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**TITLE: Functional morphology of the forelimb of living and extinct tree-kangaroos
(Marsupialia: Macropodidae)**

NATALIE M. WARBURTON^{1,2,3}, KATHRYN J. HARVEY², GAVIN J. PRIDEAUX^{3,4}
AND JAMES E. O'SHEA²

¹School of Veterinary and Biomedical Sciences, Murdoch University

²School of Animal Biology, The University of Western Australia

³Department of Earth and Planetary Sciences, Western Australian Museum

⁴School of Biological Sciences, Flinders University

SHORT TITLE: Forelimb morphology of tree-kangaroos

Corresponding Author: Dr Natalie Warburton

Senior Lecturer in Anatomy, School of Veterinary and Biomedical Sciences, Murdoch
University. South Street, MURDOCH, Western Australia 6150

Email: N.Warburton@murdoch.edu.au

Phone: +61 8 9360 7658

Fax: +61 8 9360 4144

ABSTRACT

Tree-kangaroos are a unique group of arboreal marsupials that evolved from terrestrial ancestors. The recent discovery of well-preserved specimens of extinct tree-kangaroo species (genus *Bohra*) within Pleistocene cave deposits of south-central Australia provides a unique opportunity to examine adaptive evolution of tree-kangaroos. Here, we provide the first detailed description of the functional anatomy of the forelimb, a central component of the locomotor complex, in the extant *Dendrolagus lumholtzi*, and compare its structure and function with representatives of other extant marsupial families. Several features were interpreted as adaptations for coping with a discontinuous, uneven and three-dimensional arboreal substrate through enhanced muscular strength and dexterity for propulsion, grasping and gripping with the forelimbs. The forelimb musculoskeletal anatomy of *Dendrolagus* differed from terrestrial kangaroos in the following principal ways: a stronger emphasis on the development of muscles groups responsible for adduction, grasping and gripping; the enlargement of muscles that retract the humerus; and modified shape of the scapula and bony articulations of the forelimb bones to allow improved mobility. Many of these attributes are convergent with other arboreal marsupials. Tree-kangaroos, however, still retain the characteristic bauplan of their terrestrial ancestors, particularly with regard to skeletal morphology, and the muscular anatomy of the forelimb highlights a basic conservatism within the group. In many instances, the skeletal remains of *Bohra* have similar features to *Dendrolagus* that suggest adaptations to an arboreal habit. Despite the irony of their retrieval from deposits of the 'Treeless' Plain, forelimb morphology clearly shows that the species of *Bohra* were well adapted to an arboreal habitat.

KEY WORDS: arboreality; functional anatomy; marsupial; myology

INTRODUCTION

Tree-kangaroos (*Dendrolagus*) belong to the macropodoid subfamily Macropodinae, which includes all extant kangaroos and wallabies (Flannery, 1989; Prideaux and Warburton, 2010; Raven and Gregory, 1946). Bipedally hopping macropodoids evolved from arboreal phalangeriform ancestors via a quadrupedal evolutionary stage exemplified by the extant *Hypsiprymnodon moschatus*. A reversion then to the trees within one derived clade (Dendrolagini), particularly in light of the highly specialised anatomy associated with terrestrial locomotion in macropodids, provides an interesting natural experiment to investigate evolutionary adaptation to arboreality. The adaptation of the hind foot of tree kangaroos is characterized not only by relatively short and stout metatarsals, but also by significant modification of the tarsal articular complexes, resulting in enhanced mobility and flexibility to facilitate stability and balance within the discontinuous, three-dimensional arboreal environment (Flannery, 1982; Szalay, 1994; Warburton and Prideaux, 2010). Here, we investigate whether commensurate changes exist within the morphology of the tree kangaroo forelimb.

The forelimb of terrestrial macropodids is disproportionately small compared with other marsupials due to their principally bipedal locomotor behaviour (Grand, 1990; Hopwood, 1981), and is apparently relatively unspecialised for manipulative functions (Iwaniuk et al., 2000; Weisbecker and Archer, 2008). Species of *Dendrolagus*, however, have relatively more equal ratios of forelimb to hind limb length and muscle weight, as well as

overall reduction in relative muscle mass, when compared with terrestrial kangaroos and wallabies (Grand 1990). These morphological differences between terrestrial and arboreal macropodids relate to differences in both locomotor pattern and feeding behaviours.

Windsor and Dagg (1971) identified four gaits variably used by macropodids: slow pentapedal progression, in which the tail participates in support and progression as a fifth 'limb', a quadrupedal walk, quadrupedal bound and bipedal hop. Procter-Grey and Ganslosser (1986) reclassified the latter two locomotor patterns as hopping and bipedal leaping. They also identified a galloping hop, where the forelimbs were not placed down simultaneously as in the quadrupedal bound. Species of *Dendrolagus* use all four gaits to some extent, although the preference varies between species (Flannery et al., 1996; Ganslosser, 1992; Martin, 2005). *D. lumholtzi* and *D. inustus* use bipedal leaping when moving on the ground between trees, while *D. matschiei* prefers hopping. *D. dorianus* never leaps bipedally but rather utilises a quadrupedal walk (Procter-Grey and Ganslosser, 1986). When moving arboreally, the gait utilised is correlated with substrate size and orientation. Procter-Grey and Ganslosser (1986) also describe the typical method of climbing vertically, which involves an initial spring from the hind limbs and simultaneous landing with the fore- and hind limbs, followed by climbing in which forelimbs are wrapped around the bole and move alternately with rapid hopping of the hind-limbs. Descent is generally tail first with the arms wrapped around the sides of the vertical bole (Procter-Grey and Ganslosser 1986).

Tree-kangaroos have a greater degree of manual dexterity than terrestrial macropodids. They have a high degree of freedom of movement of the upper forelimb in contrast to other groups, and, in at least one species, have some independent digital movement (Iwaniuk et al., 1998; Iwaniuk et al., 2000). The use of the hands during feeding is variable among *Dendrolagus* species and the mode of grasping and picking up food differs (Iwaniuk et al. 1998). Most species (*D. lumholtzi*, *D. goodfellowi*, *D. matschiei*, and *D. dorianus*) have been observed to manually pick up food with the hands, while *D. inustus* takes food with its mouth before using both hands for manipulation. *D. matschiei* and *D. dorianus* are more dextrous, often using only one hand to hold the food (Iwaniuk et al., 1998; Procter-Gray and Ganslosser, 1986).

Flannery and Szalay (1982) described the first fossil tree-kangaroo from Australia as *Bohra paulae*. Three other species have since been placed in this genus, one Late Pliocene and two Middle Pleistocene. *Bohra* is allied with living tree-kangaroos *Dendrolagus* on the basis of marked similarities in craniodental and hind limb elements (Dawson, 2004; Flannery and Szalay, 1982; Hocknull, 2005; Prideaux and Warburton, 2008; 2009; 2010). Functional studies of the hind foot also indicate that species of *Bohra* are adapted to moving in an arboreal environment (Warburton and Prideaux 2010). *Bohra illuminata* and *B. nullarbora* from Pleistocene deposits in caves beneath the Nullarbor Plain of south-central Australia are represented by near-complete skeletons including cranial, vertebral, forelimb and hindlimb elements.

To extend our understanding of the locomotor capabilities and palaeobiology of *Bohra*, and the evolution of arboreality in tree-kangaroos, this study investigates adaptive modifications of the forelimb. Anatomical description and functional analysis of *Dendrolagus* precedes and is subsequently utilised to elucidate the functional morphology of *Bohra*. This provides a test of hypotheses concerning the arboreal adeptness of *Bohra* previously raised on the basis of hind limb evidence (Prideaux and Warburton, 2008; 2009; Warburton and Prideaux, 2010).

