and a model using CS (**modelR3c** & **modelR3d**) indicates potential differential scaling such that any allometric effect present is greater in smaller species.

Table IV.2: Results of the phylogenetic regression modelR3
*These models assess the influence on Procrustes coordinates of logCS (**modelR3a** & **modelR3b**) and CS (**modelR3c** & **modelR3d**). **modelR3a** and **modelR3c** are outputs from* procD.pgls *with a phylogenetic framework, while **modelR3b** and **modelR3d** are outputs from* procD.lm *without a phylogenetic framework. The tables provide df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in **bold italics** in green boxes.*

procD.pgls	**modelR3a**	df	SS	MS	R^2	F	Z	p
	logCS	1	0.0011	0.0011	0.0129	1.109	0.797	0.223
	Residuals	85	0.0871	0.0010	0.9871			
	Total	86	0.0883					
procD.lm	**modelR3b**	df	SS	MS	R^2	F	Z	p
	logCS	1	0.1142	0.1142	0.0557	5.012	3.895	***0.001***
	Residuals	85	1.9361	0.0228	0.9443			
	Total	86	2.0503					

procD.pgls	**modelR3c**	df	SS	MS	R^2	F	Z	p
	CS	1	0.0008	0.0008	0.0092	0.792	0.247	0.394
	Residuals	85	0.0881	0.0010	0.9908			
	Total	86	0.08890					
procD.lm	**modelR3d**	df	SS	MS	R^2	F	Z	p
	CS	1	0.0867	0.0867	0.0423	3.754	3.000	***0.003***
	Residuals	85	1.9636	0.0231	0.9577			
	Total	86	2.05028					

The relationship of logCS to the PC1-PC6 morphospace was examined in a phylogenetic framework using PGLS (Table IV.3, Fig. IV.2). The results show that PC1, PC5 and PC6 are significantly related to logCS, the former being a positive correlation and the latter two being negative. The consistent aspect of shape change on these axes which can be associated with increased size is enlargement of the glenoid fossa (see Appendix IV.2 for shape change on PC5 and PC6).

Table IV.3: Results of allometric PGLS regressions on PC1-6

*Results of phylogenetic regressions of the first six PCs against log centroid size (logCS), including correlation coefficient (R^2), Pagel's lambda (λ), and p-values. Significant p-values are indicated in **bold italics**.*

	R^2	λ	p
PC1	0.034	1.00	***0.048***
PC2	0.003	0.62	0.261
PC3	0.031	0.86	0.055
PC4	0.021	0.94	*0.098*
PC5	0.055	0.00	***0.016***
PC6	0.049	1.00	***0.022***

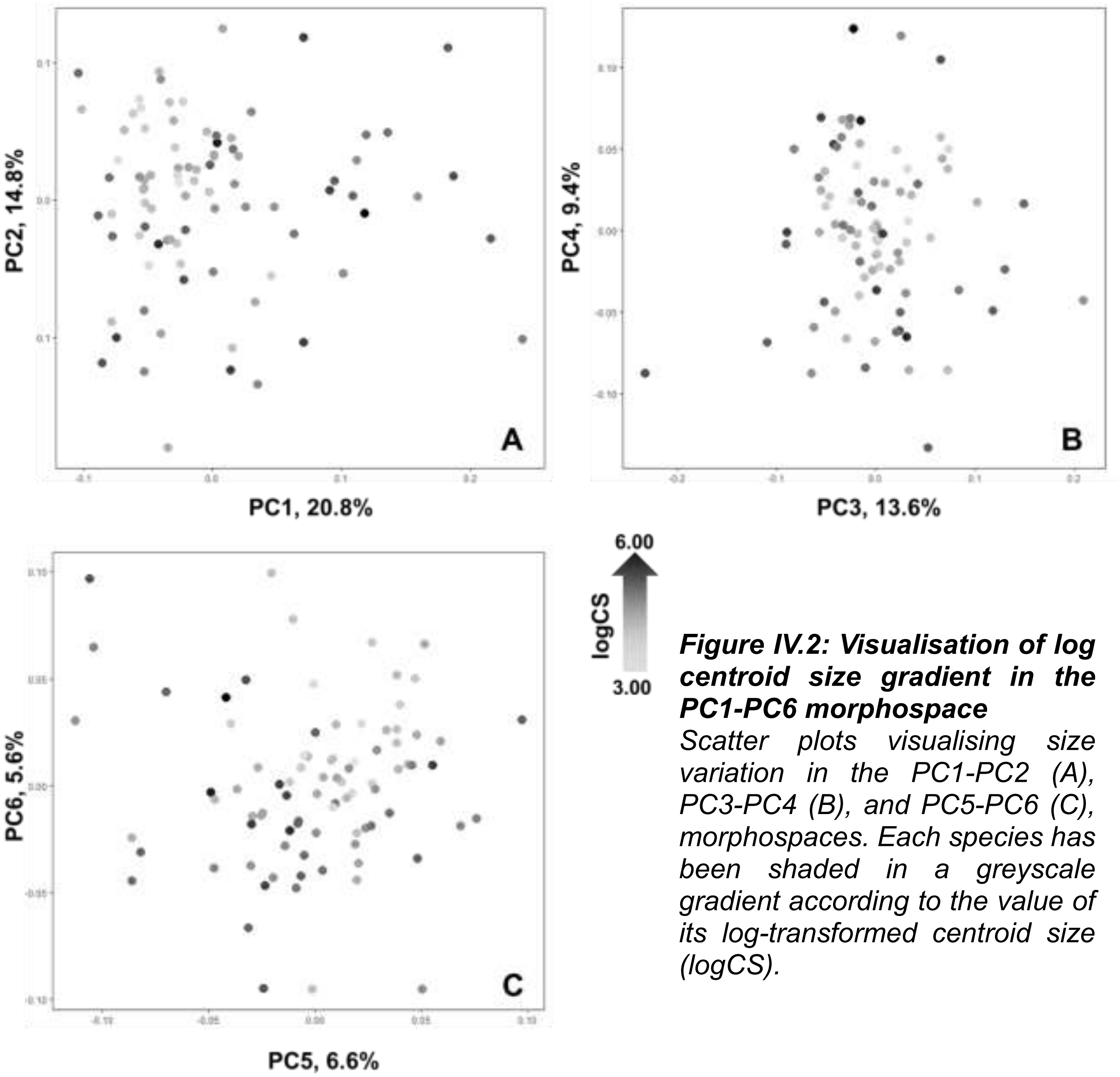
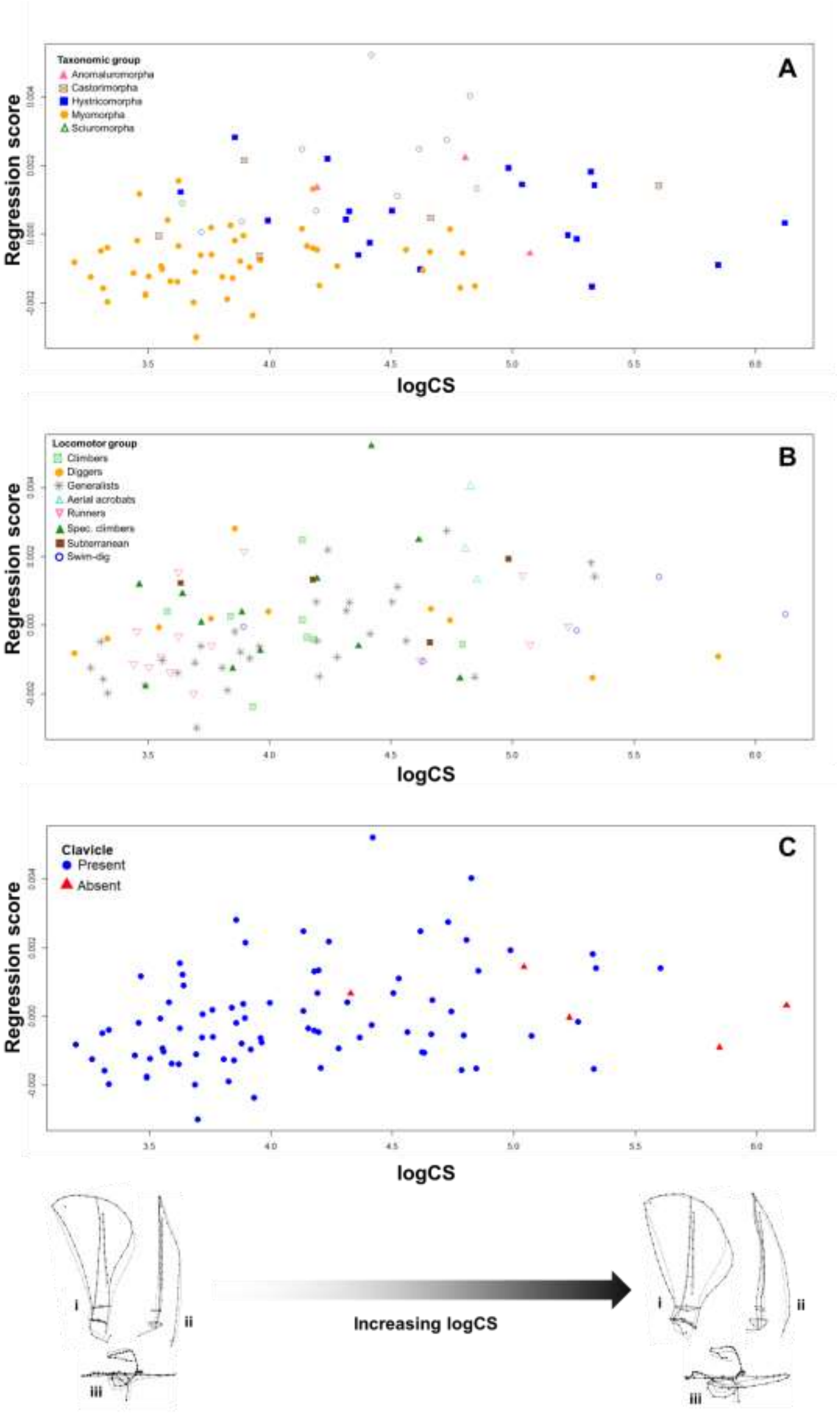


Figure IV.2: Visualisation of log centroid size gradient in the PC1-PC6 morphospace
Scatter plots visualising size variation in the PC1-PC2 (A), PC3-PC4 (B), and PC5-PC6 (C), morphospaces. Each species has been shaded in a greyscale gradient according to the value of its log-transformed centroid size (logCS).

As in Chapter III, change in logCS was directly related to shape change by inspecting the configurations associated with their regression scores arising from **modelR3a** (Fig. IV.3). This visualisation further explains the results of the models – it is particularly clear in Fig. IV.3A that different taxonomic groups generally differ in size (hystricomorphs being largest and myomorphs smallest). However, across rodents as a whole, there is a distinguishable morphological shift associated with increased size which may still be functionally relevant: increased logCS is generally associated with blade width, ventralisation of the bulk of the supraspinous fossa, enlargement of the glenoid fossa, enlargement of the area of attachment for the *m. teres major*, reduction of the acromion, and increased prominence of the metacromion.

When pairwise comparisons of allometry were investigated (S.IV.2.), no significant differences were found between locomotor groups or between claviculate and aclaviculate taxa. However, significant differences were found among taxonomic groups (S.IV.2.C) outwith a phylogenetic framework (using *procD.lm* rather than *procD.pgls*). The magnitude of shape change associated with logCS is significantly different in **Sciuromorpha** compared to all other groups, and the sciuromorph slope has a significantly different orientation from those of **Anomaluromorpha** ($p = 0.026$) and **Castorimorpha** ($p = 0.019$). The magnitude of allometric shape change and orientation of the slope in **Hystricomorpha** is significantly different from that of **Castorimorpha** (magnitude: $p = 0.021$; orientation: $p = 0.020$) and **Myomorpha** (magnitude: $p = 0.008$; orientation: $p = 0.013$). Additionally, though their slopes do not exhibit significantly different magnitudes of allometric shape change, the slopes in **Anomaluromorpha** and **Hystricomorpha** have significantly different orientations ($p = 0.043$). This supports the assertion that increased size does influence scapular morphology, but this is strongly along phyletic lines.

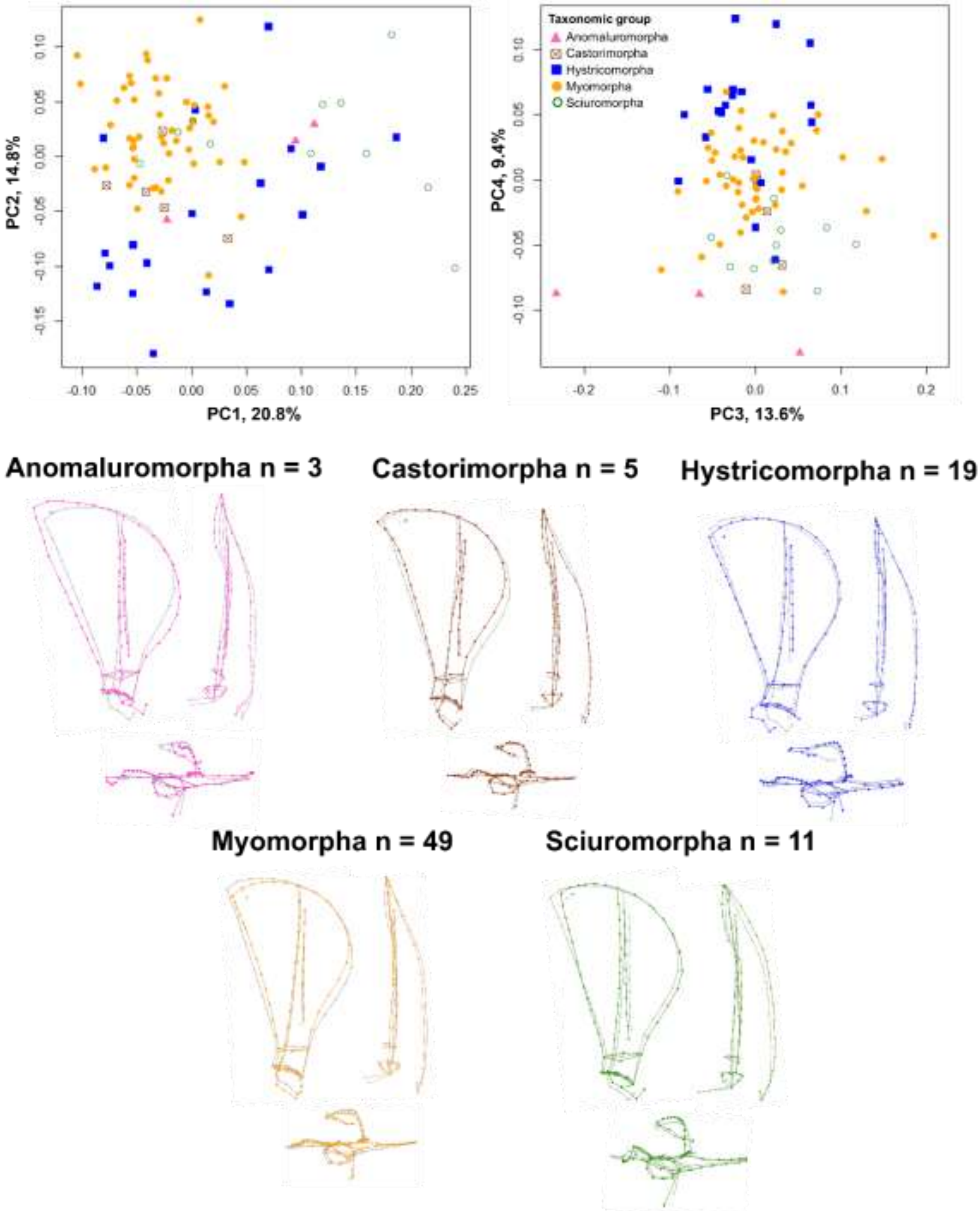
Figure IV.3: Shape change associated with increased logCS
Visualisation of the phylogenetic regression of Procrustes coordinates against log centroid size (logCS), by A) taxonomic group, B) locomotor group, and C) clavicle presence. The wireframes (relative to the mean shape in grey) are displayed in three views: i) lateral; ii) caudal; iii) glenoid.


Taxonomic group
Anomaluromorpha
Castorimorpha
Hystricomorpha
Myomorpha
Sciuromorpha
A
Regression score
-0.002
0.000
0.002
0.004
logCS
3.5
4.0
4.5
5.0
5.5
6.0
Locomotor group
Climbers
Diggers
Generalists
Aerial acrobats
Runners
Spec. climbers
Subterranean
Swim-dig
B
Clavicle
Present
Absent
C
i
ii
iii
Increasing logCS

IV.3.4. Evolutionary history

The phylogenetic signal in scapular morphology was found to be moderately strong (Bloomberg's K = 0.55), in line with the prediction of **$H_{III.2}$,** and this signal is larger than was found in scapular morphology across therians. As evidenced by the results of phylogenetic regression models and pairwise comparisons, the influence of functional variables cannot be readily disentangled from phylogenetic structure. Evolutionary history appears to play an important role in the arrangement of the PC1-PC4 morphospace (Fig. IV.4). The **Myomorpha** are almost entirely distinct from the **Hystricomorpha** in the PC1-PC2 morphospace (Fig. IV.4A) along a diagonal which aligns very closely with the linear position of the three **Anomaluromorpha**. **Myomorpha** are located in the negative half of PC1 and the positive half of PC2, with two exceptions which are found amongst the **Hystricomorpha**: the Indomalayan pencil-tailed tree mouse (*Chiropodomys gliroides*) and the lesser Egyptian jerboa (*Jaculus jaculus*). The **Hystricomorpha** are located across much of PC1, and in the negative half of PC2, with three exceptions which are located amongst the **Myomorpha**: the lowland paca (*Cuniculus paca*), the crested porcupine (*Hystrix cristata*), and the long-tailed chinchilla (*Chinchilla lanigera*). This arrangement indicates that **Myomorpha** and **Hystricomorpha** are generally differentiated by blade width, with myomorph scapulae being slimmer and more gracile, while hystricomorph scapulae are wider with a longer vertebral border. **Castorimorpha** and **Sciuromorpha** are similarly spatially separated along the opposing diagonal (Fig. IV.4A). The **Castorimorpha** are generally located below 0.0 on PC1, with the exception of the Panamint kangaroo rat (*Dipodomys panamintinus*). **Sciuromorpha** are divided into two entirely distinct groups. At the lower end of PC1, up to around -0.02, and in the centre of PC2 is a group of four **sciuromorphs**: the three glirids and the alpine marmot (*Marmota marmota*). Higher on PC1, from around 0.1 onwards, is another sciuromorph group: the remaining 6 scuirids and the mountain beaver (*Aplodontia rufa*). This latter group is distributed widely across PC2, especially at high values of PC1. The **Castorimorpha** and **Sciuromorpha** are generally distinguished on the basis of caudal angle prominence, orientation of the acromion, and ratio of the lateral fossae. In **sciuromorphs**, the caudal angle is less prominent, the acromion has a more cranially-oriented tip, and the supraspinous fossa is enlarged relative to the infraspinous.