MATERIALS AND METHODS

Dendrolagus lumholtzi inhabits the upland closed forest of north eastern Queensland (Van Dyck and Strahan, 2008). Though it is reportedly common in suitable habitat, few specimens are collected and made available for anatomical dissection. An adult male road-killed specimen was collected in the Atherton Tableland region and made available for dissection by the Queensland Environmental Protection Authority. Specimens available for dissection are rare, thus we needed to base this study on the dissection of only one specimen. However, in our experience, differences between species are generally greater than the variation observed within (e.g. Harvey and Warburton 2010). The specimen was skinned, eviscerated and embalmed in 10% formalin 4% glycerol solution for one week, before being stored in 70% ethanol (The University of Western Australia 2006). Standard dissecting techniques were used. Muscles were identified, their attachments recorded and removed from the skeleton. X-rays of the specimen were made at Murdoch University Veterinary Hospital and were used as supplementary information during the dissection process. Isolated muscles from the left forelimb were air dried at

40°C for 48 hours and dry-weights are obtained on a Mettler BasBal digital scale (2006) and converted to a percentage of total limb muscle mass. Anatomic descriptions and percentage muscle masses for extrinsic forelimb muscles are presented in Table 1. The right side was subsequently dissected for review and consistency of the initial description (Murdoch University 2009).

After muscle removal, skeletal material was boiled to remove any traces of flesh. Measurements of skeletal elements were completed using PES electronic digital callipers. Comparative skeletal material was accessed in the mammal collection at the Western Australian Museum, Perth (2006-2009). A summary of these measurements is provided in Tables 2 and 3.

To facilitate comparative analysis of the forelimb musculature among marsupials and interpretation of the literature, additional ethically sourced cadaver specimens, in accordance to the regulations of the Western Australian Department of Conservation and the Animal Ethics Committee guidelines of the University of Western Australia, were dissected following the technique described above (sample size of specimens in parentheses); *Macropus eugenii* (5), *M. fuliginosus* (3), *M. rufus* (2), *Setonix brachyurus* (2), *Trichosurus vulpecula* (2). The details of these dissections are published elsewhere (Harvey and Warburton, 2010). Published accounts of marsupial anatomy were consulted with respect to the following taxa *Macropus* (Badoux, 1965; Boardman, 1941; Hopwood, 1974; Owen, 1876; Windle and Parsons, 1898), *Petrogale* (Parsons, 1896), *Phalanger*

(Sonntag, 1922), *Phascolarctos* (Grand and Barboza, 2001; Macalister, 1865; Sonntag, 1922; Young, 1882), and *T. vulpecula* (Barbour, 1963).

Fossil remains of two recently described species of *Bohra* are housed in the Western Australian Museum. *B. illuminata* (Prideaux and Warburton, 2008) is represented by a partial adult skeleton (WAM03.5.10) including the following forelimb elements: fragments of right and left scapulae; left clavicle; right humerus (missing proximal epiphysis); right ulna; fragments of radius; triquetrum, hamatum, metacarpals and carpal phalanges, and a partial juvenile skeleton (WAM 02.7.16) including proximal fragment of left scapula; proximal fragment of right humerus; numerous carpals and metacarpals. A single individual of *B. nullarbora* (Prideaux and Warburton, 2009; WAM 05.4.70) includes left and right clavicles, humerus (left proximal and distal fragments, right partial diaphysis), left ulna, left radius (diaphysial fragment), carpals (right hamatum, left scaphoid), metacarpals (left and right III, left IV–V), and manual phalanges (digits I–IV proximal; digits III–V medial; digits III–IV distal). Images of postcranial elements of *B. illuminata* and *B. nullarbora* are provided in Prideaux and Warburton (2008, 2009) respectively.

RESULTS

Scapular form and function

Scapulae of australidelphian marsupials range in shape from rectangular in *Isoodon*, roughly trapezoidal in the terrestrial macropodids *Macropus* and *Setonix*, to more triangular shaped in the arboreal *Trichosurus* and *Phascolarctos* (Fig. 1). *Dendrolagus* is intermediate in shape between the terrestrial macropodids and the arboreal taxa, tending

toward a triangular shape. The cranial border is sinuous in outline, the angle between the vertebral and cranial borders is smoothed, the vertebral border is relatively long compared to the length of the scapula, and the angle made between the vertebral and caudal borders is more acute. This morphology is more pronounced in the ‘short-footed’ New Guinean species of tree-kangaroo (e.g., *D. dorianus*) than in the ‘long-footed’ *D. bennettianus*, *D. lumholtzi*, and *D. inustus*.

In *D. lumholtzi*, the scapular spine is high and flattened proximally. The scapula spine tapers sharply, approximately three quarters of the way along the scapular blade. The spine is inflected over the infraspinous fossa and is noticeably thickened approximately two thirds of the way along the spine, for the attachment of the m. deltoideus pars spinalis (Table 4). The infraspinous fossa is noticeably broader and larger in area than the supraspinous fossa. Among macropodines, *Dendrolagus* have relatively the widest infraspinous fossa (Table 2).

In *Dendrolagus*, the caudal angle of the scapula is posteriorly extended and the bone is noticeably thicker than the rest of the scapular boundaries. The m. teres major arises from the ventral surface of the caudal border (Fig. 2) and is relatively large in *Dendrolagus* (Table 1). A distinct thickening of the caudal border more proximally reflects the origin of the long head of the m. triceps brachii. This ridge is measurably longer in *Dendrolagus* than in any of the other macropodids observed (Table 2), reflecting the role of the long head of the triceps as a stabiliser of the elbow joint preventing elbow flexion when the limb is weight-bearing and also in humeral retraction. This muscle would function as a

synergist of the *m. latissimus dorsi* during extension of the shoulder when the limb is weight-bearing.

The *m. deltoideus pars acromialis* extends more laterally in *D. lumholtzi* than in terrestrial kangaroos, covering the medial two thirds of the spinalis portion of the deltoid along the scapular spine (Fig. 2). The acromial part of the deltoideus muscle is thickened and medially differentiated into two layers at its insertion; the superficial portion inserts onto the aponeurosis of the *m. brachialis*; the deeper portion inserts to the pectoral ridge. The omotransverse muscle inserts to the acromion, and is relatively larger in *D. lumholtzi* than in terrestrial macropodids (Table 1). The coracoid process is robust but not especially long, and is irregular in outline, protruding medio-cranially above the glenoid fossa.

The clavicle, which articulates with the acromion, is robust in *Dendrolagus* with a distinct dorso-ventral curvature. The sternal articulation is expanded and bulbous; the acromial (lateral) extremity is more modestly expanded. Medially, the clavicle is dorso-ventrally compressed. Mesially, the shaft ‘twists’, such that it appears to be antero-posteriorly compressed at the acromial end. The anterior (clavicular) portion of the trapezius is more strongly developed in *D. lumholtzi* than in terrestrial kangaroos, and inserts along the distal two thirds, rather than one third, of the clavicle.

The fragmentary scapular remains of *Bohra illuminata* and *B. nullarbora* share a number of features with *Dendrolagus*. The medial end of the spine, including the acromion, is placed high above the body of the scapula. The acromion appears to be relatively broad

and robust. It projects over the cranial edge of the glenoid fossa. The supraspinous fossa is apparently smaller than that of the infraspinous fossa, and the angle formed at the scapular notch is intermediate in form between *Dendrolagus* and *Macropus*. There is distinct concavity for the insertion of the m. triceps longus that extends a short distance from the glenoid cavity on the caudal edge. The coracoid process is globular with an indistinct outline protruding above the ventro-cranial (subscapular) edge of the glenoid fossa.

The clavicles of *Bohra* are moderately robust and dorso-ventrally curved; the edge of the ventral facet is straighter than the more rounded dorsal edge and with broadened articular ends. The sternal end is only slightly broader than the shaft. It bends ventrally and is thickened and semi-ovate in cross section. On the acromial end there is a large fossa for articulation with the acromion. A line of muscle attachment for pectoral muscles along anterior edge is present.

Glenohumeral joint form and function

The glenoid cavity of *Dendrolagus* is oval in outline and concave (Fig. 2). The cranial portion is distally extended and inflected. The length to width ratio of the glenoid fossa in *Dendrolagus* is generally high (Table 2), although the single specimen of *D. matschiei* is round (L/W 99%). In comparison, terrestrial macropodids (*Macropus*, *Setonix*, *Thylogale*) have a more circular glenoid cavity with less development of the cranial projection, and the length to width ratio is close to 100. *Onychogalea* and *Petrogale* have elongated glenoid fossae, similar to *Dendrolagus*. In *Dendrolagus*, the humeral head is

noticeably larger in surface area than the glenoid, only moderately convex and more posteriorly projected.

The glenoid fossa of *B. illuminata* and *B. nullarbora* closely resemble the oval-shaped fossa of *D. lumholtzi*. In *Bohra* the glenoid fossa is roughly oval in outline, though broader caudally than cranially. The cranial portion is elongate and curved over the relatively flat surface of the glenoid fossa at an angle of approximately 45°.

Humeral form and function

The four tree-kangaroo species measured here have longer humeri (relative to trunk length) when compared with terrestrial macropodids (Table 3). The proximal humerus comprises the head and two low and broad tuberosities. The bicipital groove is shallow and relatively wide. The shaft is robust with a well-developed pectoral ridge, and obvious teres tubercle (particularly in *D. bennettianus*; Fig. 3, 4). The distal humerus is broad mediolaterally, and the medial epicondyle is large.

The pectoral muscles are large in *D. lumholtzi* when compared to terrestrial macropodids. They arise over a relatively larger area and are relatively large in mass (Fig. 4, Table 4). The superficial pectoral muscle (pectoralis major), in particular, is enlarged. Characteristic of *Dendrolagus* is an enlarged medial crest for the insertion of the teres major and latissimus dorsi muscles. This insertion is more distally placed in comparison to terrestrial kangaroos, as previously noted by Flannery (1996). Both the teres major and

latissimus dorsi are relatively large in *D. lumholtzi* (Table 4) and their attachments to the humerus are broad and strong.

Dendrolagus have larger medial epicondyles compared with the terrestrial forms and relatively larger flexor muscles (see below). Both terrestrial kangaroos and tree-kangaroos possess a long supinator (lateral epicondylar) ridge which provides the origin for the m. brachioradialis. In *Dendrolagus* the supinator ridge is thickened proximally; the m. brachioradialis is approximately twice the mass in *D. lumholtzi* (1.5% of forelimb musculature) than in terrestrial kangaroos.

The humerus of *B. nullarbora* is similar in morphology to that of *Dendrolagus*. The humerus is robust with strongly developed pectoral and deltoid ridges, and a deep bicipital groove. The teres tubercle is observed as a distinct rugosity on the proximal half of medial shaft; the humeral shaft is relatively robust. The distal end of the humerus is transversely broad and marked by a large capitulum and a long lateral supracondylar ridge. The medial epicondyle is large and robust. These features suggested strong development of the shoulder flexors, humeral adductors and retractors and antebrachial muscles as in *Dendrolagus*. The humeral morphology of *B. illuminata* is similar to that of *B. nullarbora* and *Dendrolagus*, but is overall less robust and the development of the pectoral insertion is weaker.

Elbow joint form and function

Dendrolagus species are characterised by humero-ulnar joints with a wide humeral trochlea, a shallow trochlear furrow together with a relatively long and shallow trochlear notch of the ulna, and shallow olecranon, anconeal and radial fossa. The anconeal and coronoid processes (and their respective humeral fossa) in tree-kangaroos are both less protuberant and relatively narrow transversely than in terrestrial macropodines. The humeral capitulum is larger than the trochlea anteriorly and posteriorly. There is a relatively deep medial trochlear flange; most strongly in the New Guinean ‘short-footed’ group of tree-kangaroos. The radial notch of the ulna is tear-drop shaped, converging at the lip of the coronoid process and is oriented ventrally. The radial notch is ventrally orientated in tree-kangaroos in contrast to a more lateral orientation in terrestrial macropodids. Consequently, the interosseous space between the radius and ulna is larger in the forearm in tree-kangaroos. The radial head is more circular in shape in *Dendrolagus*; in terrestrial kangaroos the radial head is more oval-shaped.

On the ulna, *Bohra* and *Dendrolagus* share a reduced coronoid process, narrow semilunar notch, and enlarged, deep radial facet. The distal condyle of humerus of *Bohra* is transversely broad, with large articular surfaces, particularly the capitulum. The trochlea notch is elongate and relatively ‘open’; the coronoid process and anconeal process project cranially and slightly away from each other. The radial facet is very flat and deep longitudinally; in *B. nullarbora* it is buttressed out slightly from shaft. The radial head is circular in outline.

Antebrachial form and function

The length of the radius is relatively shorter in tree-kangaroos than in terrestrial kangaroos. In *Dendrolagus* the radius is roughly equal in length to the humerus (Table 3) while in terrestrial macropodids the brachial index ranged from 111 in *P. brachyotis* to greater than 130 in the larger species of *Macropus*.

The radius is robust and sinuous in shape; the shaft curves laterally in the proximal portion and the medially along its distal half. The proximal radius is circular in section with a large, oval-shaped tubercle for the insertion of the m. biceps brachii. This insertion is more medially placed than in terrestrial macropodids. The diaphysis becomes transversely compressed but dorso-ventrally broad distally. The interosseous space is long and wide. The distal epiphysis is roughly oval in shape. From our observations, in terrestrial macropodids, the radial diaphysis is more cylindrical along its entire length and the interosseous space is reduced such that the radius and ulna are in contact over the distal half (or more) of the antebrachium. The distal articular surface of the radius is large relative to the size of the shaft, and the styloid process is relatively shorter and more obliquely aligned in comparison to *Macropus*.

The ulna of *Dendrolagus* is robust, laterally compressed, and dorsoventrally curved (Fig. 5). It is broadest proximally and tapered distally. The olecranon is moderately long, robust, medially curved and roughly square in section. Concave fossae on both the lateral and medial surfaces of the olecranon extend along the proximal shaft. The shaft is semicircular in section with a strongly developed interosseous ridge along the cranial

border in the distal half. There is a strong, concave, posterolateral notch marking the passage of the flexor tendons on the distal ulna epiphysis of *Dendrolagus*.

Fragments of radius of *Bohra* are similar in form to *Dendrolagus*. The radial shaft is robust, the radial tuberosity is massive and the interosseous ridge is strongly developed in *B. nullarbora*. The disc-like proximal epiphysis of *B. illuminata* is roughly circular, rather than oval, in shape. The ulna is long with a transversely compressed shaft, anteroposteriorly expanded proximally and distinctly tapered distally elongate and transversely compressed. The anteroposteriorly expanded shaft is also deeper in *Bohra* and *Dendrolagus* than in terrestrial kangaroos. The proximal half of the diaphysis is dorso-ventrally broad with a deep proximomedial sulcus, which suggests a well-developed deep digital flexor muscle. The olecranon is large and robust. A rugose scar is present for the m. brachialis anterior to the trochlear notch as in *Dendrolagus*. The interosseous border bears a strong ridge in distal half. The styloid process is large with a hemispherical articular surface. The flexor notch is less developed in *Bohra* than *Dendrolagus*, but is more strongly developed than in the terrestrial macropodine genera.