In the PC3-PC4 morphospace (Fig. IV.4B), the **Myomorpha** are distributed widely around the mean. The **Anomaluromorpha** are located lowest on PC4 of any species, occupying their own region of the morphospace despite being spread apart on PC3. This represents a scapula with a highly cranial acromion and elongated coracoid process, as well as a high caudal angle. The notably lowest species on PC3 is the anomaluromorph springhare (*Pedetes capensis*). PC4 almost separates the **Hystricomorpha** from the **Sciuromorpha**, with only a few exceptions. The **hystricomorphs** are generally found in the positive half of PC4, with two species located within the **Sciuromorpha** region: the North American porcupine (*Erethizon dorsatum*) and the Cape dune mole-rat (*Bathyergus suillus*). The **sciuromorphs**, meanwhile are found in the negative half of PC4, with two glirid species located higher within the **hystricomorph** region: the forest dormouse (*Dryomys nitedula*) and the European edible dormouse (*Glis glis*). This relative opposition of **hystricomorphs** and **sciuromorphs** in the morphospace indicates that the groups are distinguished primarily by the position of the acromion, length of the coracoid, and the relative height of the caudal angle. Lastly, all **Castorimorpha** are located close to 0.0 on PC3, and spread across the lower half of PC4. This represents scapulae with intermediate blade width, generally more cranial acromion processes, and more elongated coracoid processes.



Anomaluromorpha n = 3 Castorimorpha n = 5 Hystricomorpha n = 19

Myomorpha n = 49 Sciuromorpha n = 11

Figure IV.4: PC1-PC4 morphospace visualised by taxonomic group, with mean shapes for taxonomic groups

Visualisation of the PC1-PC4 morphospace, with points are differentiated into the five taxonomic groups. Mean scapular shapes (relative to the mean shape in grey) are visualised as wireframes in three views: lateral (left); caudal (right); glenoid (bottom).

IV.3.5. Clavicle presence

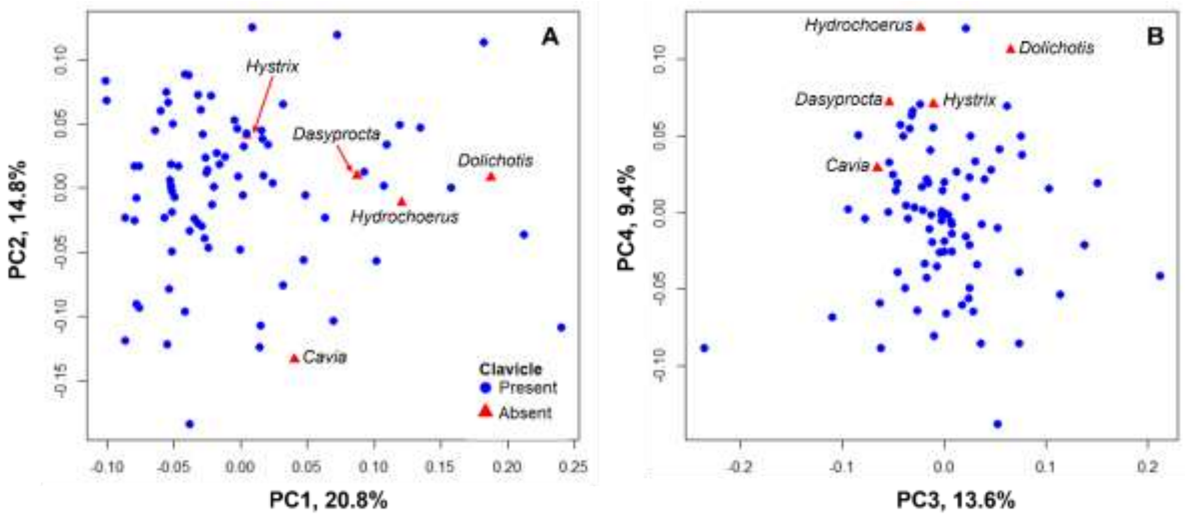


Figure IV.5: PC1-PC4 morphospace visualised by clavicle presence
Visualisation of the PC1-PC4 morphospace, with points differentiated by clavicle presence, and aclaviculate species labelled.

Clavicle presence does not appear to have a significant influence on scapular morphology in rodents which could be tangibly uncovered via phylogenetic regression modelling (**modelR1a & modelR2a** Table IV.1, **modelR7a** Table IV.4), but when a phylogenetic framework is not used, clavicle presence has a consistent significant influence (**modelR1b & modelR2b** Table IV.1, **modelR7b** Table IV.4). Additionally, clavicle presence does not appear to play a key role in the arrangement of the PC1-PC2 morphospace (Fig. IV.5A), though the five aclaviculate species in this dataset do all have positive PC1 scores. The lowest aclaviculate species on PC1 is the crested porcupine (*Hystrix cristata*). The wild guinea pig (*Cavia tschudii*) is lower on PC2 than any of the other aclaviculate species, with the other four being located close to 0.0 on PC2. In the PC3-PC4 morphospace (Fig. IV.5B), the aclaviculate species remain undifferentiated from the claviculate species, but are all located in the positive half of PC4 which represents a scapula with a highly caudally-directed acromion, reduced coracoid, and relatively dorso-ventrally low caudal angle with shallow attachment for the *m. teres major*.

Table IV.4: Results of the phylogenetic regression modelR7
These models assess the influence on Procrustes coordinates of clavice presence (a binary category) within a phylogenetic framework using procD.pgls *(**modelR7a**) and outwith said framework (**modelR7b**).. The table provides df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in **bold italics** in green boxes.*

	modelR7a	df	SS	MS	R^2	F	Z	p
procD.pgls	Clavicle	1	0.0014	0.0014	0.0162	1.400	1.129	0.142
	Residuals	85	0.0875	0.0010	0.9838			
	Total	86	0.0889					
procD.lm	**modelR7b**	df	SS	MS	R^2	F	Z	p
	Clavicle	1	0.1187	0.1187	0.0579	5.224	3.559	***0.001***
	Residuals	85	1.9316	0.0227	0.9421			
	Total	86	2.0503					

It is very important to reiterate that all aclaviculate rodents are hystricomorphs. This is why the presence of a phylogenetic framework in the model indicates no significant influence of clavicle presence. Therefore, it is valuable to assess the difference in morphology between claviculate and aclaviculate hystricomorphs in order to understand the potential influence of clavicle loss on scapular morphology in rodents. Comparing the lateral views of the mean claviculate and aclaviculate hystricomorphs (Fig. IV.6) reveals four main morphological differences: aclaviculate hystricomorphs have i) a reduced acromion, ii) a lower caudal angle, iii) a slimmer, elongated scapular neck, and iv) enlarged supraspinous fossa.

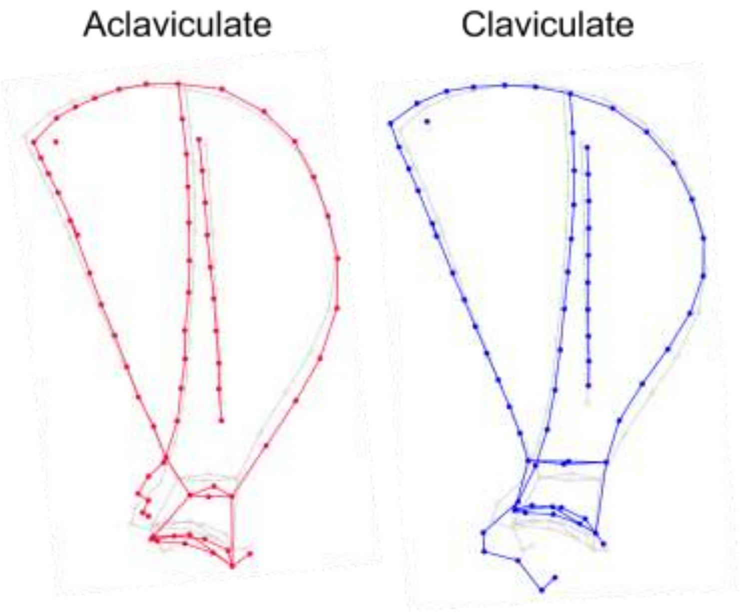


Figure IV.6: Mean claviculate and aclaviculate hystricomorph scapular shape
Mean claviculate (blue, n = 14) and aclaviculate (red, n = 5) hystricomorph scapular shape relative to the mean hystricomorph shape (grey), shown in lateral view.

Due to low sample size and phylogenetic constraint on clavicle loss in rodents, limited conclusions can be drawn regarding clavicle loss across Rodentia and its influence on scapular morphology. However, clavicle loss within Hystricomorpha does appear to have identifiable morphological correlates (supporting **H$_{\mathbf{IV.3A}}$**), including acromion reduction (supporting **H$_{\mathbf{IV.3B}}$**) and change in vertebral border morphology, both of which were the case across therians in Chapter III.

IV.3.6. Locomotion behaviour

According to **modelR1**, locomotor groups have significantly different scapular morphology but this is obfuscated by phylogenetic structure. Similarly, results of **modelR2** show significant influences of climbing, running and aerial movement behaviours which are obfuscated within a phylogenetic framework. Swimming and digging ability do not have significant influences on scapular morphology in these models. In single predictor models (**modelR8-12**, Table IV.5), the same pattern is generally borne out, except in the case of digging behaviour which is significant as a single term in the *procD.lm* model (**modelR10b**). This indicates that another variable in the larger **modelR2b** absorbs variance which is otherwise attributed to digging ability in the single predictor model. Therefore, it appears that climbing, running, and aerial movement abilities significantly influence scapular morphology, but this is obfuscated by phylogenetic structure.

Table IV.5: Results of the phylogenetic regression modelR8-12

These models of n = 87 species assess the influence on Procrustes coordinates of each of the five locomotor ability scores as single terms, both using procD.pgls *(all -a models) and* procD.lm *(all -b models). The tables provide df (degrees of freedom), SS (sum of squares), MS (mean squares), R^2 (determination coefficient), F-statistic, Z-statistic (effect size) and p-value. Significant terms are in* ***bold italics*** *in green boxes.*

procD.pgls	**modelR8a**	df	SS	MS	R2	F	Z	p
	Swim	1	0.0008	0.0008	0.0090	0.771	0.078	0.452
	Residuals	85	0.0881	0.0010	0.9910			
	Total	86	0.0889					
procD.lm	**modelR8b**	df	SS	MS	R2	F	Z	p
	Swim	1	0.0256	0.0256	0.0125	1.073	0.338	0.349
	Residuals	85	2.0247	0.0238	0.9875			
	Total	86	2.0503					

procD.pgls	**modelR9a**	df	SS	MS	R2	F	Z	p
	Climb	1	0.0009	0.0009	0.0105	0.900	0.365	0.3648
	Residuals	85	0.0880	0.0010	0.9895			
	Total	86	0.0889					
procD.lm	**modelR9b**	df	SS	MS	R2	F	Z	p
	Climb	1	0.1001	0.1001	0.0488	4.361	3.734	***0.001***
	Residuals	85	1.9502	0.0229	0.9512			
	Total	86	2.0503					

procD.pgls	**modelR10a**	df	SS	MS	R2	F	Z	p
	Dig	1	0.0012	0.0012	0.0133	1.142	0.590	0.275
	Residuals	85	0.0877	0.0010	0.9867			
	Total	86	0.0889					
procD.lm	**modelR10b**	df	SS	MS	R2	F	Z	p
	Dig	1	0.0878	0.0878	0.0428	3.801	3.171	***0.001***
	Residuals	85	1.9625	0.0231	0.9572			
	Total	86	2.0503					

Continued overleaf

procD.pgls	**modelR11a**	df	SS	MS	R2	F	Z	p
	Run	1.0000	0.0014	0.0014	0.0153	1.318	1.001	0.162
	Residuals	85.0000	0.0875	0.0010	0.9847			
	Total	86.0000	0.0889					
procD.lm	**modelR11b**	df	SS	MS	R2	F	Z	p
	Run	1	0.0920	0.0920	0.0449	3.995	3.372	***0.001***
	Residuals	85	1.9583	0.0230	0.9551			
	Total	86	2.0503					

procD.pgls	**modelR12a**	df	SS	MS	R2	F	Z	p
	Aerial	1	0.0010	0.0010	0.0116	0.999	0.627	0.281
	Residuals	85	0.0879	0.0010	0.9884			
	Total	86	0.0889					
procD.lm	**modelR12b**	df	SS	MS	R2	F	Z	p
	Aerial	1	0.0832	0.0832	0.0406	3.595	2.813	***0.001***
	Residuals	85	1.9671	0.0231	0.9594			
	Total	86	2.0503					

Modelling results somewhat reflected in the arrangement of the PC1-4 morphospace, particularly when visualised as ability gradients (Fig. IV.7). The gradients which can be visually identified are subtle, and likely constrained by taxonomic separation in these morphospaces. In the PC1-PC2 morphospace, the most discernible gradient is an increase in digging ability towards the negative extreme of PC1 (Fig. IV.7G). On PC4, however, there are three visible gradients: i) running ability increases as PC4 increases (Fig. IV.7B); ii) climbing ability increases as PC4 decreases (Fig. IV.7D); and iii) aerial ability increases as PC4 decreases (Fig. IV.7F). The running ability gradient is not entirely consistent across PC4, with the majority of high scores appearing around the centre of the axis rather than the positive extreme. These PC4 gradients are notably analogous to those observed in the therian PC1-PC2 morphospace, including the opposition of running ability to climbing and aerial abilities.

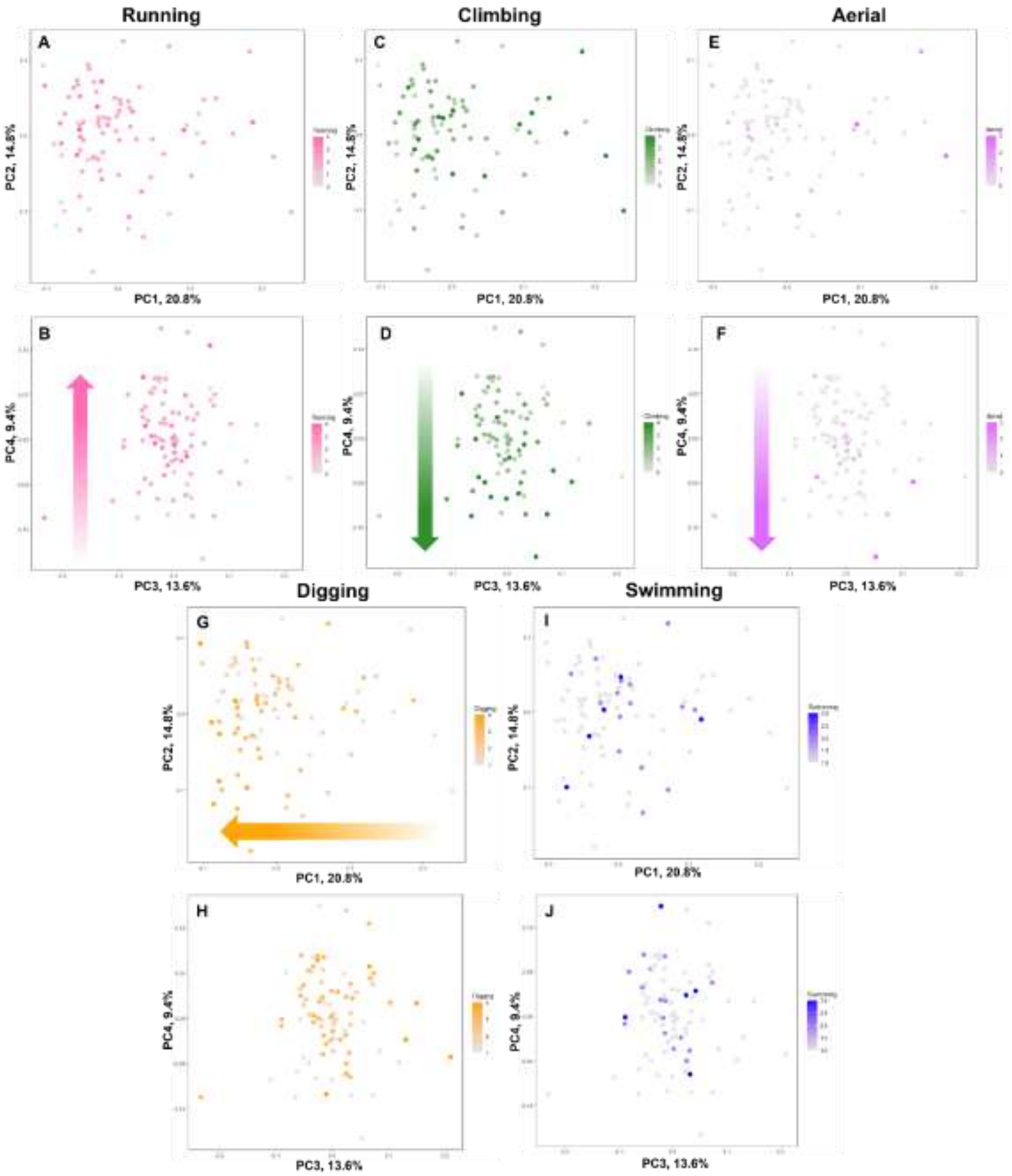


Figure IV.7: PC1-PC4 morphospace visualised with locomotor ability gradients
Visualisation of the PC1-PC4 morphospace, with points coloured in gradients according to locomotor ability score in each locomotor scoring variable. Arrows loosely indicate ability gradients.

Locomotor group membership does not appear to substantially influence the PC1-PC2 morphospace (Fig. IV.8A). However, the **subterranean** species are all found at the low extreme of PC1, representing a slimmer scapular blade with relatively smaller supraspinous fossa, slim and elongate scapular neck, and prominent and ventrally-directed acromion (in line with the prediction of **$H_{IV.4D}$**). Other **diggers** and the **swim-dig** group are also all found in the lower half of PC1, with the exception of the paca (*Cuniculus paca*, a digger) and the capybara (*Hydrochoerus hydrochaeris*, within swim-dig), which are both aclaviculate. **Aerial acrobats** are found at the positive extreme of PC1, representing a wide scapular blade with relatively large supraspinous fossa, high caudal angle, short acromion with cranially-directed tip, and elongated coracoid (in line with the prediction of **$H_{IV.4B}$**).

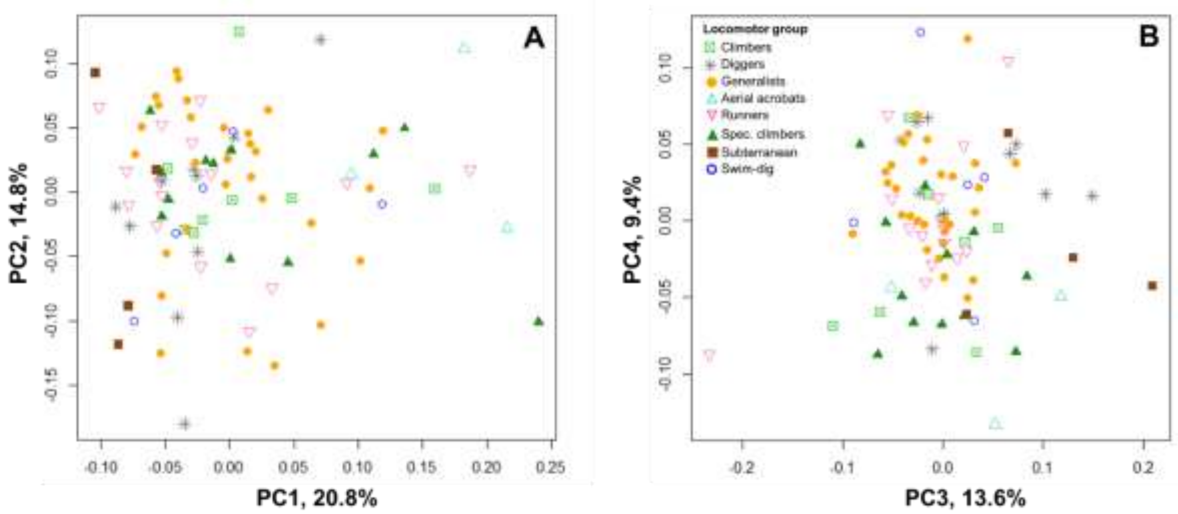


Figure IV.8: PC1-PC4 morphospace visualised by locomotor group
Visualisation of the PC1-PC4 morphospace, with points differentiated into the eight locomotor groups generated by cluster analysis.