Form and function of carpus and manus

The proximal articular surface of the scaphoid is large and transversely elongate (Fig. 6). The remainder of the scaphoid is long and proximodistally compressed, and follows an arc shaped path toward the base of the first metacarpal. The triquetrum is roughly cubic in shape and long in comparison to *Macropus*; the styloid fossa, however, is relatively shallower (Fig. 6). The hamate is large with a stepped distal face with articular facets for

the capitate medially and metatarsals IV and V distally. There is a long, proximolateral projection on the ventral aspect of the hamate of *Dendrolagus*. The capitate is longer than it is wide and the trapezoid and trapezium are relatively large.

The metacarpals of *Dendrolagus* are distinguished from terrestrial kangaroos by their massively enlarged heads; the transverse width of the metacarpal head is rough twice the width of the shaft. The enlarged metacarpal head provides a large surface area for the metacarpophalangeal joint which is further strengthened by strong collateral ligaments. The proximodorsal surface of metacarpals II and III are marked by oval shaped tubercles for the insertion of the extensor musculature. The phalanges are more elongate than those of terrestrial kangaroos, and the articular facets reflect a strongly flexed posture. The distal (ungual) phalanges have very long, laterally compressed and sharply curved claws. In contrast, the claws of terrestrial kangaroos are broader and less curved.

The large m. flexor carpi ulnaris has a long muscle belly, rather than long tendon, which inserts to the elongate pisiform (Fig. 6). The m. flexor digitorum profundus is relatively massive and has an additional, medial segment that inserts along the ventral side of the ulna. The radial head of that muscle took a longer origin from the ulna in *D. lumholtzi* than in the terrestrial kangaroos. The combined mass of flexors is more than double the combined mass of extensors, and approaches 15% of the total muscle mass of the forelimb in *D. lumholtzi*.

The carpal elements of *Bohra* are intermediate in relative size between *Dendrolagus* and those of terrestrial kangaroos. The palmar process of the hamate, which is broad in *Dendrolagus*, is more elongate in *Bohra*. The metacarpals of *Bohra* are robust with enlarged heads; broader than the corresponding proximal bases. The proximo-dorsal surface of metacarpal III is marked by an irregular depression. The proximal phalanges are more elongate than the middle phalanges. The distal carpal phalanges are long, strongly curved and laterally compressed (Fig. 6).

DISCUSSION

Locomotion in tree-kangaroos

For many animals, the gait used in arboreal habitats is not dissimilar to their terrestrial relatives. *Dendrolagus* utilise a number of different gaits, when moving at different speeds and in different conditions (Windsor and Dagg, 1971). When moving terrestrially or on large horizontal substrates *Dendrolagus* employ a slow pentapedal progression or bipedal hopping, similar to terrestrial macropodids, or a quadrupedal bounding gait (similar to *Setonix*; Windsor and Dagg, 1971). Where branch thickness does not allow simultaneous use of the fore- or hindlimbs, *Dendrolagus* employ a slow walk in which the hindlimbs are used asynchronously; a unique gait among macropodids (Windsor and Dagg, 1971). Forelimb suspension has been observed and animals are able to return from a hanging position using their arms (Proctor-Gray and Ganslosser, 1986). *Dendrolagus* has less than three-quarters the relative mass of muscle in body composition as *Macropus*

and is in this characteristic convergent with other slow-moving arboreal climbers (Grand, 1990). However, reduction in muscle mass has occurred particularly in hindlimb and axial systems, while the forelimb has relatively the greatest muscle mass of any of the marsupials studied by Grand (1990). The detailed description of the muscular anatomy of the tree-kangaroo forelimb provided here, suggests that, while muscular anatomy of the forelimb is relatively conservative among macropodids, significant adaptations for enhanced mobility and shifted emphasis on actions has been achieved by relatively slight modifications in muscle attachments and relative muscle proportions.

Grasping – maintaining contact

In *D. lumholtzi*, there is a strong emphasis on the development of muscles groups responsible for adduction, grasping and gripping that function to provide pressure on uneven arboreal surfaces in order that the animal may maintain contact with the substrate. Enhanced muscle mass and mechanical advantage from adduction and grasping is seen, particularly in the pectoral muscle group and flexor muscles of the carpus and digits. The pectoral ridge is relatively longer and more laterally placed in *Dendrolagus* than in terrestrial kangaroos (Fig. 3). The arrangement of the m. pectorales is similar in all macropodids, however, in *D. lumholtzi* enlargement of the pectoral muscles is apparent both in the extent of muscular attachments, the thickness of the muscle sheets and the large relative mass. In *D. lumholtzi* the pectoral muscle group made up 13% of the total muscle mass of the limb, in contrast to 7.6% for *M. eugenii* and 10.7% for *M. fuliginosus* (Harvey and Warburton 2010). The enlarged and more distal insertion could improve the mechanical advantage of that muscle during vertical ascent. The relatively reduced length

of the antebrachium could further improve the mechanical advantage by reducing out-lever length of the adductor muscles. The pectoral ridge of *Bohra* is strongly developed and distinctly more laterally placed than in terrestrial kangaroos, suggesting that the pectoral muscles are derived in this group for enhanced adduction. Muscles that medially rotate the arm, including the subscapularis, teres major and latissimus dorsi may also contribute to adduction strength, and are relatively strongly developed in *Dendrolagus* (as discussed below).

The paws of *Dendrolagus* appear to be adapted for maintaining contact with substrate through enhanced frictional resistance. Gripping with claws requires strong flexion of the digits, wrist and hand. The digital flexor muscles in *D. lumholtzi* are relatively large in mass and have thickened tendons of insertion and enlarged bony attachment sites. The muscles of the antebrachium comprise over 23% of the total forelimb musculature in the tree-kangaroo, rather than 16–18% in *Macropus* (Harvey and Warburton, 2010). The medial epicondyle of the humerus serves as the principle site of origin for the flexor muscles of the forearm and is obviously enlarged in *Dendrolagus* in comparison to other macropodid groups. A wide medial epicondyle provides a greater surface area and leverage for the attachment of carpal and digital flexor muscles, and has been interpreted to facilitate enhanced gripping and clinging, and are characteristic of arboreal mammals for example arboreal didelphids (Argot, 2001) and viverrids (Taylor, 1974). Additional strengthening of the flexor muscles is evidenced by the enlarged bony attachments deep digital flexor (particularly the radial head) and the robust shafts and enlarged flexor tubercles of the metacarpals and phalanges. The noticeably flared and robust medial

epicondyle in *Bohra* is reminiscent of well-developed flexor muscles of the forearm and wrists similarly implying an enhanced grasping function of the fore-paws for climbing. Strong carpal and digital flexion in *Bohra* are further indicated by the deep medial concavity beneath the trochlear notch on the ulna which suggests well-developed digital flexor muscles and thus enhanced gripping.

Propulsion

In *Dendrolagus*, vertical climbing is achieved by synchronous bounding of the hindlimbs alternated with strongly adducted forelimbs (Procter-Gray and Ganslosser, 1986). In this phase of locomotion, the muscles that draw the humerus backwards effectively pull the trunk forward during flexion of the shoulder, and thus provide propulsion and act against gravity. In the strongly flexed and adducted posture, the muscles responsible for retracting the humerus are primarily the m. latissimus dorsi and m. teres major. These muscles are massively developed in *D. lumholtzi*, with extended origins, more distally placed and greater relative mass than in terrestrial kangaroos. (The latissimus dorsi comprises 12% of total forelimb muscle mass in *Dendrolagus* in comparison to less than 9% in *M. eugenii* and *S. brachyurus* (Harvey and Warburton, 2010)). The skeletal features that reflect the strengthening of these muscles are the thickened caudal angle of the scapula for the origin of the teres major, and the enlarged and distally placed teres tuberosity. *Bohra* similarly has a strongly developed teres tuberosity. These characteristics reflect strengthening and improved mechanical advantage of these muscles for improved leverage for adduction and retraction of the arm from a raised position. The m. tensor fascia antebrachii may also contribute to forelimb retraction and is relatively

large in *D. lumholtzi*. When moving along horizontal substrates, these muscles may similarly provide propulsive force when the forelimbs are weight-bearing.

During climbing, the elbow is held in a strongly flexed posture such that the elbow flexor muscles (m. brachialis, m. biceps brachii and m. brachioradialis) transmit the weight to the substrate when climbing, by bringing the body close to the tree, then lifting the body vertically against gravity (Argot, 2001; Oxnard, 1963; Procter-Gray and Ganslosser, 1986; Stalheim-Smith, 1984). This is in contrast to terrestrial groups, in which extension of the elbow via the triceps muscle group contributes to propulsion in the forelimb.

Enlargement of the elbow flexor muscles is apparent in *D. lumholtzi*, where together these muscles accounted for around 10% of the total forelimb musculature, and the m. biceps brachii almost 6% alone. In contrast, these muscles combined accounted for less than 8% in *M. eugenii* and around 6% in *S. brachyurus*. In *Dendrolagus*, the enlarged coracoid process of the scapula and radial tuberosity reflect the strong development of the m. biceps brachii. The origin of the m. brachioradialis is proximally extended, further improving the potential mechanical advantage of this muscle via increasing length of the in-lever. The lateral epicondylar ridge is proximally thickened in *Bohra*, implying strong development of the m. brachioradialis and thus stabilisation of the joints, resistance against extension, or strong flexion of the arm.

Enhanced joint mobility

The shape of the scapula and clavicle of tree-kangaroos reflects greater mobility of the forelimb in comparison to terrestrial kangaroos; such enhanced joint mobility would

enable contact with varied branch surfaces. Iwaniuk *et al.* (1998) noted that *Dendrolagus* species are distinct from other marsupials, including terrestrial kangaroos and dasyurids, in the high degree of freedom of movement in the pectoral girdle and upper limb. The triangular shape of the scapula is convergent with arboreal didelphids and reflects a greater range of rotation and tensile forces acting on the scapula in arboreal forms, particularly via the muscles of the serratus group (Argot 2001). The insertion of the serratus ventralis in *Dendrolagus* is restricted to the caudal border of the scapula, which may enable greater mobility of the scapula on the trunk. The extrinsic muscles which insert to the scapula also function to rotate of the scapula on the body, to allow an animal to protract and retract the limb in an adducted posture during climbing. Among marsupials there is a trend for arboreal species toward increasing the size of the infraspinous fossa relative to the supraspinous fossa (Fig. 1); the supraspinous fossa is relatively the largest in the terrestrial species and smallest in *Phascolarctos*. There is also a change in the shape of the cranial border, from an acute scapular notch in *Isoodon*, to a progressively more obtuse scapular notch in the most arboreal species. The shape of the cranial border reflects, at least in part, the origin of the supraspinatus muscle. The supraspinatus may serve to protect from anterior dislocation of the shoulder (Jenkins and Weijs, 1979) and a large supraspinatus muscle has been hypothesised to act as a shock-absorber across the shoulder during bounding or leaping locomotion in didelphids (Argot, 2001). The reduced supraspinous fossa in *Dendrolagus*, in comparison to terrestrial macropods, may reflect a change in the posture of the shoulder to act more under tension than compression in arboreal forms, in which the emphasis is placed on action of the infraspinatus muscle in when the shoulder moves through flexion and rotation.

Dendrolagus has a relatively larger acromion in comparison to terrestrial macropodines. This reflects enlargement of the omotransverse muscle, and enlargement and separation of the acromial deltoid which contribute to mobility of the pectoral girdle and limb in protraction and abduction. The m. omotransversarius rotates the glenoid (distal) portion of the scapula cranially, and would also stabilise the scapula during contraction of the acromial deltoid. Thus, the large acromion reflects both enhanced rotation of the scapula on the thorax and enlargement of the deltoids for extension and abduction of the arm. In arboreal didelphids the acromion process extends past the glenoid cavity, allowing the acromial head of the deltoid muscle to wrap further medially around the shoulder, providing added leverage for the protraction (forward elevation) than in terrestrial species (Argot, 2001). Robust development of the clavicle also reflects enhanced rotational movements of the pectoral limb, and is particularly important for grasping actions and manual dexterity (Jenkins, 1974). The dorsoventral flexion of the clavicle in *Dendrolagus* improves the mechanical advantage of the clavicular deltoid for protraction of the humerus by creating a more obtuse angle relative to its insertion on the humerus. Enlargement of the trapezius muscle, and in particular the clavicular portion, facilitates elevation of the clavicle and acromial end of the scapula that would occur when raising the arms in front of the body. *Bohra* have both an elongated acromion process and robust clavicle to support rotation of the forelimb, consistent with the ability to raise the arm above the head and reach for distant hand holds while climbing.

The oval glenoid of *Dendrolagus* reflects an increased cranio-caudal rotation of the joint, consistent with the ability to raise the arms in front of the body when climbing. Elongated glenoid fossae have been observed in arboreal primates (Miller, 1932) and didelphids (Argot, 2001). The cranially extended glenoid cavity in tree kangaroos may serve to stabilise the humeral head when the arm is raised above the head, thereby preventing dislocation when the joint is under tensile stress during climbing (Argot, 2001; Miller, 1932). Enhanced gleno-humeral mobility is further indicated by the reduced height of the humeral tuberosities, as is similarly characteristic of arboreal didelphids (Argot 2001). In *Bohra*, the glenoid fossa is oval in shape indicative of increased cranio-caudal rotation of the joint as seen in *Dendrolagus*.

Both the elbow and wrist morphology of *Dendrolagus* are consistent with a greater range of movement than in terrestrial kangaroos. At the elbow, the open trochlear notch and shorter anconeal and coronoid processes of *Dendrolagus* could enable more multi-axial movement. In contrast, terrestrial macropodids have a deeply concave trochlear notch with a corresponding deeper furrow on the humeral trochlea which would provide enhanced stability. A similar morphological pattern has been identified in arboreal versus terrestrial didelphids (Argot, 2001) and viverrids (Heinrich and Houde, 2006), and also 'grappling' versus 'non-grappling' cursorial carnivorans (Andersson, 2004); arboreal and/or grappling forms possess much more rotational ability than their terrestrial counterparts. The enlarged capitulum of *Dendrolagus* facilitate improved contact with the radius through a greater range of postures, and the more circular radial head and the large interosseous space between the radius and ulna could all reflect a much great range of

rotational movements through the forearm. Additionally, *Dendrolagus* have a relatively large, distally projecting medial trochlear flange which has been identified in other mammals with enhanced rotational ability of the elbow to provide extra stability against non-parasagittal forces (Andersson, 2004). The elbow joint of *Bohra* similarly has an elongated trochlear notch and low anconeal and coronoid, a relatively ventral radial notch and a rounded radial head, suggesting enhanced rotational mobility in comparison to terrestrial kangaroos.

Corresponding with the enhanced mobility of the elbow articulations, the rotator muscles acting at the elbow for pronation and supination are relatively large and have extended areas of attachment to the bones which enhance their mechanical advantage. The muscles involved in rotation of the antebrachium and carpus, m. brachioradialis, m. supinator and m. pronator teres have enlarged areas of attachment and have a relatively larger mass in *D. lumholtzi* (3.5% total forelimb muscle mass) than in the other marsupials dissected (Harvey and Warburton, 2010). These observations suggest modification for enhanced rotation of the forearm for arboreal locomotion.

The bones of the carpus are more globular in shape with broad articular surfaces suggesting improved mobility and manual dexterity, in contrast to the compact and tightly packed morphology in terrestrial macropodids. The morphology of the carpals could provide a greater overall length between the radiocarpal joint and the carpometacarpal articular row, accentuating freedom of movement in all planes. The triquetrum is roughly cubic and long in comparison to *Macropus*. The styloid fossa is

shallower, facilitating a greater freedom of movement. Enhanced mobility of the carpal bones corresponds with observations of dexterity in *D. matschiei* that highlighted that tree-kangaroos are capable of some independent movement of the digits (Iwaniuk et al., 1998).