In the PC3-PC4 morphospace (Fig. IV.8B), locomotor group membership plays a somewhat more important role than it does in PC1-PC2. The majority of **runners** are found in the centre of this morphospace along with most generalists, presenting scapular shapes closer to the mean. Three running species are higher on PC4 (the Patagonian mara [*Dolichotis patagonum*], the red-rumped agouti [*Dasyprocta leporina*] and the yellow-footed brush-furred rat [*Lophuromys flavopunctatus*]), and one species, the springhare (*Pedetes capensis*), is particularly low on both PC3 and PC4. The latter has been discussed in Chapter III in terms of its ricochetal locomotion behaviour being particularly hindlimb-dominated. Of the former three, the mara and agouti are aclaviculate hystricomorphs, and *Lophuromys* is a myomorph. **Subterranean** species are all found at the positive extreme of PC3, representing a very slim scapular blade with ventrally-directed acromion (in line with the prediction of $\mathbf{H_{IV.4D}}$). **Diggers** generally present high PC4 scores (with the exception of the plains pocket gopher [*Geomys bursarius*]), representing a scapula with a low caudal angle, highly caudal acromion, and reduced coracoid. Meanwhile, **climbers**, **specialised climbers**, and **aerial acrobats** are generally found in the lower half of PC4, with four exceptions: the link rat (climber, *Deomys ferrugineus*), the brown rat (climber, *Rattus norvegicus*), the orange-brown Atlantic tree-rat (specialised climber, *Phyllomys brasiliensis*), and the maned rat (specialised climber, *Lophiomys imhausi*). The lowest species on PC4 is an aerial acrobat, the cream-coloured giant squirrel (*Ratufa affinis*). The negative region of PC4 represents a scapula with a high caudal angle, a prominent and highly cranial acromion, and an elongated and caudally-directed coracoid (in line with the prediction of $\mathbf{H_{IV.4B}}$).

IV.4. Discussion

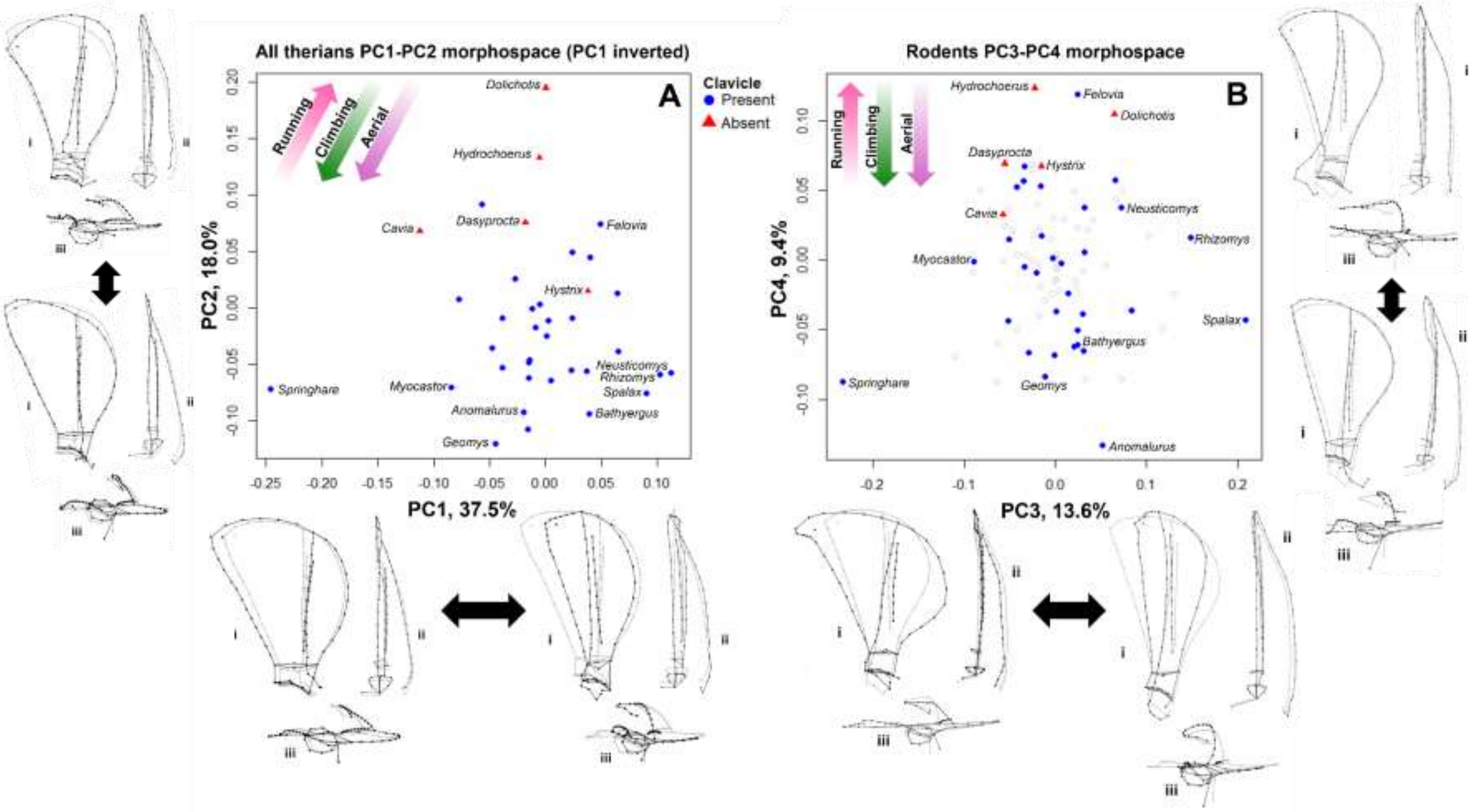
Scapular functional morphology in rodents is just as complex and nuanced as it is across therians, with phylogenetic structure obfuscating functional results to a greater degree than was observed in Chapter III. Modelling without a phylogenetic framework made it possible to establish real influences of functional variables on scapular morphology, but it remains the case that share devolutionary history drives much of scapular variation in rodents. Nevertheless, associations between scapular morphology and functional variables were found which align with those identified across therians.

IV.4.1. Overall scapular variation

Across therians in Chapter III, the most variable aspects of the scapula are blade width and relative dominance of the lateral fossae, the acromion region, the coracoid process, and curvature of the vertebral border and caudal angle height. These are also identified here as the most variable aspects of scapular shape in rodents specifically. Variation in these regions can consistently be related to differences in functional demands, but appear to also vary in direct association with taxonomic differences in rodents. In particular, the arrangement of the PC1-PC2 morphospace is predominantly related to differentiating the rodent subclades. However, PC3-PC4 is more revealing, being influenced by function as well as evolutionary history.

When comparing the results of this chapter to the therian-wide results of Chapter III, the therian PC1-PC2 morphospace and the rodent PC1-PC2 morphospace do not appear to share identifiable characteristics in their arrangement. This is because the therian PC1-PC2 morphospace is influenced by multiple factors and their interactions which could be identified in Chapter III, but the rodent PC1-PC2 morphospace appears to be influenced primarily by evolutionary history. However, examining the rodent PC3-PC4 morphospace shows that it does share many characteristics with the therian PC1-PC2 morphospace, even including the relative positions of several species (Fig. IV.10). Firstly, there are many similarities in shape change within these morphospaces. Shape changes on both therian PC1 and rodent PC3 are predominantly related to blade width and acromion morphology, while shape changes on therian PC2 and rodent PC4 predominantly relate to acromion morphology and caudal angle position. Secondly, in therians, PC2 differentiates claviculate and aclaviculate species with aclaviculate taxa at the positive end and, though it is less clear in rodents, this is also the case in the rodent PC4. Finally, both morphospaces have identifiable climbing, aerial and running ability gradients. In both cases, climbing and aerial ability have the same gradient, and running ability increases in the opposing direction. These similarities between the therian PC1-PC2 morphospace and rodent PC3-PC4 morphospace indicate that Rodentia can aptly represent a microcosm of therian mammals, containing much of the same functional information. However, evolutionary history appears to play such a significant role in scapular shape variation in rodents that this obfuscates functional influences to a much greater extent than is observed in therians more broadly.

Figure IV.10: Comparison of the therian PC1-2 morphospace and the rodent PC3-4 morphospace
Illustration of the similarities between the therian PC1-2 and rodent PC3-4 morphospaces with reference to clavicle presence, shape changes, and locomotion ability gradients. A) Scatter plot showing the rodents present in the therian dataset in the all therians PC1-PC2 morphospace with PC1 inverted. B) Scatter plot showing the rodents present in the therian dataset in the rodent only PC3-PC4 morphospace, with all other rodent species in this dataset shown in grey. Several relevant species are highlighted in both scatter plots. The wireframes (relative to the mean shape in grey) are displayed in three views: i) lateral; ii) caudal; iii) glenoid.


All therians PC1-PC2 morphospace (PC1 inverted)
A
Clavicle
● Present
▲ Absent
Running
Climbing
Aerial
PC2, 18.0%
PC1, 37.5%
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.25
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
Dolichotis
Hydrochoerus
Cavia
Dasyprocta
Felovia
Hystrix
Neusticomys
Rhizomys
Spalax
Bathyergus
Springhare
Myocastor
Anomalurus
Geomys
Rodents PC3-PC4 morphospace
B
Running
Climbing
Aerial
PC4, 9.4%
PC3, 13.6%
0.10
0.05
0.00
-0.05
-0.10
-0.2
-0.1
0.0
0.1
0.2
Hydrochoerus
Felovia
Dolichotis
Dasyprocta
Hystrix
Cavia
Neusticomys
Rhizomys
Myocastor
Spalax
Bathyergus
Springhare
Geomys
Anomalurus
i
ii
iii

IV.4.2. Size and allometry

Hypothesis IV.1A ($H_{IV.1A}$): Body size will significantly affect scapular morphology.

Hypothesis IV.1B ($H_{IV.1B}$): Large size will be associated with an enlarged vertebral border.

Based on the results of Chapter III and the biomechanical implications of weight-bearing on the scapula, it was expected that increased body size would influence scapular morphology in rodents, and that this would be reflected in an enlarged vertebral border to house enlarged weight-bearing musculature. However, previous rodent research has found little to no influence of size on scapular morphology in some hystricomorphs (Morgan 2009; Carvalhaes et al. 2022), and a variable effect in sciuromorphs dependent on locomotion behaviour (Wölfer et al. 2019).

The results of this chapter demonstrate a relationship between increased scapular size and morphology, greatly affected by evolutionary history due to the differences in mean size between taxonomic groups. For example, the myomorphs in this dataset have a mean logCS of 3.86 ± 0.44 (n = 49), while hystricomorphs have a mean of 4.78 ± 0.68 (n = 19). However, looking across rodents as a whole it is apparent that there are morphological shifts which occur in tandem with increased size, which align closely with those identified across therians. Based on a significant relationship between logCS and shape change on PC1 (Fig. IV.2), P5 and PC6 (Appendix IV.2), as well as visualisations of allometric shape changes in the rodent scapula (Fig. IV.3), increased size in rodents is associated with increased blade width, ventralisation of the bulk of the supraspinous fossa, enlargement of the glenoid fossa, enlargement of the area of attachment for the *m. teres major*, reduction of the acromion, and increased prominence of the metacromion. Increased blade width results in an enlarged vertebral border, supporting **$H_{IV\text{-}1B}$**. Allometry in rodents clearly varies along phyletic lines. Sciuromorpha and Hystricomorpha are particularly different from other taxonomic groups in this regard. There does not appear to be any evidence of significant differences in allometry between locomotor groups, or in claviculate versus aclaviculate rodents, at least in a phylogenetic framework. The former somewhat contradicts the findings of Wölfer et al. (2019) who identified differences in allometry related to differences in locomotor behaviour within Sciuromorpha, though this was not explicitly tested here.

The results of this chapter strongly support the findings of Chapter III and **$H_{IV.1A}$ & $H_{IV.1B}$**. As across therians, increased size is associated with increased blade width and enlargement of the vertebral border to facilitate large musculature involved in weight-bearing. Previous research failed to identify strong relationships between size and scapular morphology in certain hystricomorph groups (Morgan 2009; Carvalhaes et al. 2022), but this may be related to clavicle loss. In Morgan (2009)'s study, *Hystrix* – an aclaviculate species – is used as the outgroup to which caviomorphs are compared. It can then be seen that all the aclaviculate species in their dataset are closely aligned in their position on PC1. It is likely that the difference in allometric trends between claviculate and aclaviculate hystricomorphs (Fig. IV.9) was important in Morgan's results not demonstrating a significant influence of size on scapular morphology in caviomorphs. In the case of Carvalhaes et al. (2022), which focuses on echimyids, there is very little crossover in dataset composition with this thesis. It is possible that, in this group, scapular shape is not significantly related to size, but this could not be supported here.

IV.4.3. Evolutionary history

Hypothesis IV.2 ($H_{IV.2}$): There will be a significant effect of evolutionary history on scapular morphology, potentially greater than that of the other factors.

Evolutionary history appears to play a very significant role in influencing scapular morphology in rodents. In fact, the rodent scapula dataset is more phylogenetically structured than therians as a whole (Bloomberg's K = 0.55 in rodents versus K = 0.46 across therians). The arrangement of the PC1-PC2 morphospace is almost entirely attributable to differentiation of taxonomic groups, and much of the PC3-PC4 mophospace too. Maximum likelihood values for Pagel's lambda arising from models of PCs against logCS, from λ = 0.00 for the PC5 regression to λ = 1.00 for the PC1 and PC6 regressions, highlighting a variable phylogenetic signal across regions of the scapula in rodents. Additionally, allometric variation occurs along phyletic lines, as it does in therians more broadly.

These results in rodents support **$H_{IV.2}$**, demonstrating a strong and significant effect of evolutionary history on scapular morphology. The dominance of evolutionary history in the PC1-PC2 morphospace supports the assertion that phylogeny has a greater influence on scapular variation than functional demands, as do the allometric differences among taxonomic groups. These findings are also in line with previous research which has found a dominant phylogenetic effect on scapular morphology in sciurids (Swiderski 1993), caviomorphs (Morgan 2009), echimyids (Carvalhaes et al. 2022), and the genus *Cerradomys* (de Oliveira et al. 2025).

IV.4.4. Clavicle presence

Hypothesis IV.3A ($\mathbf{H_{IV.3A}}$): Scapular morphology will significantly differentiate claviculate and aclaviculate species.

Hypothesis IV.3B ($\mathbf{H_{IV.3B}}$): Aclaviculate species will exhibit a reduced acromion and more curved vertebral border (with lower caudal angle).

While rodents represent an unusual example of a mammal order in which clavicle presence is not universal, only a few species are aclaviculate and all belong to the Hystricomorpha. Unfortunately, this means that statistical tests in the context of clavicle presence in rodents have relatively low power and need to be interpreted with caution. Therefore, it cannot be said that $\mathbf{H_{IV.3A}}$ is well-supported by the results of this chapter. However, the fact that not all hystricomorphs are aclaviculate does make it possible to assess the influence of clavicle loss on morphology within this group, and comparison of the claviculate and aclaviculate hystricomorph scapula reveals specific morphological traits associated with clavicle loss in rodents (Fig. IV.6). In complete alignment with $\mathbf{H_{IV.3B}}$ and the findings of Chapter III across all therians, aclaviculate rodents present a reduced acromion and a lower caudal angle. Since the clavicle articulates with the acromion when present, loss of this articulation results in reduction of the acromion. The difference in caudal angle position and associated change in vertebral border curvature is likely due to the difference in scapular position between claviculate and aclaviculate taxa (Voisin 2006), which alters muscle lines of action, particularly those attached to the vertebral border and vertebral column. Two traits are observed in aclaviculate rodents that were not highlighted in the therian study: elongation of the scapular neck and an enlarged supraspinous fossa. The former serves to increase the dorso-ventral height of the scapula, increasing the mechanical efficiency of cranio-caudal pendulum motions of the scapula during stride. The latter may be associated with increased stability of the shoulder joint (by providing larger attachment sites for *m. supraspinatus* and *subscapularis*), necessary in the absence of the cranially-stabilising clavicle (Jenkins 1974).

IV.4.5. Locomotion behaviour

Hypothesis IV.4A ($H_{IV.4A}$): There will be identifiable morphological distinctions between functionally different locomotor groups.

Hypothesis IV.4B ($H_{IV.4B}$): Aerial movement adaptation will be associated with an elongated coracoid.

Hypothesis IV.4C ($H_{IV.4C}$): Climbing/aerial and running specialisations will be associated with opposing morphologies.

Hypothesis IV.4D ($H_{IV.4D}$): Subterranean specialisation will be associated with a very slim scapula blade.

As predicted in **$H_{IV.4A}$** and found across therians, locomotion behaviour identifiably influences scapular morphology in rodents. However, this is somewhat less clear and more greatly obfuscated by phylogenetic effects than was the case across therians.

IV.4.5.1. Climbing and aerial abilities

While the influence of climbing and aerial abilities on scapular morphology is non-significant within a phylogenetic structure, models which do not include phylogeny demonstrate a significant relationship between both of these behaviours and morphology (**modelR9** & **modelR12**). Climbing and aerial abilities are closely linked in rodents, as they were across therians, and are associated with negative values of PC4. This translates to scapulae with a high caudal angle, large area of attachment for the *m. teres major*, highly cranial acromion, and elongated coracoid. These features are directly associated with increased shoulder mobility and stability through a wide range of motion, as well as positioning of the scapula more dorsally on the thorax (Argot 2001; Taylor & Slice 2005; Voisin 2006; Preuschoft et al. 2010). This aligns entirely with the findings of Chapter III regarding these behaviours, and supports the prediction of **$H_{IV.4B}$** that increased aerial ability is associated with elongation of the coracoid. Wölfer et al. (2019) identified that, in sciuromorphs, the transition from climbing to increased aerial movement is associated with a reduction of the metacromion and increased prominence of the acromion tip (hamatus process). This is reasonably supported here across all rodents, with the climbing to aerial gradient on

PC4 reflecting the same shape chnges. Based on experimental evidence in lab mice, Kimes et al. (1981) and Green et al. (2012) identified an association between increased climbing behaviour and decreased scapular width with infraspinous dominance. While the results of this chapter do not suggest that climbing behaviour is linked to decreased blade width, it does appear that increased size of the infraspinous fossa is associated with climbing.

IV.4.5.2. Running

Running ability was found to significantly influence scapular morphology in rodents when a phylogenetic structure is not included (**modelR11b**). While running ability did not have a consistent morphological signal across therians in Chapter III, it was generally the case that runners possess a moderately slim scapular blade. Beyond this there is considerable difference between claviculate and aclaviculate runners. In rodents specifically, runners are mostly found in the densest areas of the PC1-4 morphospace. The majority are relatively low on PC1 and central on PC2, central on PC3 and widely distributed on PC4. The concentration of highest running scorers is slightly below centre on PC4. This indicates that high running ability is associated with the mean scapular shape in rodents. However, the mean rodent scapula is unlike the mean therian scapula, being slimmer, with a prominent and ventrally-directed acromion region, and infraspinous-dominance. This is, in fact, in line with scapular morphology associated with high running ability in claviculate taxa in Chapter III. These features are associated with increased efficiency when moving the limbs within the parasagittal plane, often at the expense of power in movements outwith this plane (Taylor 1974; Argot 2001; Seckel & Janis 2008).