Conclusions

Our inferences of stabilised arm movements, increased strength and reach in the forearm and arm, and strong gripping mechanisms in the forelimb of the extinct tree-kangaroo *Bohra* confirm prior functional appraisal of the hind foot (Warburton and Prideaux, 2010). Our analysis suggests that species of *Bohra* are evidently equally as well adapted to the functional demands of an arboreal environment as extant species of *Dendrolagus*, despite weighing up to twice as much (Flannery and Szalay, 1982), and despite their occupation of habitats not previously considered within the domain of tree-kangaroos, namely semi-arid woodland/shrubland mosaics (Prideaux et al., 2007; Warburton and Prideaux, 2010). The differences observed between *Dendrolagus* and *Bohra*, namely a relatively larger body to the size of the head, and relatively longer limbs (Prideaux and Warburton, 2008) reflect ecological differences that could be required for *Bohra* to survive in these more open environment. Long forelimbs would be advantageous for climbing, while efficient terrestrial locomotion through semi-arid woodland or shrubland would require hindlimbs with sufficient mechanical advantage (McGowan et al., 2008). The short limbed, more compact body morphology of *Dendrolagus* likely reflect adaptation under the selective pressure imposed by a more closed habitat (both canopy and understory) of the rainforest environments in which they are found.

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Figures

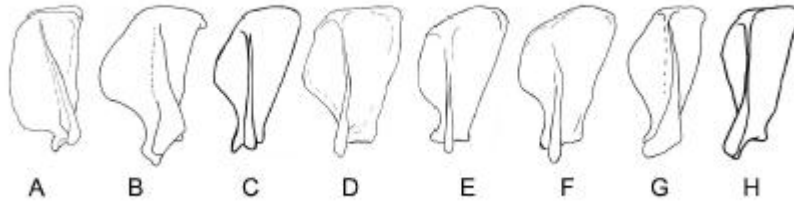


Figure 1 - Left scapula of marsupials, lateral view. A, *Isoodon obesulus*; B, *Dasyurus geoffroii*; C, *Setonix brachyurus*; D, *Macropus fuliginosus*; E, *Dendrolagus bennettianus*; F, *Dendrolagus dorianus*; G, *Trichosurus vulpecula*; H, *Phascolartos cinereus*. Not to scale.

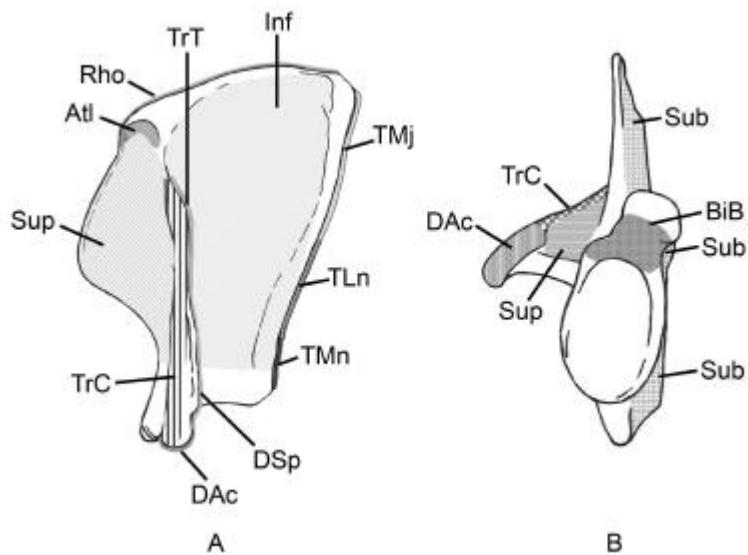


Figure 2 - Left scapula of *Dendrolagus lumholtzi* showing key landmarks and areas of muscular origin (Or) and insertion (In). A lateral view, B glenoid view. Atl, Atlantoscapularis In; BiB, Biceps brachii Or; DAc, Deltoideus pars acromialis Or; DSp, Deltoideus pars spinalis Or; Inf, Infraspinatus Or; Rho, Rhomboideus In; Sub, Subscapularis Or; Sup, Supraspinatus Or; TMj, Teres major Or; TMn, Teres minor Or; TrC, Trapezius pars cervicis In; TrT, Trapezius pars thoracis In; TLn, Triceps pars longum Or.

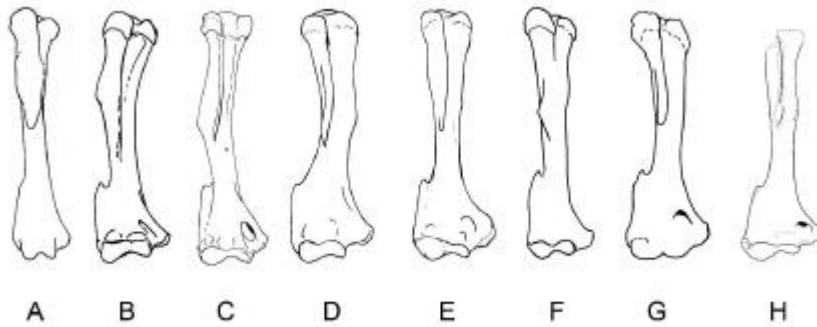


Figure 3 – Right humerus of marsupials, lateral view. A, *Dasyurus geoffroii*; B, *Macropus eugenii*; C, *Macropus fuliginosus*; D, *Dendrolagus bennettianus*; E, *Dendrolagus dorianus*; F, *Trichosurus vulpecula*; G, *Phascolarctos cinereus*; H, *Bohra illuminata*. Not to scale

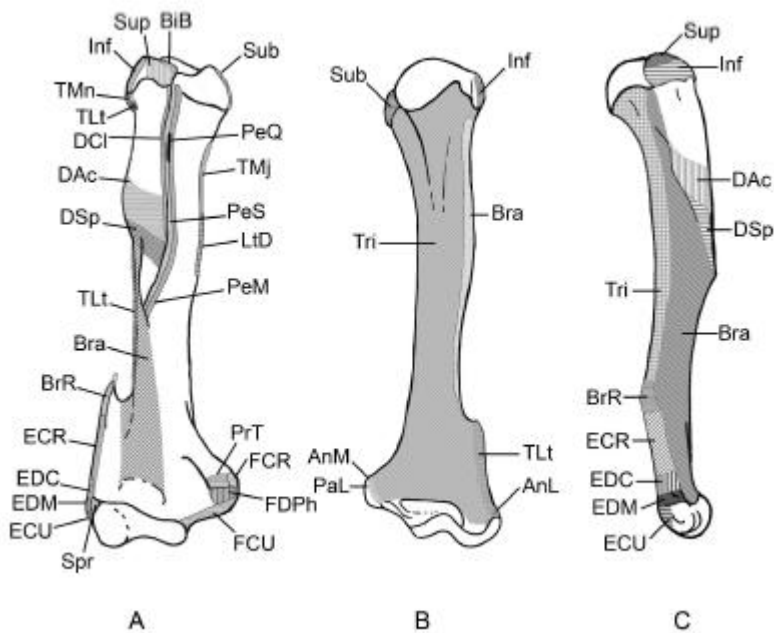


Figure 4 – Right humerus of *Dendrolagus lumholtzi* showing areas of muscular origin (Or) and insertion (In). A cranial view, B caudal view, C medial view. AnL, Anconeus lateralis Or; AnM, Anconeus medialis Or; Bra, Brachialis Or; BrR, Brachioradialis Or; DAc, Deltoid pars acromialis In; DCI, Deltoid pars clavicularis In; DSp, Deltoid pars spinalis In; ECR, Extensor carpi radialis Or; ECU,

Extensor carpi ulnaris Or; EDC, Extensor digitorum communis Or; EDM, Extensor digitorum minimus Or; FCR, Flexor carpi radialis Or; FCU, Flexor carpi ulnaris Or; FDPH, Flexor digitorum profundus humerale Or; Inf, Infraspinatus Or; LtD, Latissimus dorsi In; PaL, Palmaris longus Or; PeM, Pectoralis minor (profundis); PeQ, Pectoralis quartus In; PeS, Pectoralis superficialis In; PrT, Pronator teres Or; Spr, Supinator Or; Sub, Subscapularis Or; Sup, Supraspinatus In; TMj, Teres major In; TMn, Teres minor Or; Tri, Triceps Or; TLt, Triceps caput lateral Or.

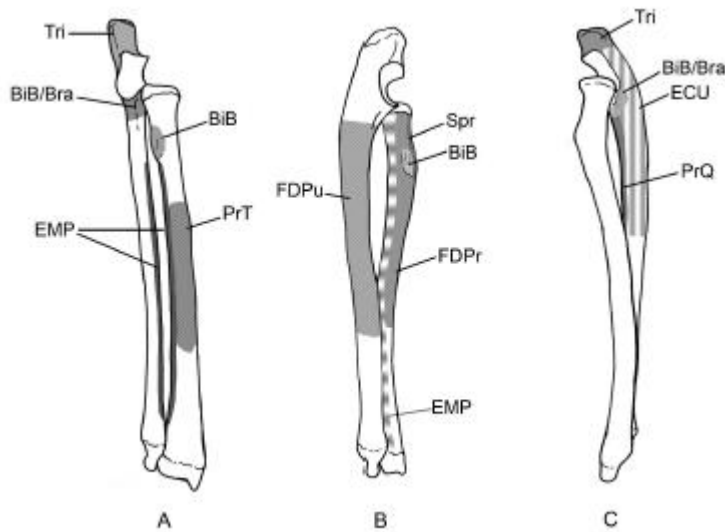


Figure 5 – Right radius and ulna of *Dendrolagus lumholtzi* showing areas of muscular origin (Or) and insertion (In). A cranial view, B lateral view, C medial view. BiB, Biceps brachii In; Bra, Brachialis In; ECU, Extensor carpi ulnaris Or; EMP, Extensor ossis metacarpus pollicis; FDP, Flexor digitorum profundus radiale Or; FDPu, Flexor digitorum profundus ulnaris Or; PrQ, Pronator quadratus Or; PrT, Pronator teres In; Spr, Supinator In; Tri, Triceps In.



Figure 6 – Right carpus of *Dendrolagus lumholtzi* (x-ray).

Table 1 – Anatomical description and muscle mass proportions of the extrinsic muscles of the pectoral limb of *Dendrolagus lumholtzi*

Muscle	Origin	Insertion	Muscle mass % as proportion of total limb
<i>M. trapezius pars cervicis</i>	Fleshy fibres from nuchal crest along dorsal midline to spinous process T2	Fleshy fibres along the acromial half and cranial aspect of the scapular spine, acromion process and lateral 3/4 of the clavicle	3.12
<i>M. trapezius pars thoracis</i>	Fleshy fibres along dorsal midline from spinous processes of T2 - T6/C7	Aponeurotic sheet along the distal 3 rd of scapular spine	
<i>M. serratus ventralis</i>	Fleshy fibres from lateral aspect of the 6 anterior ribs and transverse processes of the T6 and T7	Thick, fleshy insertion on the vertebral border of scapula (<i>facies serrata</i>)	Combined serratus ventralis and levator scapulae 4.37
<i>M. levator scapulae</i>	Fleshy origin from transverse process of T3 to T5	Fleshy fibres onto the cranial angle of scapula, the facies serrata, adjacent to insertion of <i>M. serratus anterior</i>	
<i>M. atlantoscapularis.</i>	Aponeurotic fibres from transverse process of atlas (C2), deep to the <i>M. atlanto-acromialis</i>	Fleshy fibres onto the vertebral border and proximal end of scapular spine bordering the supraspinous fossa	0.31
<i>M. omotransversarius (atlanto-acromialis)</i>	Fleshy fibres from transverse process of atlas (C2), superficial to <i>M. atlantoscapularis</i>	Fleshy and aponeurotic fibres onto the distal half of scapula spine, and cranial aspect of the acromion process.	1.45
<i>M. latissimus dorsi</i>	Dorsal midline, from level of caudal angle of the scapula, to the spinous process and rib of T12 and thoracolumbar fascia	Tendon to proximomedial humeral shaft, immediately distal to tendon of <i>m. teres major</i>	11.98
<i>M. rhomboideus</i>	Lateral aspect of upper neck, close to level of nuchal crest	Along entire edge of scapular vertebral border (thick, strong)	1.9

	(fleshy fibres, not a strong attachment) as well as a midline origin of thicker fleshy fibres from the 1st to the 3rd spinous process.	fleshy fibres).	
<i>M. pectoralis superficialis</i>	Thick fleshy fibres from the ventral midline from manubrium of sternum to 5 th costal cartilage	Fleshy and aponeurotic fibres to the medial half of clavicle, and along entire length of pectoral ridge of humerus; fuses distally with the <i>m. deltoideus pars clavicularis</i> .	13.02 Combined pectoral mass
<i>M. pectoralis minor</i>	Fleshy fibres between the clavicle and 2 nd and 3 rd costal cartilages on the ventral midline	Aponeurotic sheet proximal to the <i>m. pectoralis quadratus</i> on the proximal half of the pectoral ridge, medially on the greater tubercle, and the posterior aspect of the clavicle.	
<i>M. pectoralis quartus</i>	Fleshy fibres from the ventral midline between the 3 rd & 6 th costal cartilages	Thin aponeurotic sheet to central segment of the pectoral ridge deep to the insertion of the <i>m. pectoralis superficialis</i>	
<i>M. subclavius</i>	Fleshy fibres from medial 3rd of 1st rib and lateral edge of the manubrium.	Medial deep 3/4 of clavicle.	

Table 2– Measurements of the scapula in kangaroos and wallabies. Where n>1, data are species means and standard errors (S.E.) are included within parentheses.

	Length of the scapula (mm)	Width of infraspinous fossa / scapula length (%)	Length of tricep crest/ scapula length (%)	Glenoid fossa length / width (%)
<i>Dendrolagus bennettianus</i> (n=2)	57.6 (1.43)	61	37	114
<i>Dendrolagus dorianus</i> (n=2)	57.6 (0.68)	64	72	143
<i>Dendrolagus lumholtzi</i> (n=6)	55.6 (1.43)	65	66	158
<i>Dendrolagus matschei</i> (n=1)	54.8	67	45	99
<i>Dorcopsis veterem</i> (n=1)	59.4	54	28	124
<i>Lagorchestes conspicillatus</i> (n=5)	36.5 (0.35)	39	NA	153
<i>Macropus eugenii</i> (n=6)	44.8 (3.57)	62	29	101
<i>Macropus fuliginosus</i> (n=4)	96.7 (13.81)	61	25	105
<i>Macropus rufus</i> (n=4)	95.1 (18.08)	59	24	123
<i>Onychogalea unguifera</i> (n=4)	44.8 (1.92)	41	NA	166
<i>Petrogale brachyotis</i> (n=3)	45.6 (1.70)	55	NA	142
<i>Petrogale lateralis</i> (n=6)	39.0 (1.12)	59	NA	137
<i>Setonix brachyurus</i> (n=4)	45.2 (1.65)	47	28	100
<i>Thylogale billardierii</i> (n=1)	71.2	46	33	96

Table 3– Measurements of the humerus and radius in kangaroos and wallabies. Where n>1, data are species means and standard errors (S.E.) are included within parentheses.