There are two aclaviculate runners in this dataset, the red-rumped agouti (*Dasyprocta leporina*) and the Patagonian mara (*Dolichotis patagonum*), which are both members of the Hystricomorpha. While the scapulae of these two species do differ considerably, there are some notable commonalities which can be associated with running behaviour based on the results of Chapter III, specifically a convex border with low caudal angle and significantly reduced acromion. The scapula of the agouti is wide, with a prominent caudal angle, reduced coracoid process, and short acromion region with very prominent metacromion. The prominent metacromion is particularly notable because this feature has been associated with running behaviour in small mammals (Seckel & Janis 2008, a dataset which included the same species of agouti). This is because it brings muscle attachments associated with the metacromion more caudal to the centre of shoulder rotation, thereby more effectively preventing shoulder collapse in response to high ground reaction forces. The scapula of the mara, meanwhile, is slim and elongated with a triangular shape akin to that of ungulates. The acromion is reduced but without a prominent metacromion. Unlike ungulates, the glenoid of the mara is notably caudally-directed relative to the blade, likely reflecting the difference in limb posture between unguligrady and digitigrady. The differences between the agouti and mara scapulae are likely attributable to the differences in forelimb use in the two species. While maras use their forelimbs almost exclusively for locomotion (walking, hopping and galloping), agoutis additionally use their forelimbs for digging and food handling (Nowak 1999).

IV.4.5.3. Climbing/aerial versus running

One notable finding in Chapter III was evidence of opposing morphological specialisation associated with aerial movement (and related climbing ability) versus running ability. This is the premise of $\mathbf{H}_{\mathbf{IV.4C}}$, and this prediction is somewhat supported in rodents. Firstly, looking at the locomotor profiles within this rodent dataset shows that high scores in aerial or climbing ability preclude high running scores (and vice versa). That is, no species scoring ≥ 3 in climbing or aerial ability scores higher than 2 in running ability. Likewise, no species scoring ≥ 3 in running scores more than 2 in climbing or aerial ability.

In a morphological context, there is evidence of climbing/aerial specialists and running specialists having distinct and opposing morphologies. Specifically, climbers/aerial species have a higher caudal angle, more prominent and cranially-directed acromion, and elongated coracoid. However, the evidence that running rodents are most likely to have mean-shaped scapula means that, in reality, the only conclusion that can be drawn here is that climbers tend to diverge from the mean shape.

IV.4.5.4. Digging

While digging ability does not appear to significantly influence scapular morphology in rodents, subterranean specialisation exhibits the same signatures as are observed across therians. A great many rodent species engage in digging behaviour as part of a more varied locomotor profile due to the prevalence of burrowing in rodents, so it may be expected that a specific signature of digging behaviour in rodents would be elusive. However, digging ability does appear to influence the arrangement of species in the PC1-PC4 morphospace (Fig. IV. G & H), with digging ability increasing towards the negative end of PC1. This indicates that digging ability is associated with a relatively slim blade with a slim and elongated scapular neck, prominent caudal angle, and ventrally-directed acromion. The four species classified as subterranean in this dataset (the naked mole-rat [*Heterocephalus glaber*], the Cape dune mole-rat [*Bathyergus suillus*], the Middle East blind mole-rat [*Spalax ehrenbergi*], and the Siberian zokor [*Myospalax myospalax*]) are all found at the negative extreme of PC1. While the former two of these species are located near the centre of PC3, *Spalax* has the highest PC3 score across the dataset, and *Myospalax* is quite close. These scores represent a particularly slim scapular blade with a ventrally-directed acromion. This is identifiably similar to the findings on subterranean taxa across therians in Chapter III, associated with re-orientation of the scapula such that the glenoid is highly cranial to facilitate a ‘breaststroke-like digging’ motion (Reed 1951; Gambaryan & Kielan-Jaworowska 1997; Warburton 2003). This also supports **H$_{\mathrm{IV.4D}}$** within the scope permitted by the low sample size and how heavily rodent scapular shape is constrained in different clades.

However, it is important to address the different types of digging behaviour in rodents, because this is not necessarily a forelimb-dominant behaviour. In fact, several rodents use their large incisors to break and move substrate (known as chisel-tooth digging) as their exclusive digging strategy or in combination with forelimbs (Lessa & Stein 1992; Doubell et al. 2020). Notable primarily chisel-tooth diggers within this dataset are the naked mole-rat (*Heterocephalus glaber*), the Maule tuco-tuco (*Ctenomys maulinus*), and the Middle East blind mole-rat (*Spalax ehrenbergi*), all of which are entirely or mostly subterranean. Of course, the functional demands on the forelimb differ greatly between species which dig exclusively with their forelimbs and those which dig primarily using their teeth, so it follows that this is likely to influence forelimb morphology. This is the case in the closely related *Heterocephalus* and *Bathyergus* (the former of which is a chisel-tooth digger and the latter of which is a forelimb-dominated digger), which have notably different morphologies in all components of the forelimb (Doubell et al. 2020). It is expected that chisel-tooth diggers will lack scapular adaptations related to the functional forelimb demands of digging, while those species which primarily use their forelimbs will exhibit clearer functional adaptations towards digging behaviour. However, it can be seen in Fig. IV.11 that differences in digging type do not clearly influence the position of digging species in the PC1-4 morphospace. While there may be consistent morphological differences in the scapula between different digging types, these are not aligned with the axes of greatest variation across rodents, and further investigation would be required to better understand how digging type influences scapular morphology in digging rodents.

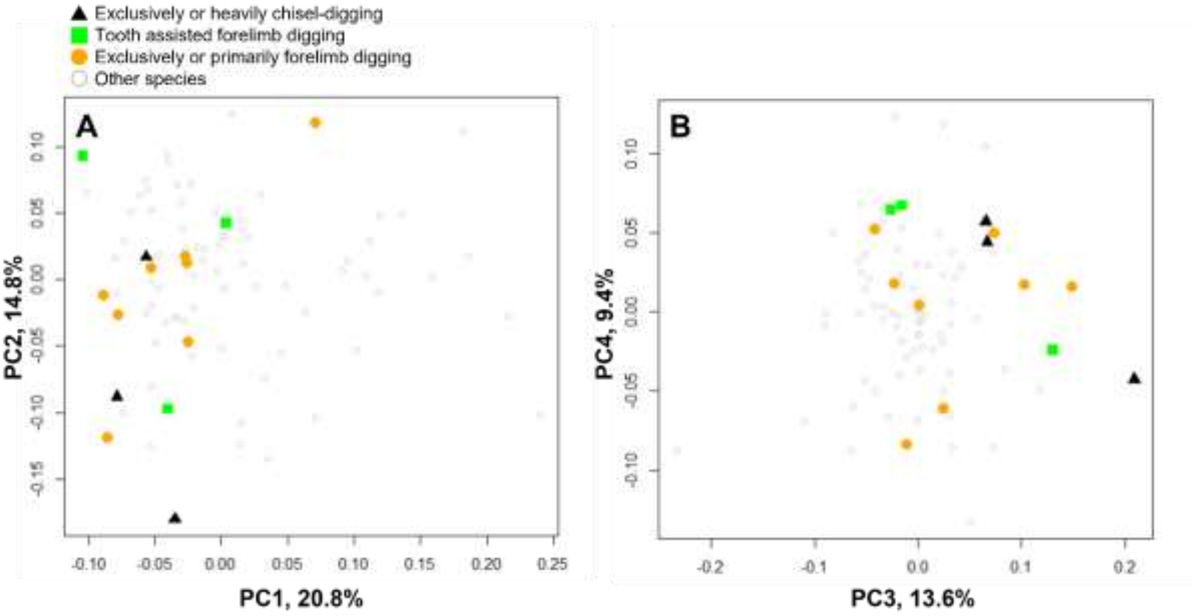


Figure IV.11: Position of diggers and subterranean species utilising functionally different digging behaviours in the PC1-4 morphospace
Scatter plots highlighting all species classified as diggers or subterranean, with type of digging behaviour indicated (from predominantly chisel-tooth digging to predominantly forelimb digging), in the PC1-PC4 morphospace. All other species are shown as grey circles.

IV.4.5.5. Swimming

Swimming ability does not significantly influence scapular morphology within or outwith a phylogenetic structure in the model (**modelR8**), and this ability has no visually discernible influence on the PC1-PC4 morphospace (Fig. IV.7I & IV.7J). This indicates that any morphology associated with high swimming ability does not align with the major shape variations represented by PC1-PC4. Further investigation at larger sample sizes of proficient swimmers within rodents would be necessary to confidently identify aspects of scapular morphology directly linked to swimming ability.

IV.4.6. Rodents as a microcosm of therians

The taxonomic breadth of Chapter III came with the aim of identifying large-scale generalisable trends in scapular functional morphology across therians. However, in order to validate the findings, it was necessary to reduce the taxonomic breadth of the dataset to a single group which could appropriately represent the functional diversity of mammals. Rodents were chosen for this, being numerous, diverse in their locomotion behaviour and size, as well as exhibiting clavicle loss in some species. Following the results of this chapter, the question arises, are rodents appropriately representative of therian mammals in the context of scapular functional morphology?

Firstly, the most variable regions of the scapula in rodents are the same as those across therians. This is encouraging evidence that these regions are particularly diverse in therians and are, therefore, the most relevant regions to investigate in scapular functional morphology. For example, when constructing landmark configurations for researching scapular morphology in therians, capturing these regions should be prioritised. Secondly, allometric shape change in rodents appears to generally reflect the allometric results across therians (despite clear influences of evolutionary history in rodents). This validates the findings across therians, and strengthens the conclusion that increased size is directly associated with increased blade width, elongation of the vertebral border, and enlargement of the glenoid fossa. Finally, with regards to locomotion behaviour, rodents are certainly representative of therians more broadly in exhibiting a particularly wide variety of locomotor profiles. No rodents are capable of powered flight, though multiple species are specialised gliders. Likewise, no rodents are fully aquatic but many are proficient swimmers. This means that rodents provide a comparison for non-chiropteran and non-cetacean therians. Since chiropterans and cetaceans consistently represented isolated morphological extremes in Chapter III, the absence of these behavioural profiles within rodents does not detract from comparison to the rest of therians. In Chapter III, it was found that aerial and running abilities significantly influence scapular morphology across therians. The same is the case here in rodents. Aerial acrobatics (and associated climbing ability), both across therians and in rodents specifically, are associated with a high and prominent caudal angle, elongated coracoid process, and highly cranial acromion in rodents. This supports the association of gliding behaviour with these scapular characteristics, and indicates that rodents are representative of therians more broadly in this regard. The significance of running ability to influence scapular morphology across therians is reflected in rodents (particularly in aclaviculate species), as are the opposing trends of scapular morphologies adapted for climbing/aerial movement and those adapted for high running ability. Though high running ability in rodents appears to be associated with a mean scapular shape, this shape reflects several of the characteristics of claviculate runners across therians – slim, infraspinous-dominated blade with ventral acromion region.

It is clear that rodent scapular functional morphology reflects that of therians broadly in several key ways. There are, however, some notable caveats. The obfuscating influence of phylogeny in rodents, though somewhat representative of therians generally, means that rodents do not offer a clear insight into the functional morphology of the scapula disentangled from potential phylogenetic constraints, as originally intended. Certainly, the rodent dataset does not improve upon the therian dataset in this regard, and is arguably subject to greater phylogenetic influence than therians broadly. This is particularly apparent in the significant differences in allometric trends between taxonomic groups within rodents. Additionally, the fact that clavicle loss in rodents has only occurred within Hystricomorpha, coupled with the reduced number of available aclaviculate species, results in decreased statistical power for most analyses on the influence of clavicle loss on rodent scapular shape.

Overall, rodents are promisingly representative of therians more broadly in the context of scapular morphology, particularly with regard to scapular adaptation associated with functional demands. The strong influence of phylogenetic variation on scapular shape and limited clavicle loss in rodents are disadvantageous for studies such as these, but the former at least can be accounted for in statistical analyses which factor in phylogeny. Ultimately, there is no alternative therian group which offers the same functional diversity as rodents. Marsupials have this potential, but assertions that their forelimb functional morphology is constrained by the necessity of precocial climbing behaviour (Sears 2004; Astúa 2009) means that marsupials are not an appropriate choice. Carnivorans exhibit substantial functional diversity, in size and locomotion behaviour, and considerable work has been done on scapular functional morphology in this group (Taylor 1974; Gálvez-López 2014; Gálvez-López & Casinos 2022). However, since all carnivorans are aclaviculate, they cannot be said to represent therians more broadly. The results of this chapter support rodents as the most suitable microcosm for therian mammals in the study of scapular functional morphology.

IV.5. Conclusions

IV.5.1. Overall scapular variation

The most variable aspects of the rodent scapula are the same as the most variable regions across therians:

- blade width and relative dominance of the lateral fossae
- acromion region morphology
- coracoid process morphology
- curvature of the vertebral border and caudal angle height.

IV.5.2. Size and allometry

Though size differences are tied to evolutionary history across much of rodents (with hystricomorphs generally larger than myomorphs, for example), increased size in rodents is associated with increased blade width and subsequent enlargement of the vertebral border. This was also observed across therians, and allows attachment of larger weight-bearing musculature at the vertebral border. Additionally, allometry consistently varies along phyletic lines in rodents.

IV.5.3. Evolutionary history

Evolutionary history has a distinct effect on scapular morphology in rodents, apparently obscuring the influences of other factors. The differentiation of taxonomic groups appears to be particularly influential on scapular variation (see the PC1-PC2 morphospace, Fig. IV.4), and allometry.

IV.5.4. Clavicle presence

Clavicle loss has only occurred in some species of Hystricomorpha. As compared to claviculate hystricomorphs, aclaviculate species exhibit the same characteristics associated with clavicle loss across therians: acromion reduction and relatively low caudal angle. In addition, they also have a slim scapular neck and enlarged supraspinous fossa.

IV.5.5. Locomotion behaviour

Differences in locomotion behaviours and their respective functional demands clearly influence scapular morphology in rodents.

- Increased aerial ability is associated with a highly cranial acromion process, as well as elongated and caudally-directed coracoid process. These features were also found to be characteristic of aerial behaviours across therians, and are directly associated with increased shoulder mobility and stability in a wide range of motion.
- Increased running ability is associated with the mean scapular shape in rodents – a scapula with slim, infraspinous-dominated blade and ventrally-directed acromion region. These features were associated with running behaviour across claviculate therians, and are related to efficient and stabilised movement in the parasagittal plane.

IV.5.6. Rodents as a microcosm of therians

Functional morphology of the scapula in rodents reflects results in therians more broadly with some caveats, but still indicating that rodents are the most suitable study group in this context.

Appendix IV.1: Rodent locomotor quantification

The method laid out in Chapter II was utilised in order to obtain a locomotion scoring matrix (S.IV.1.B) and locomotion categorical variable for the specific dataset of 87 species included in Chapter IV. The results of the three cluster validation methods (App. IV.1 Fig. 1) indicate a consistent optimum at k = 8 and, upon inspection, these clusters are biologically informative.

The groups are as follows (App. IV.1 Fig. 2):

Climbers (n = 8): This cluster is defined by scores of 2 or 3 in climbing ability, a score of 1 in digging ability, and a score of 0 in aerial ability.

Specialised climbers (n = 12): This cluster is defined by a score of 4 in climbing ability not associated with aerial scores above 0.

Diggers (n = 10): This cluster is defined by scores of 3 or 4 in digging ability not associated with scores of at least 1 in all other abilities except aerial, and no scores of > 2 in any other ability.

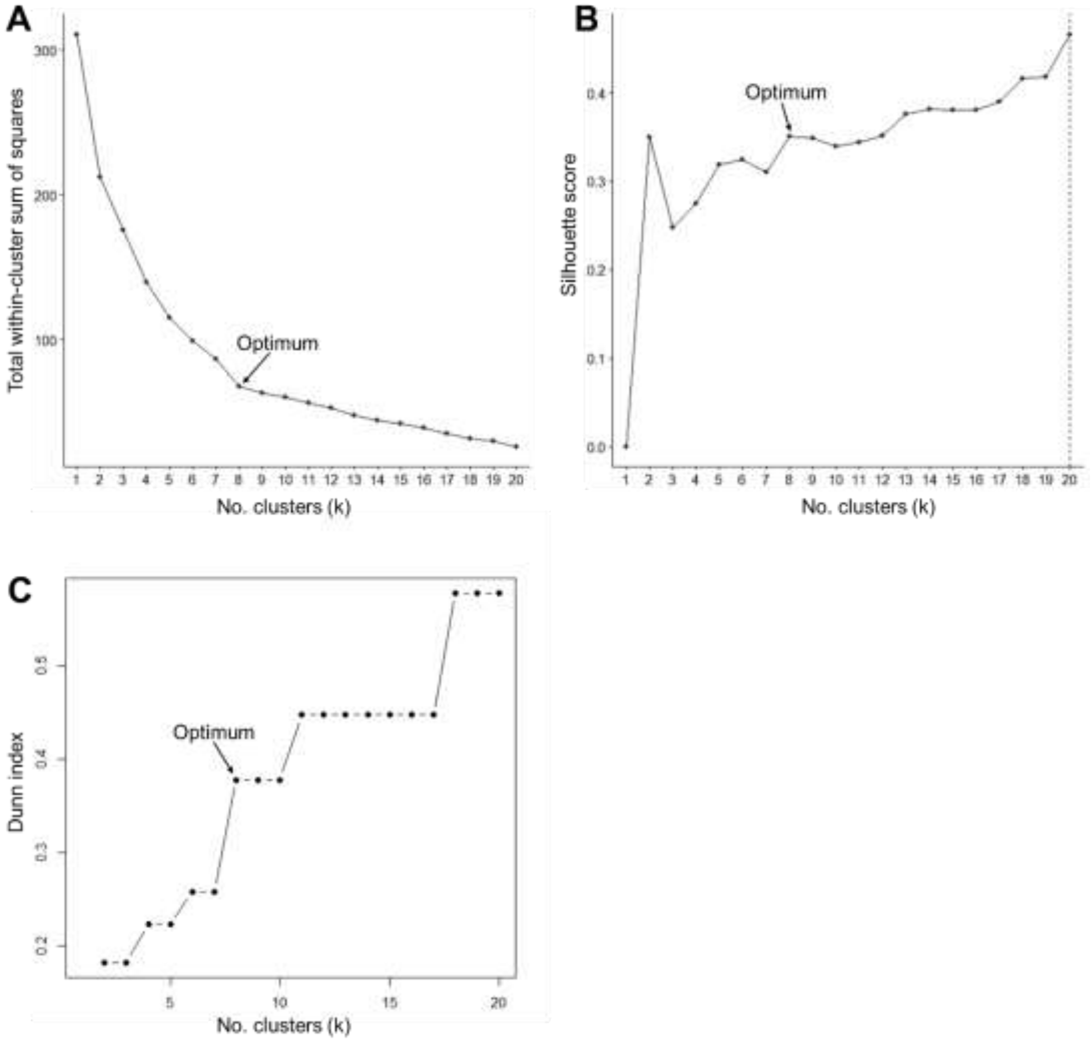
Generalists (n = 30): This cluster is defined by scores ≥ 2 in at least two abilities (most commonly 3) and a score of 0 in aerial ability only.