	Humerus Length (mm)	Ant-post W trochlea / humerus length (%)	Radius length (mm)	Brachial Index (radius length / humerus length)
<i>Dendrolagus bennettianus</i> (n=2)	96.1 (3.23)	19	101.4 (2.15)	106
<i>Dendrolagus dorianus</i> (n=2)	105.2 (0.49)	25	103.5	99
<i>Dendrolagus lumholtzi</i> (n=6)	98.4 (1.91)	18	103.5 (1.06)	103
<i>Dendrolagus matschei</i> (n=1)	101.8	21	96.9	95
<i>Dorcopsis veterem</i> (n=1)	78.8	10	93.0	118
<i>Lagorchestes conspicillatus</i> (n=5)	44.6 (0.78)	21	56.0 (1.10)	124
<i>Macropus eugenii</i> (n=6)	63.91 (5.60)	12	77.4 (6.57)	121
<i>Macropus fuliginosus</i> (n=4)	148.4 (22.0)	10	240.4 (25.77)	134
<i>Macropus rufus</i> (n=4)	143.5 (23.73)	13	222.9 (47.67)	133
<i>Onychogalea unguifera</i> (n=4)	63.4 (3.49)	22	82.1 (3.65)	130
<i>Petrogale brachyotis</i> (n=3)	58.8 (1.47)	21	67.2 (1.80)	111
<i>Petrogale lateralis</i> (n=6)	57.7 (1.53)	18	65.4 (2.04)	113
<i>Setonix brachyurus</i> (n=4)	53.4 (1.16)	13	62.7 (1.16)	118

Table 4 - Anatomical description and muscle mass proportions of the intrinsic muscles of the pectoral limb: muscles of the shoulder and brachium of *Dendrolagus lumholtzi*

Muscle	Origin	Insertion	Muscle mass % as proportion of total limb
<i>M. deltoideus</i> <i>pars spinalis</i>	Fleshy fibres from medial 2/3 rd of scapula spine and fascia that covers the infraspinatus	Aponeurotic fibres laterally on delto-pectoral ridge of the humerus; medially inseparable from <i>pars acromialis</i> and <i>M. brachialis</i>	3.17 Combined deltoid mass
<i>pars acromialis</i>	Fleshy fibres from acromion process	Immediately distal to the <i>pars spinalis</i> on the delto-pectoral ridge, fuses to <i>m. brachialis</i> .	
<i>pars clavicularis</i>	Fleshy fibres from central 3 rd of the clavicle	Aponeurotic fibres to the anterior and proximal 3 rd of the humerus, the distal extension of the greater tubercle with superficial pectoral	
<i>M. supraspinatus</i>	Fleshy fibres from supraspinous fossa and cranial edge of scapula spine; shares an aponeurosis with the subscapularis in the cranial notch.	Dorso-laterally on the greater tuberosity of the humerus by a strong fleshy & aponeurotic tendon.	1.94
<i>M. infraspinatus</i>	Fleshy fibres from the infraspinous fossa and caudal aspect of scapula spine; sharing an aponeurotic membrane with the m. subscapularis in the caudal notch.	Strong tendon to the lateral aspect of the greater tuberosity of humerus.	3.49
<i>M. teres minor</i>	Small muscle from distal caudal border of scapula	Base of greater trochanter	0.09
<i>M. subscapularis</i>	Fleshy fibres from subscapular fossa, covers almost entire medial surface; facies serrata very narrow.	Fleshy and aponeurotic fibres insert medially onto the lesser humeral tuberosity.	5.19
<i>M. biceps brachii</i>	Two heads from the coracoid process and from beneath the supraglenoid tubercle; thick tendons combine passing over the anterior facet of the lesser tuberosity and shallow bicipital groove.	Superficial portion to the bicipital notch of the radius; deep portion to proximal ulna with the brachialis	5.81
<i>M. coracobrachialis</i>	Coracoid process of scapula.	Medial and distal on lesser tuberosity of humerus.	0.08
<i>M. brachialis</i>	Lateral humeral shaft, between the deltoid and supinator ridge, and anterior distal humerus	Aponeurotic fibres onto ulna, distal to trochlear notch & coronoid process	2.76
<i>M. triceps</i> <i>brachii caput lateral</i>	Aponeurotic and fleshy fibres from postero-lateral humeral neck and shaft.	Lateral olecranon	10.49 Combined triceps brachii mass
<i>brachii caput medial</i>	Fleshy fibres from the medial and distal 2/3rds of the humeral shaft.	Medial olecranon	
<i>brachii caput longum</i>	Fleshy and aponeurotic fibres from the distal half of	Proximal olecranon	

	the caudal border of the scapula.		
<i>M. tensor fasciae antebrachii</i>	Fleshy fibres from mid m. latissimus dorsi.	To antebrachial fascia, fascia of medial triceps and olecranon	1.40
<i>M. anconeus</i>			0.31

Table 5 - Anatomical description and muscle mass proportions of the intrinsic muscles of the pectoral limb: muscles of the antebrachium and carpus of *Dendrolagus lumholtzi*

Muscle	Origin	Insertion	Muscle mass % as proportion of total limb
<i>M. pronator teres</i>	Fleshy and aponeurotic fibres from the anterior face of the medial epicondyle, deep to the origin of the flexor carpi radialis	Fleshy fibres to anteromedial radius	1.40
<i>M. flexor carpi radialis (FCR)</i>	Fleshy and aponeurotic fibres from medial epicondyle superficial to the pronator teres.	Inserts by tendon onto the scaphoid bone of the carpus.	1.21
<i>M. flexor carpi ulnaris (FCU)</i>	Medial epicondyle, passes along medial aspect of ulna	Pisiform (accessory carpal)	1.44
<i>M. palmaris longus</i>	Fleshy origin from the medial epicondyle, deep to the FCR.	Deep fascia of ventral carpus	0.73
<i>M. flexor digitorum superficialis</i>	Distal medial epicondyle with FDPPrH.	Tendons along superficial belly of FRPr extending to each of the digits.	
<i>M. flexor digitorum profundus (FDPPrH)</i>	Fleshy fibres from distal medial epicondyle of the humerus; proximal 2/3rds of medial facet of ulna; proximal 2/3 rd s of medial face of radius	The large tendons of each portion unite and then give rise to one thick insertion for each distal phalanx.	11.20 Combined digital flexor mass
<i>M. brachioradialis</i>	Fleshy fibres from proximal third of the supinator ridge, and distal aponeurosis of lateral head of the triceps.	Tendon to dorsum of metacarpal I.	1.54
<i>M. extensor carpi radialis</i>	Supinator ridge distal to brachioradialis, and lateral radius. Longus and brevis portions not easily separable at origin.	Longus portion to dorsum metacarpal II. Brevis portion with thick tendon to dorsum of metacarpal III.	2.27
<i>M. extensor carpi ulnaris (ECU)</i>	Lateral epicondyle and proximal lateral ulna	To pisiform bone and intercarpal ligaments	0.39
<i>M. supinator</i>	Lateral epicondyle of the humerus and capsule of the elbow joint.	Fleshy fibres to the proximal third of the medial border of the radius.	0.56
<i>M. extensor digitorum communis (EDC)</i>	Aponeurotic fibres from the anterior aspect of lateral epicondyle distal to ECRB (two heads)	Four tendons to insert medial digit 3, medial digit 4, lateral digit 4 (small) and medial digit 5; deeper portion gives tendons to lateral digit 1 and medial digit 2.	0.90
<i>Extensor ossis metacarpi pollicis (EMP)</i>	Fleshy fibres from the medial border of radius and ulna	Tendinous insertion onto the base of metacarpal I.	0.73