Aerial acrobats (n = 3): This cluster is defined by a climbing score of 4 as well as aerial scores of 2 or 3.

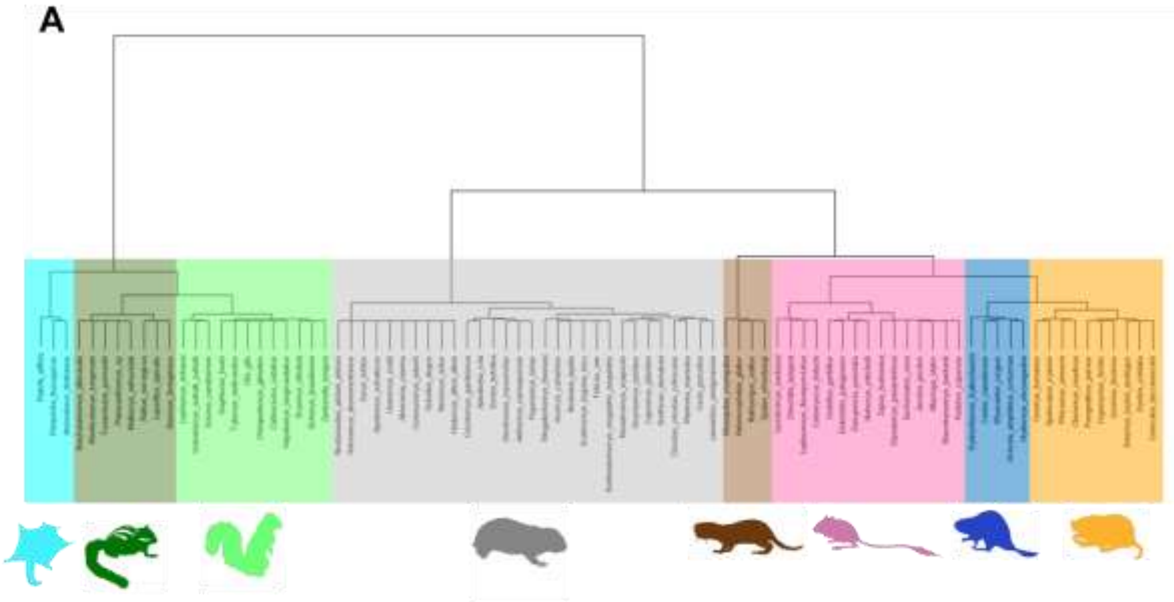
Runners (n = 15): This cluster is defined by scores of 3 or 4 in running ability.

Subterranean (n = 4): This cluster is defined by a score of 4 in digging ability associated with a score of 0 in climbing ability.

Swim-dig (n = 5): This cluster is defined by a swimming score of 3. This is generally associated with digging ability of 2 or 3, though the capybara (*Hydrochoerus hydrochaeris*) scores 1 in digging ability.



Appendix IV.1 Figure 1: Results of optimal cluster number tests
Plots showing results of (A) Elbow method: total within-cluster sum of squares against cluster number; (B) Silhouette method: Silhouette scores against cluster number; and (C) Dunn Index values against cluster number. All plots show results for up to 20 clusters (k = 1 to 20) with local optima indicated.



B

	Aerial acrobats	Climbers	Spec. climbers	Generalists	Subterranean	Runners	Swim-dig	Diggers
n	3	8	12	30	4	15	5	10
Swimming	1 ± 0	1 ± 0	1 ± 0	1 ± 0.38	1 ± 0	1 ± 0	3 ± 0	1 ± 0.38
Climbing	4 ± 0	3 ± 0.5	4 ± 0	2 ± 0	0 ± 0	1 ± 0	1 ± 0	1 ± 0
Digging	1 ± 0	1 ± 0	1 ± 0.13	3 ± 0.5	4 ± 0	3 ± 0.5	3 ± 0.5	3 ± 0.38
Running	2 ± 0.25	2 ± 0	2 ± 0	2 ± 0	0 ± 0.13	3 ± 0.5	2 ± 0.5	2 ± 0.5
Aerial	3 ± 0.25	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 0.5	0 ± 0.5	0 ± 0

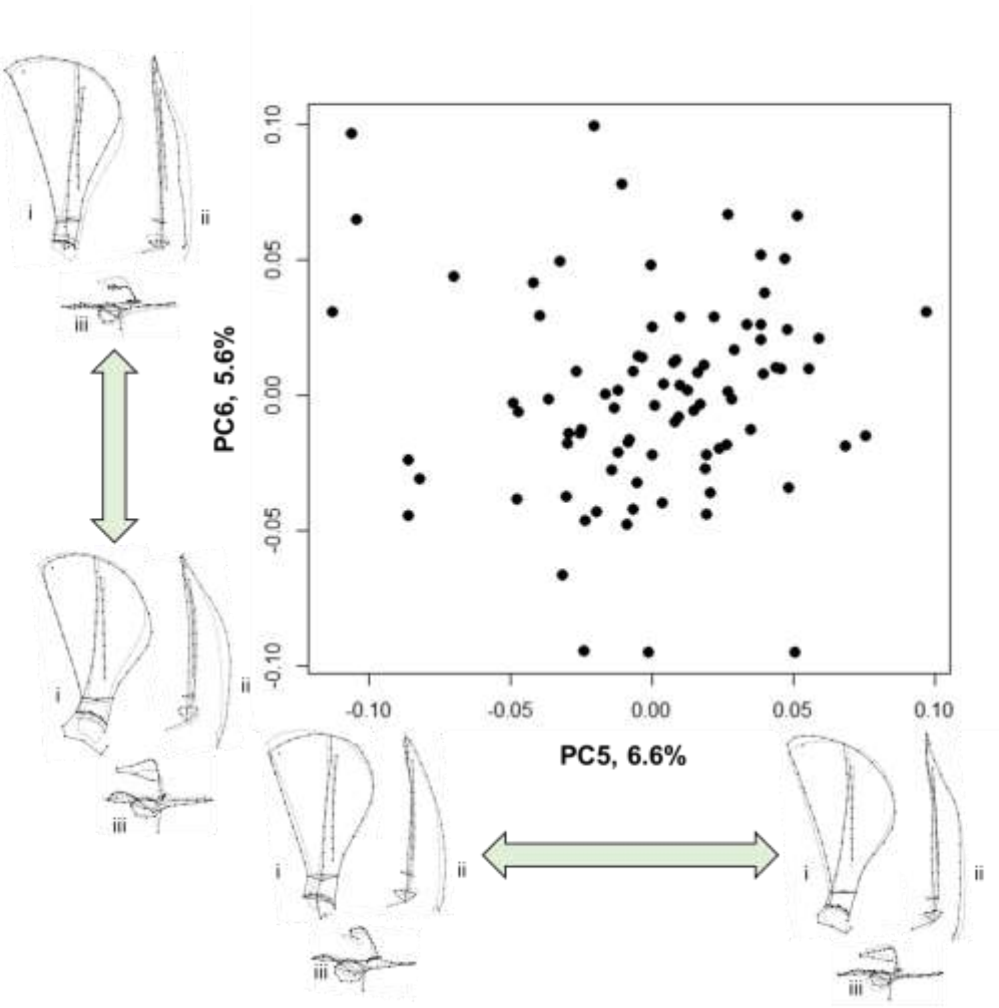
Appendix IV.1 Figure 2: Summary of final locomotor clusters arising from hierarchical cluster analysis

(A) Dendrogram showing the hierarchical relationships of the 87 species based on their locomotor profiles, calculated using Ward's method. The identity of the eight clusters established previously as optimal are visualised and colour coded here. Animal silhouettes are modified from PhyloPic (www.phylopic.org); species as follows from left to right: Petaurus breviceps *(sugar glider),* Funambulus pennantii *(Northern palm squirrel),* Sciurus carolinensis *(grey squirrel),* Aplodontia rufa *(mountain beaver),* Heterocephalus glaber *(naked mole-rat),* Jaculus jaculus *(Lesser Egyptian jerboa),* Castor canadensis *(N. American beaver), and* Geomys bursarius *(Plains pocket gopher).*

(B) The table provides median scores and quartile deviations (QD) for each locomotor variable in each cluster. In addition, the number of species in each cluster (n) is provided.

Appendix IV.2: PC5-PC6 results

Shape variation



Appendix IV.2 Figure 1: PC5-PC6 morphospace with shape changes
Scatter plot visualising principal components (PCs) five and six, accounting for a total of 12.2% or total variation in the dataset. Shape changes on each axis are visualised as wireframes from MorphoJ ver. 1.07a (Klingenberg et a. 2011), each relative to the mean shape (grey). The wireframes are displayed in three views: i) lateral; ii) caudal; iii) glenoid.

Shape change on PC5 (6.6%, App. IV.2 Fig. 1) is primarily related to vertebral border curvature, acromion morphology (especially of the metacromion), spine height, and glenoid fossa size. At the **negative extreme**, the scapula blade is approximately equal in width to the mean shape with a slightly larger infraspinous fossa than supraspinous. The caudal angle is low, being lower than the vertebral end of the scapular spine. The acromion is somewhat reduced relative to the mean shape, highly ventrally-oriented, and the metacromion is not identifiable. The coracoid is slightly longer than in the mean shape, but otherwise unchanged. The scapular spine is tall, particularly at the acromion end. The glenoid fossa is enlarged. At the **positive extreme**, the scapula blade is also approximately the same width as the mean shape, with equal lateral fossae. The caudal angle is considerably higher than the vertebral end of the spine. The acromion is prominent with a distinct metacromion, and highly cranially-directed acromion tip. The coracoid is sightly shorter than in the mean shape, and slightly more caudally-oriented. The scapula spine is lower than the mean shape at the acromion end. The glenoid fossa is small.

Shape change on PC6 (5.6%, App IV.2 Fig. 1) is primarily related to size of the supraspinous fossa, caudal angle prominence, acromion prominence, scapular spine height, scapular neck morphology, and glenoid fossa size and morphology. At the **negative extreme**, the supraspinous fossa is wider than in the mean shape, particularly in the lower (ventral) half of the blade, while the infraspinous fossa is unchanged. The caudal angle is slightly reduced, but remains the highest point of the vertebral border, The acromion is significantly enlarged with a prominent metacromion and cranio-ventrally-oriented acromion tip. The coracoid process is elongated but otherwise unchanged from the mean shape. The scapular spine is tall, especially at the centre of the blade. The scapular neck is shortened. The glenoid fossa is cranio-caudally elongated. At the **positive extreme**, the supraspinous fossa is reduced while the infraspinous is unchanged. The caudal angle is prominent and remains the highest point of the vertebral border. The acromion is significantly reduced, barely extending beyond the glenoid, and without a distinct metacromion. The coracoid process is reduced. The scapular spine is lower than in the mean shape. The scapular neck is slim and elongated, ending in a relatively small and circular glenoid fossa.

Size and allometry

Both PC5 and PC6 are significantly negatively correlated with size (App. IV.2 Table 1; App. IV.2 Fig. 2). This means that, on both axes, increased size is associated with curvature of the vertebral border such that the caudal angle is lower than the vertebral end of the scapular spine, and enlargement of the glenoid fossa.

Appendix IV.2 Table 1: Results of the allometric PGLS regressions
These tables provide the results of PGLS regressions PC5 and PC6 against log centroid size (logCS). The tables provide p-values, adjusted correlation coefficient (R^2), and Pagel's lambda (λ).

	R^2	**λ**	**p**
PC5	0.055	0.00	***0.016***
PC6	0.049	1.00	***0.022***

Evolutionary history

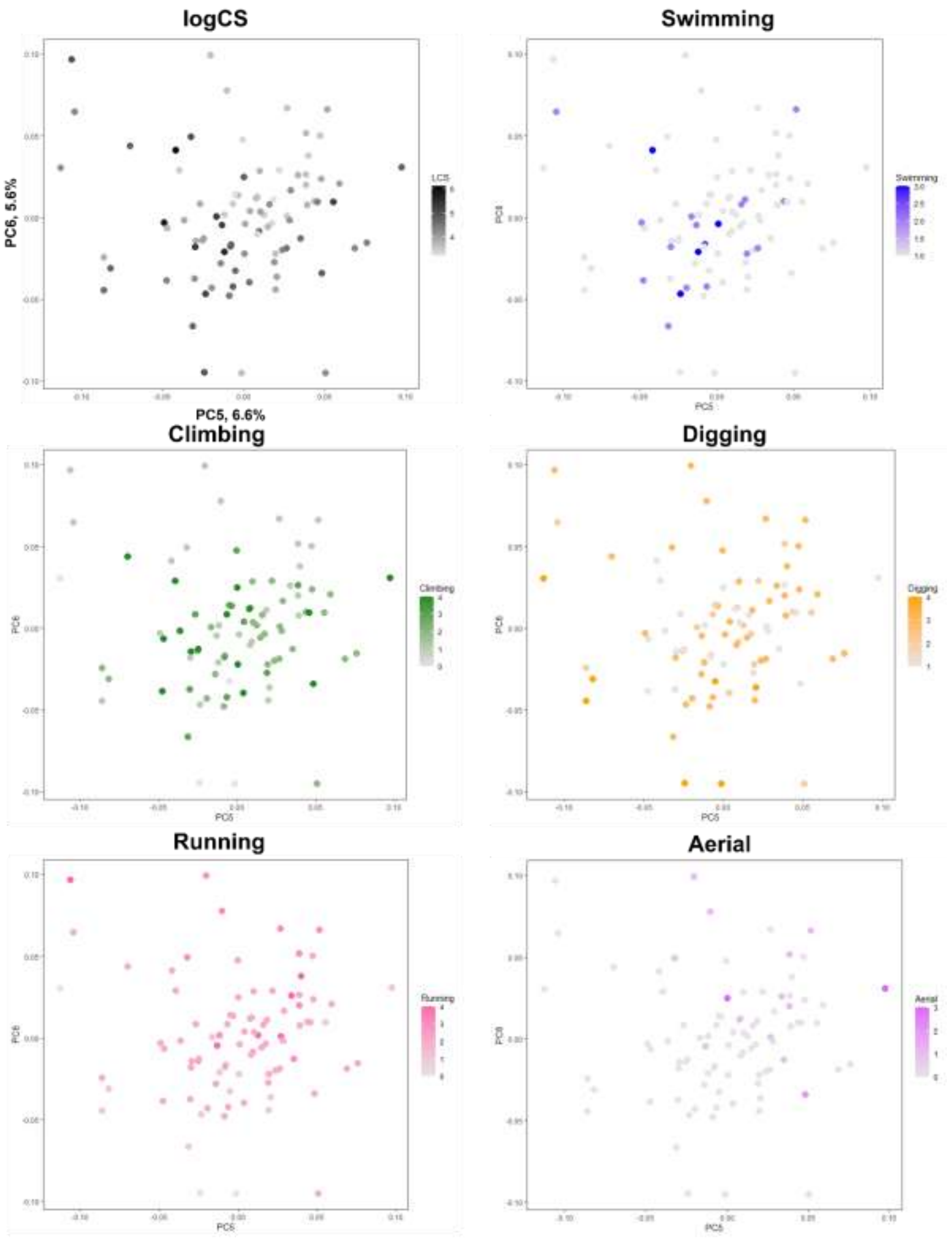
Similarly to the PC1-PC2 morphospace, a diagonal line through this morphospace serves to almost distinguish **Myomorpha** from **Hystricomorpha** (App. IV.2 Fig. 3A). **Sciuromorpha** are generally found in the lower half of PC6. Within **Castorimorpha**, two species are found in the lower half of PC5 (the plains pocket gopher [*Geomys bursarius*] and the Eurasian beaver [*Castor fiber*]), while the other three are found in the upper half of PC5 (Great Basin pocket mouse [*Perognathus parvus*], panamint kangaroo rat [*Dipodomys panamintinus*], and Desmarest's spiny pocket mouse [*Heteromys desmarestianus*]).

Clavicle presence

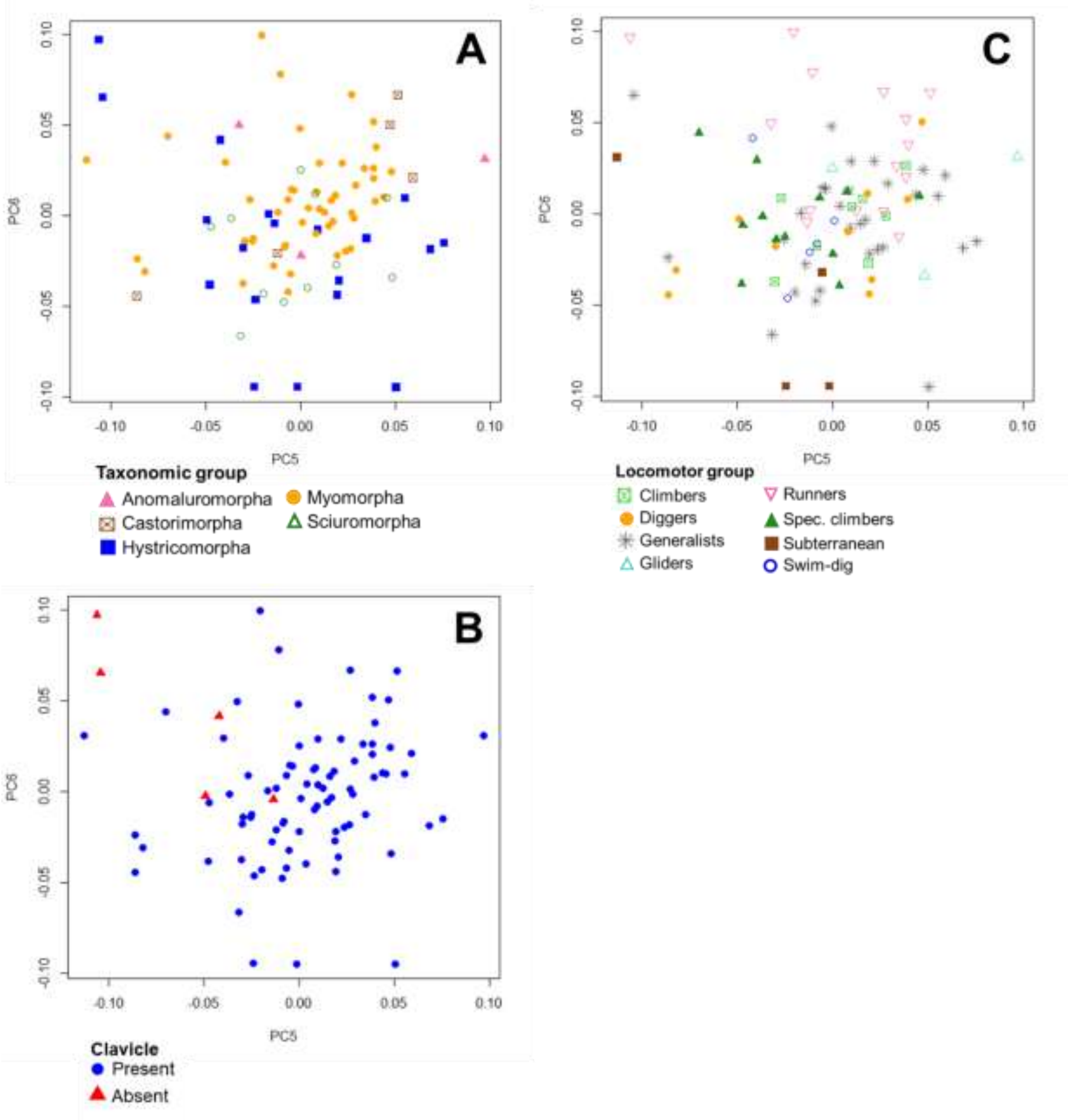
All five of the aclaviculate species are found in the lower half of PC5, and generally in the upper half of PC6 (App. IV.2 Fig. 3B). Two species (the Patagonian mara [*Dolichotis patagonum*] and the montane guinea pig [*Cavia tschudii*]) are located at the low extreme of PC5 and the high extreme of PC6. The common feature of shape change associated with positions low on PC5 and high on PC6 is reduction of the acromion.

Locomotion

In the PC5-PC6 morphospace, locomotor groups are relatively widely distributed (App. IV.2 Fig. 3C) and without clear ability gradients (App. IV.2 Fig. 2). Generally, the runners are located in the upper half of PC6, while climbers, specialised climbers, and diggers are mostly found in the lower half.



Appendix IV.2 Figure 2: PC5-PC6 morphospace with size and ability gradients
Scatter plots visualising the PC5-PC6 morphospace, with gradients of increasing size and ability in each of the five locomotor ability categories.



Appendix IV.2 Figure 3: PC5-PC6 morphospace with shape changes
Scatter plots visualising the PC5-PC6 morphospace, A) by taxonomic group, B) by locomotor group, and C) by clavicle presence.

Chapter V

Discussion:

Synthesising evidence of scapular functional morphology in therians

The work of this thesis has achieved the aim of empirically relating scapular morphology to functional demands across therian mammals. Firstly, in Chapter II locomotion behaviour was quantified at high resolution to provide a robust representation of the functional demands placed on the scapula during locomotion. Next, in Chapter III scapular morphology across all extant therian orders was related to the functional demands of locomotion, as well as increased size, and loss of the clavicular articulation. The results of this chapter revealed identifiable and biomechanically interpretable associations between aspects of scapular morphology and the various functional demands investigated. Finally, in Chapter IV the results across therians were validated within the taxonomically more restricted but functionally representative order, Rodentia, providing increased confidence in the functional conclusions and demonstrating the potential for rodents to be used as a model order in the study of mammal functional morphology.

V.1. Quantifying locomotion behaviour is foundational for understanding scapular functional morphology

Multivariate quantification of mammal locomotion has facilitated robust and nuanced analysis of the relationship between locomotion behaviour and scapular morphology.

When contemplating this project and the prospect of investigating how scapular morphology relates to functional demands in therians, it became clear early on that quantifying locomotion behaviour effectively would be a key component. Since it was necessary to represent the full diversity of locomotion behaviour across the whole of Theria, this required careful consideration. Unsatisfied with existing solutions in the literature, namely the use of categorical variables to represent locomotion behaviour, the work of Chapter II sought to develop an improved method for quantifying locomotion to be used in the subsequent analyses of scapular functional morphology. The use of a categorical variable to represent locomotion behaviour is well-established in functional morphology. However, there are two major caveats associated with this – significant loss of functional information when reducing behavioural profiles to single categories, and subjectivity in category selection and species assignment. The method developed in Chapter II addresses both of these caveats. Using a scoring system to quantify locomotor profiles dramatically increases the information contained within the behavioural quantification variable. Having locomotion represented in this way also facilitated novel ways of investigating scapular functional morphology in subsequent chapters. Specifically, including these numerical behavioural scores in regressions on the Procrustes coordinates made it possible to establish which locomotor abilities contributed most to scapular variation, and it was possible to visualise gradients of different locomotor abilities within the PCA morphospaces. Nevertheless, a categorical variable representing locomotion behaviour was also valuable. At this taxonomic scale, using pre-determined categories runs the risk of conflating species with very different locomotor profiles and functional demands into a single category. Instead of determining a series of categories prior to data collection and manually assigning each species to a single category (both points at which subjectivity are introduced), a categorical variable representing locomotion behaviour was generated mathematically using Ward’s hierarchical cluster analysis. In this way, the number of categories was optimised to best capture key distinctions between locomotor profile groups.

Throughout this thesis, this method for quantifying locomotion is used on three different datasets – 250 extant mammals (Chapter II), 201 extant therians (Chapter III), and 87 extant rodents (Chapter IV). This is an opportunity to explore how variation in the dataset influences the clustering (Table V.1). Five clusters arise consistently across the three datasets: **aerial acrobats**, **climbers**, **runners**, **generalists** and **subterranean** species. Though median scores vary somewhat in these categories across the datasets due to differences in species composition, the consistent recovery of these identifiable clusters suggests that these behavioural profiles are particularly prevalent in extant mammals. While the **volant** and **aquatic** categories do not appear in rodents, since no extant rodents are capable of powered flight or specialised aquatic life, it is expected that they would appear any time that such species are included in the dataset, making them as consistent as the other five clusters. A **dig-run** category arises in the large Chapter II dataset but not in subsequent chapters. Instead, species with this profile appear to be included in the runners category in Chapters III and IV, increasing the median digging score in this category. This also accounts for the lower percentage of the dataset represented by the runners in the Chapter II dataset. This is simply due to dataset composition – the Chapter II dataset contains more species exhibiting a profile with high scores in both running and digging than the Chapter III dataset, so they agglomerate into the runners category in the latter. In Chapter IV, digging behaviour is common across many rodent behavioural profiles, so a dig-run category is not distinguished from the runners category. In essence, the dig-run cluster can be considered a specialist subgroup within runners that is substantiated by cluster validation methods only when species composition supports its individuality. Similarly, a **swim-dig** category arises in both the Chapter II and Chapter IV datasets, but not Chapter III. There are seven species with this profile included in the Chapter II dataset which are absent from the Chapter III dataset (including the two monotreme species), and the remaining species are predominantly allocated to the generalist category in Chapter III. In the Chapter IV rodent dataset, there are five species in this category, but within the context of this smaller dataset, that is a significant enough proportion of species with this profile to make this category valuable to distinguish. This is another clear example of specialist subgroups arising based on differences in dataset composition. The Chapter IV rodent dataset also includes two novel categories not arising in the previous datasets – **diggers** and **specialist climbers**. As mentioned, digging behaviour is a common component of rodent behavioural profiles, so the main distinction between the diggers category and other categories is not the high digging score, it is the lack of a high score in climbing ability. The specialist climbing category distinguishes species with climbing scores of 3 (the climbers category) from those with scores of 4. Essentially, this draws a distinction between species which would traditionally have been categorised as scansorial and arboreal. Similar to the dig-run and swim-dig clusters, specialist climbers can be considered a specialised subgroup within the context of the rodent dataset. It is also worth noting that the only novel cluster arising in the Chapter III dataset is ‘other’ – an artificially created category to separate three outliers which were erroneously included in the aquatic category due to overall low scoring. This is important to highlight because it reflects the nature of determining the locomotor groups mathematically using Ward’s method – though outliers do not cause erroneous splinters in the dataset as they might in divisive clustering, they may appear within biologically-incongruous clusters due to the greedy nature of the algorithm. This is why cluster composition must be examined with care. Finally, while the rodent dataset is smaller than the others, instead of producing fewer clusters, validation methods suggest a similar cluster number with greater resolution in the category distinctions. Differences in clustering are expected with different dataset sizes and composition, and this is an advantage of the method – the categorical variable is tailored to the dataset. The consistency in the appearance of five to seven of the clusters indicates that these locomotor profiles were particularly prevalent across the three datasets. Whether this holds true across other taxonomic groups and datasets which otherwise deviate considerably from these is open to further investigation.

Finally, it is worth discussing the specialisation triangles mentioned in Chapter II. Grossnickle (2021) noted the appearance of these triangles in several mammal morphospaces, citing Samuels & Van Valkenburgh (2008), Chen & Wilson (2015) and Grossnickle et al. (2020), in which a triangle can be drawn with vertices at the specialist diggers, runners and aerial acrobats. This triangle appears in the PCA behavioural space too (Fig. II.5), extending to include aquatic and volant vertices, highlighting the parallel between form and function. However, no such specialisation triangles can be identified in the scapular morphospaces produced in this thesis. In all cases cited by Grossnickle, the morphospaces are constructed based on linear measurements of multiple limb bones. It appears to simply be the case that this triangle does not arise in the scapula datasets because the scapular PCA morphospaces are dictated by a mosaic of factors, of which locomotion is not dominant.

Table V.1: Summary of final locomotor clusters arising from hierarchical cluster analysis across three chapters
Comparison of the median scores ± quartile deviations (QD) for each locomotor variable in each cluster across the datasets for Chapters II, III and IV. In addition, the number of species in each cluster (n) and the percentage of the total dataset represented in said cluster are provided.

CH II, n = 250	Aerial acrobats	Climbers	Runners	Generalists	Subterranean	Volant	Aquatic	Swim-dig	Dig-run			
n (% of total)	21 (8.4%)	46 (18.4%)	23 (9.2%)	44 (17.6%)	8 (3.2%)	32 (12.8%)	27 (10.8%)	24 (9.6%)	25 (10.0%)			
Swimming	1 ± 0	1 ± 0	1 ± 0.5	1 ± 0.5	1 ± 0	1 ± 0	4 ± 0	2 ± 1	1 ± 0.5			
Climbing	4 ± 0	3.5 ± 0.5	1 ± 0.5	2 ± 0.5	0 ± 0	4 ± 0	0 ± 0	1 ± 0	1 ± 0			
Digging	1 ± 0	1 ± 0.5	0 ± 0.5	2 ± 0.5	4 ± 0	0 ± 0	0 ± 0	3 ± 0	3 ± 0.5			
Running	2 ± 0.5	2 ± 0	4 ± 0	2 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 0.5	4 ± 0.5			
Aerial	2 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 0	0 ± 0	0 ± 0	0 ± 0.5			

CH III, n = 201	Aerial acrobats	Climbers	Runners	Generalists	Subterranean	Volant	Aquatic			Other		
n (% of total)	17 (8.5%)	38 (18.9%)	37 (18.4%)	50 (24.9%)	7 (3.5%)	25 (12.4%)	23 (11.4%)			3 (1.5%)		
Swimming	1 ± 0	1 ± 0	1 ± 0.5	1 ± 0.5	1 ± 0	1 ± 0	4 ± 0.25			2 ± 0		
Climbing	4 ± 0	3.5 ± 0.5	1 ± 0.5	2 ± 0.5	0 ± 0	4 ± 0	0 ± 0			0 ± 0		
Digging	1 ± 0	1 ± 0.5	2 ± 1.5	3 ± 0.5	4 ± 0	0 ± 0	0 ± 0			1 ± 0		
Running	1 ± 0.5	2 ± 0	4 ± 0	2 ± 0.5	0 ± 0	0 ± 0	0 ± 0			2 ± 0		
Aerial	2 ± 0	0 ± 0	0 ± 0.5	0 ± 0	0 ± 0	4 ± 0	0 ± 0			0 ± 0		

CH IV, n = 87	Aerial acrobats	Climbers	Runners	Generalists	Subterranean			Swim-dig			Spec. climbers	Diggers
n (% of total)	3 (3.4%)	8 (9.2%)	15 (17.2%)	30 (34.5%)	4 (4.6%)			5 (5.7%)			12 (13.8%)	10 (11.5%)
Swimming	1 ± 0	1 ± 0	1 ± 0	1 ± 0.38	1 ± 0			3 ± 0			1 ± 0	1 ± 0.38
Climbing	4 ± 0	3 ± 0.5	1 ± 0	2 ± 0	0 ± 0			1 ± 0			4 ± 0	1 ± 0
Digging	1 ± 0	1 ± 0	3 ± 0.5	3 ± 0.5	4 ± 0			3 ± 0.5			1 ± 0.13	3 ± 0.38
Running	2 ± 0.25	2 ± 0	3 ± 0.5	2 ± 0	0 ± 0.13			2 ± 0.5			2 ± 0	2 ± 0.5
Aerial	3 ± 0.25	0 ± 0	1 ± 0.5	0 ± 0	0 ± 0			0 ± 0.5			0 ± 0	0 ± 0

V.2. Overall scapular variation

Specific aspects of scapular morphology are consistently more variable than others.

Both across therians and within rodents, the most variable regions of the scapula were found to be consistent and in line with previous research. Change in **blade width and ratio of the lateral fossae** was a particularly dominant component of shape change in the therian and rodent PCA morphospaces. Blade width is explicitly noted to be a primary source of variation or key descriptive feature in several studies (Argot 2001 [didelphid marsupials]; Sargis 2002 [tupaiids]; Salton & Sargis 2008 [tenrecoids]; Astúa 2009 [didelphids]; Gálvez-López 2014 [carnivorans]; Voisin et al. 2014 [primates]; Wölfer et al. 2019 [sciuromorph rodents]; Carvalhaes et al. 2022 [echimyid rodents]). Ratio of the lateral fossae was more variable across therians than within rodents, but has been recognised as highly variable in many taxa (Müller 1967 [carnivorans and ungulates]; Monteiro & Abe 1999 [xenarthrans]; Sargis 2002 [tupaiids]; Taylor & Slice 2005 [apes]; Salton & Sargis 2008 [tenrecoids]; Voisin et al. 2014 [primates]; Gálvez-López 2014 [carnivorans]; Carvalhaes et al. 2022 [echimyid rodents]). **Length and/or curvature of the vertebral border**, particularly with respect to the **position of the caudal angle** relative to the vertebral end of the spine, was found to be a considerable source of variation across therians and within rodents. These characteristics have also been identified previously as sources of significant variation in many taxa (Lehman 1963 [fossorial rodents]; Taylor 1974 [viverrid carnivorans]; Monteiro & Abe 1999 [xenarthrans]; Argot 2001 [didelphid marsupials]; Sargis 2002 [tupaiids]; Seckel & Janis 2008 [small cursors]; Astúa 2009 [didelphids]; Preuschoft et al. 2010 [primates]; Gálvez-López 2014 [carnivorans]). Finally, the **acromion region** (prominence and orientation, including both the hamatus and suprahamatus processes), was found to be particularly variable across therians and within rodents. This has certainly been identified in a range of taxa (Lehman 1963 [fossorial rodents]; Taylor 1974 [viverrid carnivorans]; Argot 2001 [didelphid marsupials]; Seckel & Janis 2008 [small cursors]; Salton & Sargis 2008 [tenrecoids]; Astúa 2009 [didelphids]; Gálvez-López 2014 [carnivorans]; Voisin et al. 2014 [primates]; Wölfer et al. 2019 [sciuromorph rodents]; Carvalhaes et al. 2022 [echimyid rodents]), with Sears (2004) deciding to exclude the acromion from their PCA due to its high variability in placentals. Importantly, the findings of this thesis provide a framework for focusing scapular shape quantification – future landmark configurations should prioritise capturing these regions. Additionally, as expanded upon throughout, all of these features can be directly related to differing functional demands as well as evolutionary history.

V.3. Chiroptera and Cetacea – specialised functions, specialised morphologies

Chiropterans and cetaceans represent two unusual taxonomic groups within therians, behaviourally and morphologically.

Chiropterans are the only therians capable of powered flight, and all representatives fly. Flight places immense functional demands on the shoulder girdle and forelimb, requiring unparalleled mobility to perform the upstroke, and significant power in forelimb adduction during downstroke (Vaughan 1970). For this reason, the chiropteran shoulder girdle is highly adapted and distinct from that of other therians. The chiropteran scapula is highly dorsally-positioned on the thorax, with a long acromion process directing the clavicle over the shoulder dorsally, thus leaving the lateral area of the joint free of osseous elements, facilitating the raising of the forelimb during the upstroke. High levels of shoulder mobility are also facilitated in bats by unusually mobile sternoclavicular and acromioclavicular joints (Panyutina et al. 2011). In fact, the bat shoulder has a range of motion of at least five degrees of freedom (Bahlman et al. 2013), which is also facilitated by the absence of significant ligaments at the glenohumeral joint, which is predominantly supported and stabilized by the tendons of the surrounding musculature (Panyutina et al. 2011). Finally, forelimb musculature is concentrated proximally to reduce weight through the wing (Amador et al. 2018; Anderson & Ruxton 2020), meaning that the bat scapula is robust and houses well-developed muscles.

Likewise, the fully aquatic life of cetaceans presents its own extreme functional demands. The forelimbs are not weight-bearing in any capacity, but instead are utilised for directional control while thrust is generated via pelvic oscillation (Cooper et al. 2007). Therefore, cetacean flippers primarily experience force in the form of drag. In order to provide effective directional control through the dense medium of water, the shoulder must be mobile but also well-stabilised. The scapula is large and wide because, as in chiropterans, the musculature of the cetacean forelimb is concentrated proximally (Cooper et al. 2007; Sekiya et al. 2023). The *m. subscapularis* is particularly large and subdivided into independent segments for increased forelimb control (Sanchez & Berta 2009). While the *m. supraspinatus* is notably small and passes between the coracoid and acromion processes, the *m. infraspinatus* and *m. teres major* are large and occupy almost the entire lateral side of the blade. These muscles are heavily involved in rotation of the flipper for steering and in its role as a hydrofoil (Smith et al. 1994; Sekiya et al. 2023). Evidently, the cetacean scapula is highly adapted for the biomechanical demands of movement through water. The subtleties of cetacean scapular morphology have been extensively studied (Strickler 1978; Smith et al. 1994; Cooper et al. 2007; Sanchez & Berta 2009; Sekiya et al. 2023) and can even be used to distinguish marine from freshwater species (Smith et al. 1994). Within the context of therian scapular anatomy more broadly, the cetacean scapula is a clear outlier, not subject to forces associated with weight-bearing, hence the likely divergence of cetacean scapular allometry from other therians.

Overall, chiropterans and cetaceans present scapular morphologies which are identifiably related to their specific biomechanical needs, which differ considerably from those of other therians. Their differentiation from the other therians is responsible for a substantial portion of scapular variation identified in the therian-wide PCA. Therefore, while understanding the scapular adaptations associated with these unique locomotor behaviours is of great value, their inclusion in further studies investigating therian scapular morphology may be unnecessary or even disadvantageous.

V.4. Differences in scapula size significantly influence morphology

Increased size is associated with increased width of the scapular blade, elongation of the vertebral border, and enlargement of the glenoid fossa.

In therians overall, log-transformed absolute scapula size (logCS) was found to be significantly related to scapular morphology within a phylogenetic framework, and the same was true in rodents outwith the phylogenetic framework due to a clear relationship between size and evolutionary history. The scapula is a weight-bearing component of the forelimb in a quadrupedal posture and, thus, it is subject to the effect of ground reaction force directed up the forelimb, through the glenoid fossa into the scapula. In climbing and suspensory behaviours, the scapula is also subjected to forces arising from body mass, though this may be via tensile rather than compressive forces.

Both in therians generally and in rodents specifically, increased absolute scapular size is associated with three main features: increased blade width and accompanying expansion of the vertebral border, increased curvature of the vertebral border, and increased size of the glenoid fossa. First, the increase in blade width and vertebral border elongation is in line with biomechanical predictions ($\mathbf{H}_{\mathbf{III.1}}$ & $\mathbf{H}_{\mathbf{IV.1B}}$) and previous findings (Young 2008 [anthropoid primates]; Astúa 2009 [didelphid marsupials]; Gálvez-López 2014 [carnivorans]). The responsibility of weight-bearing predominantly falls to musculature associated with connecting the thorax to the forelimb, primarily the *m. serratus ventralis, mm. rhomboidei* (Jenkins 1974; Stein 1981; Polly 2007; Fujiwara et al. 2009; Preuschoft et al. 2010). The *m. serratus ventralis* and the subdivisions of the *mm. rhomboidei* attach to the scapula along the vertebral border. It has also previously been found that increased size is associated with enlargement of one or both of the lateral fossae housing the *m. supraspinatus* and *m. infraspinatus* (Taylor & Slice 2005; Young 2008; Astúa 2009; Wölfer et al. 2019). Therefore, it appears that elongation of the vertebral border facilitates enlargement of this musculature, directly increasing weight-bearing capacity. Second, increased size was found to be related to increased curvature of the vertebral border such that the caudal angle is generally lower than the point at which the scapular spine meets the vertebral border. The most likely explanation for this is the difference in forelimb posture in small versus large mammals. Small mammals commonly exhibiting a crouched or 'zigzag' limb posture to maximise manoeuvrability over uneven terrain (Fischer 1994), while larger mammals tend to have their joints stacked increasingly vertically to better manage high ground reaction forces (Biewener 2003). This difference in limb posture alters the relationship of the scapula to the lower limb and the thorax. The curving of the vertebral border and translation of the caudal angle ventrally may function to maintain a relatively consistent muscle length and line of action for the *m. teres major* which originates at the caudal angle of the scapula and inserts into the proximal humerus. The curvature may also act to optimise function of the weight-bearing musculature attached to both the scapula and thorax with the scapula in differing postures. It is very important to bear in mind that the limitations of capturing the osseous part of the scapula only may result in loss of functional information, especially around the vertebral border where some taxa have large cartilaginous extensions of the blade. This is particularly important to bear in mind in the case of terrestrial ungulates, which have flat, straight vertebral borders even at large sizes, and have large cartilaginous expansions of the vertebral border (described in horses, Ahrari-Khafi et al. 2017). Finally, enlargement of the glenoid fossa in association with increased size is almost certainly related to increased stress and strain experienced at the glenohumeral joint when body mass is large and, therefore, ground reaction force is large (Püschel & Sellers 2016; Arias-Martorell 2018).

Differential scaling in the scapula has previously been identified in carnivorans (Gálvez-López 2014) and didelphid marsupials (Astúa 2009). That is, the allometric effect differs in small versus large taxa. The results of this thesis indicate differential scaling in terrestrial therians and in rodents such that the allometric effect is greater in smaller taxa, aligned with the findings of Gálvez-López in carnivorans (2014) and in contradiction to the findings of Astúa 2009 in didelphid marsupials. The dataset of therians used in Chapter III represents a size range of approximately six orders of magnitude, and the rodent dataset represents a range of four orders of magnitude. With Gálvez-López's dataset representing five orders of magnitude and Astúa's representing only three, it is likely that Astúa's results may not be generalisable. This differential scaling suggests that shape changes per unit size are proportionally larger in small scapulae versus large scapulae, and might explain why scapular variation appears greater in smaller species. Since each shift is large relative to the small bone, the same absolute increased in blade width would appear to be a dramatic change in small species, where it may be barely detectable in large species.

Allometry has previously been found to vary along phyletic lines in carnivorans (Gálvez-López 2014) and between locomotor groups in sciuromorph rodents (Wölfer et al. 2019). Across therians, it was found that allometry varies according to both phyletic lines and locomotor groups. In rodents, however, it was found that allometry varies strikingly along phyletic lines, but not between locomotor groups. This does not necessarily contradict the findings of Wölfer et al. (2019), since low sample size precluded further investigation of allometric differences between locomotor groups within each taxonomic group in this thesis. This leads directly into discussion of the importance of evolutionary history on scapular morphology.

V.5. Evolutionary history impacts scapular morphology

Different taxonomic groups exhibit notably different scapular morphologies and allometries.

Both across therians and within rodents, the phylogenetic signal (Bloomberg's K) in scapular morphology was moderate, demonstrating an important role of evolutionary history, but one which cannot explain scapular variation to the exclusion of functional variables. With lower taxonomic variation overall, the influence of phylogenetic structure was greater in rodents, obfuscating functional effects in regression models. Arrangement of species in the first two PCs of the rodent morphospace appears to be determined largely in association with differentiation of the five taxonomic groups, while PCs 3 & 4 are also heavily influenced by taxonomic differences alongside functional influences (Fig. IV.4). This means that taxonomic groups within rodents can be largely differentiated on the basis of the most variable aspects of scapular morphology. It is also the case that allometry varies significantly between taxonomic groups in rodents. Across therians, evolutionary history also greatly influences the arrangement of the morphospace (Fig. III.8). Though there is a great deal of overlap between taxonomic groups within the PC1-PC2 morphospace, several groups are identifiably clustered in particular regions. For example, terrestrial ungulates are all located in the positive half of PC2 and between 0.0 and -0.01 on PC1 (with the exception of the Javan warty pig [*Sus verrucosus*] which is located at 0.03 on PC1). Another example, the eulipotyphlans, are all located between -0.1 and -0.3 on PC1 (the lowest of any taxonomic group) and between -0.07 and 0.12 on PC2.

There are no specific aspects of scapular morphology which can be directly attributed to evolutionary history and no other factors in this thesis, but it is clear that scapular morphology in therians varies in relation to evolutionary history. This could be further explored using, for example, Mantel's tests comparing the phylogenetic distance matrix and the Procrustes coordinate matrix (Monteiro & Abe 1999), or ancestral state reconstruction (Gálvez-López 2014), but further exploration of the differences in scapular morphology along phyletic lines is outwith the functional focus of this thesis.

V.6. Clavicle loss has a significant influence on scapular morphology

Clavicle loss is associated with reduction of the acromion and change in vertebral border curvature.

Therian mammals have a notable evolutionary history of shoulder girdle simplification and reduction. In many extant taxa, this has gone a step further with reduction or loss of the clavicle. To varying extents, clavicle reduction/loss has occurred in multiple orders independently (Fig. III.3). The clavicle is lost entirely in ungulates, elephants, hyraxes, sirenians and pangolins, but is technically present in many carnivorans as a vestigial component of the shoulder girdle (de Souza Junior et al. 2020). This carnivoran vestigial clavicle takes the form of a 'floating' osseous element deep within the brachiocephalic muscle which does not articulate directly with the scapula or sternum via osseous articulation, but rather by ligamentous connections (de Souza Junior et al. 2020). In marsupials, the clavicle has been lost in Peramelemorphia (Garland et al. 2017; Simone et al. 2025) and reduced in the thylacine (Warburton et al. 2019). In rodents, as has been discussed previously, the clavicle is reduced and lacking osseous articulations in some species of hystricomorphs (Rocha-Barbosa et al. 2002). For the purposes of this thesis, clavicle presence was considered binary, dependent on the presence of osseous articulations with the scapula and sternum, which is a simplification of realistic clavicle diversity in therians. Nevertheless, the distinction between clavicle presence and absence proved to be highly informative in understanding scapular variation in therians.

Clavicle presence was found to be greatly influential on scapular morphology across therians in phylogenetic regression models, additionally influencing other functional variables. There are two main morphological differences between the scapulae of claviculate and aclaviculate therians identified in this thesis. First, the acromion is clearly reduced in aclaviculate taxa, even to the point of being unidentifiable in some ungulates. This was the specific prediction of $\mathbf{H_{III.3}}$ since the clavicle articulates with the acromion process when present, and loss of this articulation somewhat reduces the significance of the acromion. This is the first empirical evidence of acromion reduction in association with clavicle reduction/loss across therians. Second, the curve of the vertebral border differs between claviculate and aclaviculate taxa, specifically with the highest point of the border being the caudal angle in claviculate taxa and being the vertebral end of the scapular spine in aclaviculate taxa. This most likely arises as a consequence of differences in scapula position on the thorax in claviculate versus aclaviculate therians and the resulting biomechanical differences in relationship of the vertebral border and vertebral column, and the muscles connecting them (Voisin 2006).

Though the sample of aclaviculate rodents is limited and taxonomically constrained, the aclaviculate hystricomorphs do exhibit these two key differences relative to claviculate hystricomorphs, supporting **$H_{IV.3}$** and increasing confidence in the association of these features with clavicle loss. Aclaviculate hystricomorphs also have a slimmer scapular neck and relatively larger supraspinous fossa than the claviculate hystricomorphs. These additional features serve to increase mechanical efficiency of pendulum motions of the scapula in the parasagittal plane during stride, and provide stability to the joint cranially, which may be lost in the absence of the clavicle (Eaton 1944; Jenkins 1974).

Future work may benefit from finer subdivisions of clavicle condition or, ideally, the use of measures of relative clavicle size which are not currently available across therians, or a morphometric analysis of the clavicle itself. This would capture differences in the vestigial clavicle of carnivorans, which may vary considerably in its influence on scapular morphology depending on the size and structure of the vestigial clavicle.

V.7. Differences in locomotor profile significantly influence scapular morphology

Differences in biomechanical demands associated with differing locomotor profiles directly influence scapular morphology.

Quantifying locomotion using the novel method developed in Chapter II provided substantial multivariate data for use in Chapters III & IV. This is superior to the use of a single traditional categorical variable in many ways, one being the option to include ability scores in multivariate models (**model2, model3, model9-13, modelR2, modelR8-12**) and determine, not just that differences in locomotion behaviour influence scapular morphology (as is demonstrated in **model1** and **modelR1**), but which specific behaviours are responsible for influencing scapular morphology and to what extent. Thus, it was possible to discover that running and aerial abilities are particularly influential in both therians and rodents, and swimming ability non-significant in either dataset. Climbing ability significantly influences scapular morphology in rodents (outwith a phylogenetic framework), but not in therians. Another advantage of the multivariate scoring matrix was the ability to produce visualisations of locomotor ability gradients within the morphospace, which revealed shape changes associated with running, climbing, digging and aerial abilities. Though visualisation of the morphospace by discrete locomotor groups was informative, especially in identifying shape transition from claviculate climbers through aerial acrobats to volant species, using this visualisation alone without ability gradient visualisation would fail to represent subtleties of the relationship between scapular morphology and locomotion behaviour.

V.7.1. Swimming

It is challenging to relate swimming behaviour to scapular morphology within the context of this thesis due to the inclusion of cetaceans in Chapter III which, as has been discussed, present a unique set of scapular morphologies. The other species in the dataset highly capable of swimming appear more similar in scapular morphology to the non-aquatic species in the dataset than they are to cetaceans. Additionally, these non-cetacean aquatic taxa vary considerably in their terrestrial movement capability and, therefore, the necessity of weight-bearing on the scapula. Within rodents, no taxa are considered fully aquatic, and the least specialised member of the aquatic cluster across therians, the capybara, is one of the most aquatic rodents. However, based on previous research supported by the results of this thesis, some generalisations can be made regarding the scapulae of aquatic therians: the scapula is crescent shaped with a convex cranial border and concave caudal border, and the glenoid is caudally-oriented. These morphologies provide power in forelimb protraction and retraction, and humerus adduction and abduction, all of which are significant movements in pectoral oscillation, directional control using forelimbs, and limited terrestrial movement (Pierce et al. 2011; Gálvez-López 2014).

V.7.2. Climbing

Climbing ability was not found to significantly influence scapular morphology across therians (**model3**), but was found to be significant in rodents in non-phylogenetic models (**modelR2b**). Climbing ability gradients are identifiable in both the therian and rodent morphospaces, associated with aerial ability gradients. Given the significant biomechanical demands of specialised climbing behaviour, the lack of clear climbing behaviour signature is unexpected. However, across therians this is likely due to differences in claviculate and aclaviculate climbers, which is almost entirely linked to evolutionary history due to the very limited taxonomic variation in aclaviculate climbers – 11 of the 13 aclaviculate climbers are carnivorans (the exceptions being the African tree pangolin [*Phataginus tricuspis*] and the tree hyrax [*Dendrohyrax dorsalis*]), while nine of the 25 claviculate climbers are euarchontans and nine are marsupials. Climbing behaviour favours a shoulder which is mobile, and which is also stable and powerful in movement of the forelimb above and behind the head. The clavicle significantly supports these functions, so it follows that clavicle loss is disadvantageous in the context of climbing behaviour. The aclaviculate climbers all arise from taxonomic groups which exhibit universal clavicle loss, so their climbing ability developed within an aclaviculate context. It is important, then, to note that carnivorans being represented as aclaviculate in this thesis, when they possess a vestigial clavicle in reality, may influence the results pertaining to climbing behaviour (de Souza Junior et al. 2020). Further research to investigate the relative size/morphology of the clavicle across different behavioural profiles in carnivorans would significantly illuminate this.

Though a clear, generalisable morphological signature of climbing ability was not identified in this thesis, scapular morphology in both claviculate and aclaviculate climbers is well-studied due to the significance of the shoulder in facilitating climbing behaviour. In both claviculate and aclaviculate taxa, climbing ability has been associated with enlargement of the supraspinous fossa, enlargement of the attachment area for the *m. teres major*, and a prominent acromion (including in aclaviculate taxa, relative to other locomotor groups) (Oxnard 1968 [therians]; Taylor 1974 [viverrid carnivorans]; Monteiro & Abe 1999 [xenarthrans]; Argot 2001 [didelphid marsupials]; Sargis 2002 [tupaiids]; Taylor & Slice 2005 [apes]; Salton & Sargis 2008 [tenrecoids]; Astúa 2009 [didelphids]; Preuschoft et al. 2010 [primates]; Gálvez-López 2014 [carnivorans]; Voisin et al. 2014 [primates]; Fujiwara et al. 2019 [primates]; Wölfer et al. 2019 [sciuromorph rodents]; Oyetunde Kazeem et al. 2020 [rodents]). These features increase shoulder joint stability and mobility, as well as increasing power in shoulder flexion which facilitates lifting the thorax upwards.

V.7.3. Digging

Digging ability is significantly related to scapular morphology across therians, but the nature of the morphological relationship differs significantly in claviculate and aclaviculate taxa (**model3**). In rodents, digging ability does not appear to significantly influence scapular morphology in a meaningful way which can be uniquely attributed to this ability and no other variables (**modelR2b**). However, gradients of digging ability were identifiable on PC1 across therians and in rodents, and this is clearly associated with shape changes towards the rod-like scapulae found in subterranean species at the extremes of digging behaviour (all of which are claviculate). Beyond this, subtleties of the interaction between digging ability, size and clavicle presence, and their influence on scapular morphology prevent the identification of a clear morphological signature for digging behaviour.

As was touched upon in Section IV.4.5.4 (albeit with low sample size), digging ability as quantified here in fact reflects a diverse behaviour which may or may not be forelimb dominated. Even forelimb-dominated digging behaviours vary from extreme breaststroke-like motions in moles to more parasagittal forelimb motions in species like aardvarks, for example. Additionally, substrate varies across ecosystems, so some species are contending with hard and dry substrate, while others are moving through softer substrates. Disparities such as these in what digging behaviour looks like for different mammals may contribute to the lack of a consistent morphological digging signature across therians or in rodents, outwith the extremes of subterranean specialisation.

Subterranean species were found to consistently cluster within therian and rodent morphospaces due to the relatively well-understood independent specialisations of species to this lifestyle. Part of this is a tendency for these animals to revert to a sprawling forelimb posture in order to facilitate the ‘breaststroke-like’ digging motion they utilise for moving through the soil substrate (Gambaryan & Kielan-Jawarowska 1997). As a result, the position and orientation of the scapula on the thorax is altered, with the glenoid positioned highly cranial and close to the base of the skull while the slim and rod-like blade extends directly caudally, lying highly dorsal on the thorax (Reed 1951; Gambaryan & Kielan-Jawarowska 1997; Warburton 2003).

V.7.4. Running

Running was found to significantly influence scapular morphology across therians (**model3**) and within rodents (**modelR2b**), and in therians scapular morphology associated with running ability is significantly different in claviculate and aclaviculate taxa. This is, arguably, unsurprising. Clavicle loss has long been explained in association with increased cursorial behaviour, facilitating improved efficiency and power in parasagittal movement of the forelimb (shoulder flexion and extension) and increasing stride length (Eaton 1944; Rocha-Barbosa et al. 2002; de Souza Junior et al. 2020). In running behaviours, when the forelimb moves predominantly in the cranio-caudal plane without the need for arcuate motion at the shoulder joint, the clavicle is not necessary. Though empirical studies of this link between clavicle loss and running behaviour are lacking, the results of this thesis generally supports clavicle loss being common in association with running behaviour (73.0% or runners in Chapter III are aclaviculate). Evolutionary history also plays a significant role in this, however, with 14/27 aclaviculate runners in the Chapter III dataset being ungulates, which are ancestrally aclaviculate. This also considerably impacts interpretation of scapular morphology associated with running behaviour, as the high presence of ungulates may result in ungulate-specific features appearing erroneously to be associated with running behaviour. Nevertheless, some characteristics of the scapula in aclaviculate runners can be identified based on their position within the PC1-PC2 morphospace in Chapter III. The blade is supraspinous-dominated, with a reduced acromion (associated with clavicle loss), and convex vertebral border (caudal angle lower than vertebral end of the spine, likely also associated with clavicle loss due to the difference in position of the scapula on the thorax). It has been suggested that a large *m. supraspinatus* aids in shock-absorption, and it is also involved in shoulder extension, both important factors in effective running behaviour (Astúa 2009).

Claviculate runners would appear to be at a disadvantage, given the possible association between running and clavicle loss. Across therians and within rodents, claviculate runners have a slim scapula with a prominent and high caudal angle, and prominent, ventrally-directed acromion. The high caudal angle and prominent acromion may be attributable to the claviculate condition, but the ventral orientation of the acromion is likely important to avoid the clavicle interfering cranially with shoulder extension. The prominent caudal angle implies a large *m. teres major* which would provide powerful shoulder flexion during stride. The blade being slim may allow the scapula to function as a more effective 'pendulum' during its rotation to increase stride length (Jenkins 1974; Fischer 1994).

V.7.5. Aerial movement

Aerial movement ability was found to significantly influence scapular morphology across therians (**model3**) and within rodents (**modelR2b**). This behaviour descriptor encompasses a wide variety of specific behaviours, including brachiation, gliding, and powered flight, all of which are biomechanically demanding on the forelimbs and shoulder girdle in different ways. Generally, much like climbing behaviours but to a greater extent, aerial behaviours require that the shoulder be highly mobile, but also stable and powerful when the forelimb is positioned above or behind the head. Three main features of scapular morphology were found to be associated with aerial behaviours: a prominent and cranially-directed acromion process, a high caudal angle relative to vertebral end of spine, and an elongated and caudally-directed coracoid process. All species within Chapter III & IV which score ≥ 2 in aerial movement are claviculate, and this is because of the loss of the clavicle would significantly decrease the range of motion and stability of the shoulder. In fact, pathological loss of the clavicle in humans leads to significant weakness in load-bearing above the head (Rockwood et al. 2009). This is one reason for the prominent acromion in species adept at aerial movement, and it is cranially-oriented to direct the clavicle dorsally over the joint and avoid it interfering with lateral excursions of the humerus. This is taken to its extreme in the animals capable of powered flight, the chiropterans, where the scapula is highly dorsally-positioned with a highly cranial acromion (Vaughan 1970; Gaudioso et al. 2020). The other reason for the prominence of the acromion is its role in providing the attachment area for muscles such as the *m. acromiotrapezius* and *m. acromiodeltoideus*, which are involved in stabilisation of the scapula during complex movements. An enlarged acromion has previously been associated with gliding behaviour in sciuromorph rodents (Wölfer et al. 2019). There are a number of factors leading to the high caudal angle. Elongation of the caudal border relative to the cranial border has been associated with brachiation in primates (Preuschoft et al. 2010). This is likely linked to expansion of the *m. infraspinatus* and *m. teres major*, involved in shoulder flexion, humerus rotation, and scapular stability (Taylor 1974; Monteiro & Abe 1999; Astúa 2009; Preuschoft et al. 2010). The vertebral border is also elongated in association with the high caudal angle, and this is most likely due to the significance of musculature arising from the vertebral border in elevating the body through the shoulder girdle during ascension climbing, brachiation, and the upstroke of powered flight (Panyutina et al. 2011). Finally, the elongated and caudally-directed coracoid provides a robust attachment for the *m. coracobrachialis* with appropriate line of action around the joint to effectively stabilise it and contribute to humerus adduction.

Further investigation of scapular morphology in association with different specific types of aerial behaviour (e.g. brachiation versus gliding) would be beneficial to illuminate the subtleties of this relationship further, though this is outwith the scope of this functionally-broad thesis.

V.8. Interactions of variables

Interactions between functional and phylogenetic factors must be considered within interpretation of scapular functional morphology.

One important discussion point throughout this thesis is the interaction of evolutionary history and functional variables. Different taxonomic groups exhibit many ecological, behavioural and physiological differences, both across therians broadly and within rodents specifically. As such, including all groups of extant therians in a single dataset introduces myriad confounding factors. Still, it has been possible to make significant progress in disentangling the complex fabric of therian scapular morphology, particularly through the use of analyses within a phylogenetic framework.

Phylogenetic influence is highly relevant in many analyses through its effect on other variables. The relationship between clavicle presence and size is a clear example, as aclaviculate taxa have larger scapulae on average than claviculate taxa (mean logCS: therian claviculate = 4.36; therian aclaviculate = 6.01; rodent claviculate = 4.11; rodent aclaviculate = 5.31). Does this indicate a relationship between increased size and clavicle loss? Not necessarily. For example, amongst therians generally, the aclaviculate taxa mainly belong to Ferungulata – pangolins, carnivorans, perissodactyls, cetaceans and terrestrial artiodactyls – which contains some of the largest extant mammals. While all ferungulates are aclaviculate, not all are large or have weight-bearing scapulae. This, together with the fact that clavicle loss likely occurred early in the history of all ferungulates, means that it cannot be said that clavicle loss is necessarily associated with large size. Likewise, though aclaviculate rodents are among the largest in the dataset, the relatively small-bodied montane guinea pig is also aclaviculate. Thus, there is a clear phylogenetic influence (through ancestral clavicle loss) that complicates disentangling the relationship between clavicle loss and other factors. Nevertheless, it is possible that taxonomic groups which have clavicle loss/reduction may be able to reach larger body sizes than would have not been possible while claviculate – they may be released from a constraint imposed by the clavicle. Certainly, the clavicle is weight-bearing when present (Voisin 2006) and, just like any other skeletal element, is susceptible to failure under too great a stress. The largest extant claviculate species are apes (the chimpanzee being the largest represented in this thesis), which prioritise power in movements of the forelimb above the head for climbing where weight is borne as tensile forces. In quadrupedal primates, the majority of weight is borne by the hindlimbs (Reynolds 1985), and when the largest primates, apes, move quadrupedally it is often via a knuckle-walking posture with distal forelimb adaptations to support the body weight (Zihlman et al. 2011). Thus, this may release the clavicle somewhat from weight-related force. The largest claviculate therian of all time currently identified is the extinct marsupial *Diprotodon* (Owen 1870) which weighed up to several tonnes (Wroe et al. 2004), vastly exceeding the mass of any claviculate species in this dataset. It is particularly striking, then, that the scapula of *Diprotodon* is so highly unusual among mammals. The scapula is tall and triangular in shape, but with one vertex of the triangle being the most dorsal point of the blade, and the base of the triangle being at the joint – seemingly an inversion of the standard therian triangular scapula with the joint being a vertex of the triangle, and the vertebral border being a side (Fig. V.1). Could this be related to weight-bearing such that the clavicle is not strained beyond its capacity? Further work investigating he functional morphology of the *Diprotodon* shoulder is necessary to better understand this.

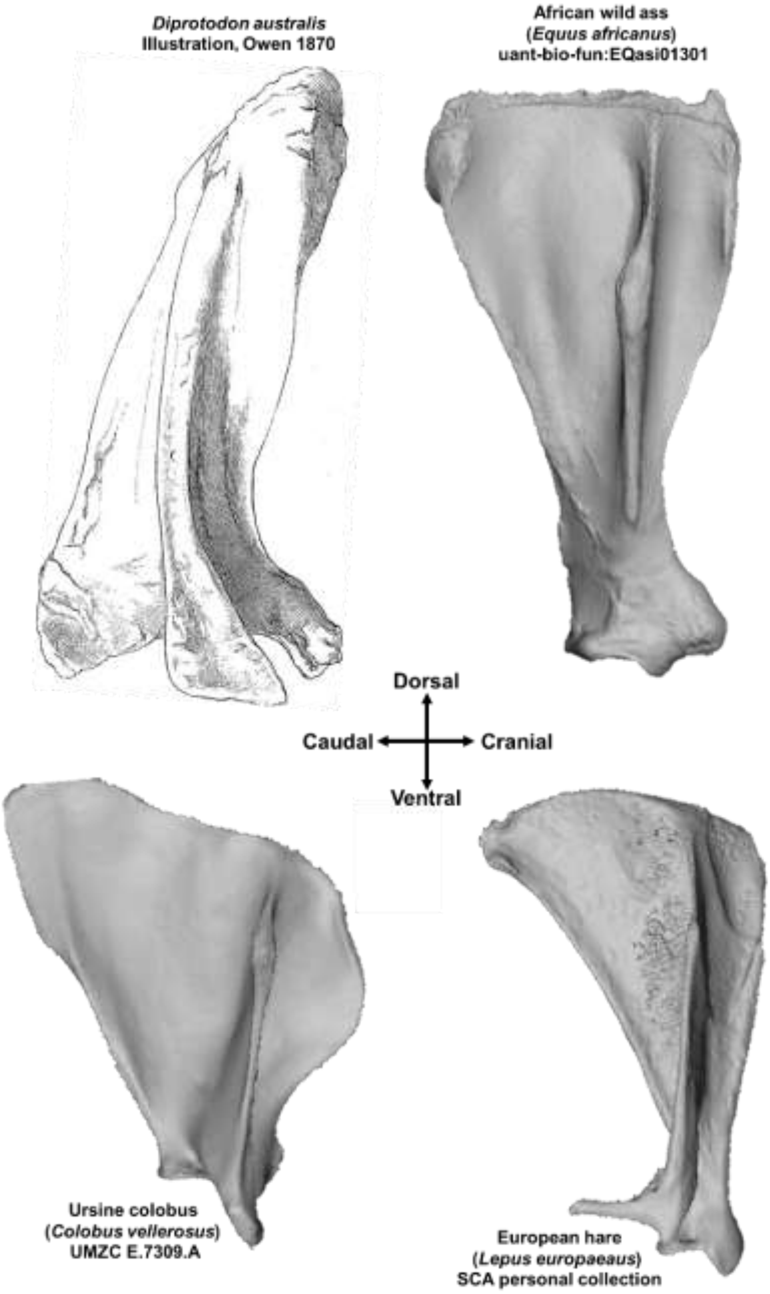


Figure V.1: Comparison of the scapula of* Diprotodon australis *to those of some extant therians

A diagrammatic representation of the left scapula of Diprotodon australis *(from Owen, 1870), compared to the scapulae of the African wild ass (*Equus africanus*, uant-bio-fun:EQasi01301), ursine colobus (*Colobus vellerosus*, UMZC E.7309.A), and European hare (*Lepus europaeaus*, SCA personal collection). Images are not to scale, but are all shown in lateral view.*

V.9. Comments on methodology

The large scale of the datasets within this thesis satisfactorily ameliorates potential sources of methodological error.

V.9.1. Species composition of datasets

The composition of the scapula datasets in Chapters III & IV was significantly affected by specimen availability. For Chapter III, the aim was to include representatives from as many families (and subfamilies where present) of extant therians as feasible. Since the scapulae were landmarked in relatively high resolution with most areas captured, only complete and undamaged adult specimens could be included. Many specimens could be obtained from MorphoSource.org. This was an efficient method for obtaining specimens, requiring no travel time or expense. Of the 201 specimens included, 82 were obtained from MorphoSource.org. On two research trips to the Natural History Museum, London, and a trip to the University of Cambridge Museum of Zoology it was possible to surface scan a further 75 specimens and request in-house CT scans for 34 specimens too small to be surface scanned. Remaining specimens were obtained from collaborators at the University of Montpellier (Dr Pierre-Henri Fabre & Dr Lionel Hautier), SketchFab.com, the Kyoto University Primate Research Institute online repository, and the University of York BioArch teaching collection. It is worth acknowledging that the dataset combines many different imaging methods from different sources (surface scanning, photogrammetry, CT segmentation which I performed, CT segmentation performed by contributors to MorphoSource.org), and with considerable variation in resolution. In studies where biological variation is low, differences in data acquisition (particularly surface scanning versus microCT) have been shown to potentially obscure results, but to a lesser extent than other sources of error (e.g. interobserver variation, and individual variation) (Robinson & Terhune 2017; Marcy et al. 2018). Given the order and clade level breadth, and the wide range of morphological variation within the datasets, mean that these sources of error should not affect the results presented here. The final dataset includes 74% of all extant families/subfamilies of therians, with each order represented by at least 50% of its families/subfamilies (Table V.2). In the case of the two orders for which only 50% of groups are represented, there are only two extant families within the order, and the absence of just one dramatically influences this percentage. For example, Lagomorpha have 50% representation because there are only two extant families, Leporidae and Ochotonidae, and a specimen from Ochotonidae could not be obtained.

In the case of the Chapter IV rodent dataset, 37 specimens were carried over from the Chapter III dataset. In total, 60 of the 87 specimens were obtained from MorphoSource.org, eight were CT scanned at the Natural History Museum in London, six were CT scanned at the University of Cambridge Museum of Zoology, four were surface scanned in person at the University of Cambridge Museum of Zoology, and eight CT scans were provided by collaborators at the University of Montpellier. Only two of the 36 extant rodent families are not represented in this dataset – Petromuridae and Dinomyidae, both of which are monotypic – and 11 of the 46 subfamilies are not represented.

It would have been preferrable to control for body side and sex in the dataset, but it was often not possible due to specimen availability. Sex of the specimen was rarely known, while body side was dependent upon specimen completeness. Though the right scapula was selected preferentially where possible, 36% of specimens in the therian-wide dataset and 41% of the rodent dataset are left scapulae. While it is possible that left-right scapula asymmetry occurs across therians or in specific species, this has not been investigated and it is generally assumed that the left and right scapulae are interchangeable within morphometric contexts (e.g. Young 2004; Astúa 2009; Wölfer et al. 2019).

Table V.2: Taxonomic composition of Chapter III dataset
Representation of extant families/subfamilies per order in the Chapter III therian-wide, dataset including percentage represented relative to total extant (following Burgin et al. 2018).

Order	No. extant families/subfamilies (Burgin et al. 2018)	No. in Ch. III dataset	Percentage of total in Ch. III dataset
Macroscelidea	1	1	100.0
Afrosoricida	6	6	100.0
Tubulidentata	1	1	100.0
Proboscidea	1	1	100.0
Hyracoidea	1	1	100.0
Sirenia	2	2	100.0
Cingulata	4	3	75.0
Pilosa	4	3	75.0
Scandentia	2	1	50.0
Dermoptera	1	1	100.0
Primates	20	19	95.0
Lagomorpha	2	1	50.0
Rodentia	71	37	52.1
Eulipotyphla	9	6	66.7
Chiroptera	37	26	70.3
Pholidota	3	3	100.0
Carnivora	34	31	91.2
Perissodactyla	3	3	100.0
Artiodactyla (terrestrial)	19	15	78.9
Artiodactyla (aquatic)	20	15	75.0
Didelphimorphia	4	3	75.0
Paucituberculata	1	1	100.0
Microbiotheria	1	1	100.0
Dasyuromorpha	4	4	100.0
Peramelemorpha	5	4	80.0
Notoryctemorpha	1	1	100.0
Diprotodontidae	15	11	73.3
Overall	**272**	**201**	**73.9**

V.9.2. Landmark configuration

The landmark configuration used in Chapters III & IV was designed to capture the 3D morphology of the scapula across the broad range of scapulae in therians. Landmark number is at the discretion of the researcher, and a minimal number of landmarks capturing only the most relevant aspects of a shape can be relatively easy to interpret, involves relatively less time landmarking, and is less computationally demanding. At the other extreme, the shape could be captured as a very high number of landmarks, potentially even covering the whole surface (e.g. Goswami et al. 2019). This ensures that all aspects of shape are captured, but introduces large amounts of noise into the data, can reduce the statistical power of subsequent analyses (particularly when the number of landmarks exceeds the number of specimens), and is time-consuming and computationally demanding (Cardini 2020). In this thesis, the aim was to capture the scapula across a very wide range of morphologies without relying on preconceptions of which areas would be most relevant to capture. Therefore, the configuration of 19 true landmarks and seven semilandmark curves was chosen to capture the whole shape in high resolution while maintaining a high level of interpretability by ensuring that all areas captured reflect distinct regions of the scapula, such as the outer border, the spine, the glenoid and the acromion. The configuration used here is an expanded version of a landmark configuration implemented by Gálvez-López (2014) for carnivorans, with additions primarily around the glenoid and spine base, and with better coverage of the *m. teres major* insertion. The landmark configuration was found to have satisfactory repeatability across disparate morphologies to be confidently used across therians (Appendix III.1). At this scale of variation, the configuration is robust to small variations arising from human error. Following the results of this research, it is clearer which areas of the scapula are highest priority for capturing and, in future studies, a reduced landmark configuration could be considered.

V.10. Future work

Several avenues of research on the therian scapula remain, and investigating them would build on the work of this thesis to continue advancing understanding scapular morphology.

V.10.1. Posture and scapular morphology

One of the most variable aspects of scapular morphology in this thesis is the curvature of the vertebral border. This curvature varies specifically in association with clavicle presence/absence and size variation, both of which are related to differences in relative position of the scapula on the body, and posture of the forelimb. Likewise, different types of locomotion behaviour are often associated with postural differences or differences in relative scapular position. For example, specialised climbing and aerial taxa tend to have dorsally positioned scapulae which facilitates a wide range of forelimb motion above the head for navigating the 3D canopy, while specialised runners tend to have more laterally positioned scapulae to increase efficiency of forelimb movement in the parasagittal plane.

The observed differences in vertebral border morphology being linked to differences in muscle lines of action associated with postural and positional differences of the forelimb and scapula is inferred from the results of this thesis, but not explicitly tested. Testing this hypothesis presents a particular challenge in developing a consistent and repeatable methodology for quantifying, or at least categorising, scapular position and forelimb posture. This cannot be achieved using articulated museum specimens because the positions of all the elements have been influenced by the preparator and may not accurately represent the position in life with associated soft tissue. Additionally, skeletal specimens are preferentially stored disarticulated so that the individual elements can be better used for research. Whole body CT scans, unfortunately, do not present a superior alternative. The position in which the animal was scanned may not represent a natural resting body position, and certainly would not represent a natural standing and weight-bearing position of the limbs. Likely the best option for acquiring such data would be 3D biplanar X-ray of live animals with XROMM (Demuth et al. 2023), which is costly, time-consuming, and requires ethical considerations.

V.10.2. Fossil scapulae

One of the key uses for functional morphology data is in a palaeontological research context. Understanding form-function relationships in extant species provides information which can be used to infer functional parameters from extinct taxa for which fossil remains have been discovered. It is apparent that mammal scapular morphology contains functional information, so it has great potential as a tool in mammal palaeontology, but unfortunately the scapula is a particularly fragile bone which does not preserve well in the fossil record. Under the assumption that dense and compact areas of bone are most likely to preserve in the fossil record (Behrensmeyer et al. 2000), the glenoid region would be expected to survive even if the rest of the scapula is fragmentary or damaged. For example, known material of Eocene mammal genus *Wyolestes* (Mesonychia: Hyaenodonta) includes a right scapula from *W. dioctes* and a left scapula from *W. apheles*, both of which are represented by the glenoid and distal portion of the scapula only, while long bones are generally more completely represented (Zack et al. 2025). Though the results of this thesis do not indicate that the glenoid region is particularly informative in the context of functional morphology relative to other regions of the scapula, further work investigating the glenoid in isolation with high resolution landmarking may reveal functional information not gathered here. The tendency of the scapula to be damaged through taphonomy also limits the examples of fossil taxa for which scapular functional morphology can be interpreted, but an excellent opportunity is presented by the near-complete scapula of *Diprotodon* (Owen 1870; Fig. V.1), which is qualitatively recognised to be morphologically unique, but the functional morphology of which has not been quantitatively explored.

V.10.3. Modularity and integration

Different regions of the scapula may vary independently or in association with other regions. Modularity refers to the division of the scapula into semi-independent anatomical or developmental regions, and integration refers to how these regions covary. Generally, the scapula is divided into four regions in this context: blade, spine and acromion, glenoid, and coracoid, though this is somewhat dependent on the particular study. This has been investigated in the context of developmental gene patterning and morphometrics (Swiderski 1993; Young 2004; Sears et al. 2013). Genetic patterning reveals integration of the coraco-gleno-acromial region (Timmons et al. 1994; Pellegrini et al. 2001), but morphometric studies identify that the acromion is independent or integrated with the spine, but not with the coraco-glenoid region (Young 2004; Sears et al. 2013). There is also evidence that patterns of modularity differ between marsupials and placentals, with marsupials having largely integrated scapulae and independent coracoid, while placentals have much more modular scapulae (Young 2004; Sears et al. 2013). Additionally, the scapula may undergo some evolutionary transitions as an integrated unit, and others in a much more modular fashion (Swiderski 1993). These studies are often limited in the resolution at which they capture the scapula and its regions, and/or in the taxonomic scope of the sample. Further investigation with high resolution landmarking across the whole of Theria may illuminate the nature of the discrepancies between different studies.

V.11. Conclusions

- Locomotion behaviour in mammals can be effectively quantified using the novel scoring system and clustering method developed in Chapter II. This method increases behavioural repertoire information contained within the locomotor variable and reduces subjectivity in the quantification process as compared to traditional behavioural categorisation.
- Increased scapular size in therians is associated with increased blade width, enlargement of the glenoid fossa, and curvature of the vertebral border such that the caudal angle is lower than the vertebral end of the spine.
- Clavicle loss in therians is associated with reduction of the acromion process and increased curvature of the vertebral border such that the caudal angle is lower than the vertebral end of the spine.
- Evolutionary history heavily influences scapular morphology in therians, especially in rodents, though this is also associated with ancestral constraints in some functional variables, e.g. all chiropterans being volant.
- Running ability and aerial ability significantly influence scapular morphology in therians, requiring opposing adaptations.
- Locomotion behaviours necessitating shoulder mobility in association with power and stability, namely climbing, aerial acrobatics and powered flight, are associated with the presence of a prominent and cranially-oriented acromion process, a high caudal angle (elongated caudal border), and elongated and caudally-directed coracoid process.
- Rodents are an effective model order for therians in the context of scapular functional morphology.

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