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Ecomorphological determinations in the absence of living analogs: the predatory behavior of the marsupial lion (*Thylacoleo carnifex*) as revealed by elbow joint morphology

Borja Figueirido, Alberto Martín-Serra and Christine M. Janis

RRH: THE PREDATORY BEHAVIOR OF *THYLACOLEO*

LRH: BORJA FIGUEIRIDO ET AL

Abstract.—*Thylacoleo carnifex*, or the “pouched lion” (Mammalia: Marsupialia: Diprotodontia: Thylacoleonidae), was a carnivorous marsupial that inhabited Australia during the Pleistocene. Although today all researchers agree that *Thylacoleo* had a hypercarnivorous diet, the way in which it killed its prey remains uncertain. Here we use geometric morphometrics to capture the shape of the elbow joint (i.e., the anterior articular surface of the distal humerus) in a wide sample of extant mammals of known behavior to determine how elbow anatomy reflects forearm use. We then employ this information to investigate the predatory behavior of *Thylacoleo*. A Principal Components Analysis indicates that *Thylacoleo* is the only carnivorous mammal to cluster with extant taxa that have an extreme degree of forearm maneuverability, such as primates and arboreal xenarthrans (pilosans). A Canonical Variates Analysis confirms that *Thylacoleo* had forearm maneuverability intermediate between wombats (terrestrial) and arboreal mammals, and a much greater degree of maneuverability than any living carnivorous placental. A Linear Discriminant Analysis computed to separate the elbow morphology of arboreal mammals from terrestrial ones shows that *Thylacoleo* was primarily terrestrial but with some climbing abilities. We infer from our results that *Thylacoleo* used its forelimbs for grasping or manipulating prey to a much higher degree than its supposed extant placental counterpart, the African lion (*Panthera leo*). The use of the large and retractable claw on the semi-opposable thumb of *Thylacoleo* for potentially slashing and disemboweling prey is discussed in the light of this new information.

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Introduction

The determination of the possible ecology or behavior of extinct animals has been an enjoyable challenge for scientists and the popular media alike. Studies of comparative anatomy, from Richard Owen to the present day, have compared the anatomy of extinct animals with extant relatives or analogs, and drawn conclusions about the behavior of the extinct forms in a qualitative fashion. During the past few decades, researchers have devoted considerable effort to the development of quantitative modes of analysis for inferring the behavior and ecology of extinct species. Such studies fall under the general rubric of “ecomorphology”, whereby the morphology of an animal is functionally correlated with its ecology or behavior (see Wainwright 1991). Ecomorphological studies of extinct species include multivariate morphometrics on various skeletal elements to statistically assess the association between the morphology of a skeletal structure (dependent variable) in the extant forms with their ecology or behavior (independent variable). Morphological traits associated with known behaviors may be used as indicators of ecology and behavior in extinct taxa (e.g., Slater and Van Valkenburgh 2008; Meachen-Samuels and Van Valkenburgh 2009; Figueirido and Janis 2011; Samuels et al. 2013; Janis and Figueirido 2014).

Biomechanical modeling can also be used to reconstruct the paleoecology of extinct species as uses the morphology of skeletal structures and the physical properties of biomaterials to evaluate functional performance of anatomical arrangements (e.g., Alexander 1985). A recent example of such an approach is finite element analysis (FEA), where the virtual performance of skeletal elements of extinct animals under simulated stress has been compared with that of their living relatives to infer performance and function

(e.g., McHenry et al. 2007; Wroe 2008; Rayfield 2007; Tseng and Wang 2010; Tseng et al. 2011; Gill et al. 2014).

Paleoecological inferences are likely to be more reliable if there are living relatives and if a clear analogy can be established with performance in an extant animal. However, we know of various types of morphologies in extinct mammals where there are no extant analogs: examples include saber-toothed carnivores (e.g., Emerson and Radinsky 1980) and large, clawed herbivores (e.g., Coombs 1983). If living relatives are absent and/or there are no analogous forms, paleoecological inferences are likely to be more ambiguous, especially in the absence of an extant phylogenetic bracket (Witmer 1995). The temptation to shoehorn an extinct animal into the ecomorphological role of an extant one may lead to premature conclusions. For example, the extinct short-legged barrel-bodied rhino *Teleoceras* is often portrayed as having a hippo-like mode of life, but careful examination of the evidence (in this instance, isotopic evidence of a preference for a terrestrial habitat) shows that to be incorrect (MacFadden 1998). Additionally, an extinct animal may behave in a way seen in no extant taxon, such as the proposed unique mode of swimming in the archaeocete *Ambulocetus* (Thewissen and Fish 1997), or the proposed bipedal walking locomotion in sthenurine kangaroos (Janis et al. 2014). In such cases, the selection of highly functional –or “taxon-free”– traits to derive ecomorphological conclusions is crucial, because analyses will then show whether or not the anatomy of an extinct animal falls within the boundaries of the range of morphologies of extant ones. If it does not fall within these boundaries, it may have had a type of ecomorphology not seen today.

There are also a number of other approaches to the ecology of extinct taxa that capture aspects of behavior during the animal’s lifetime: these could be termed “eco-physiological” as they reflect lifetime habits rather than adaptive morphology revealed by

ecomorphological or biomechanical traits. Such approaches can be invaluable for studying extinct animals without living analogs. These include wear on the teeth to determine diet, whether macrowear (e.g., Janis 1979), mesowear (e.g., Fortelius and Solounias 2000) or microwear (e.g., Solounias et al. 2010). Another approach involves geochemistry: the study of the isotopic signatures in dental and bone tissues incorporated during food and water consumption (e.g., Cerling and Harris 1999; Palmqvist et al. 2008). However, while both of these methodologies are extremely useful in the derivation of feeding behavior or habitat preference, they cannot be employed to determine other behavioral aspects of extinct species such as hunting style or locomotor strategy.

In this paper we demonstrate the potential of ecomorphological methodologies to infer aspects of behavior in extinct species without living relatives by using a functional and quantifiable morphological trait. Here we use the shape of the anterior surface of the humerus distal epiphysis (from here on referred to as the elbow joint) as a morphological indicator to infer the predatory behavior of the emblematic Australian marsupial lion (*Thylacoleo carnifex*). We propose that, despite the fact that *Thylacoleo* is usually portrayed as a cat-like predator because of its rather feline-like appearance, it may have had a predatory behavior unlike that seen in any extant carnivore.

Thylacoleo carnifex: a hypercarnivorous diprotodontid without living analogs.—
Thylacoleo carnifex, known as the pouched (or marsupial) lion, was a carnivorous marsupial of the Australian Pleistocene. It was originally described in 1859 by the renowned paleontologist Sir Richard Owen: the genus name *Thylacoleo* (from the Greek – *thylakos* and –*leo*) means “pouched lion” and the species name *carnifex* (from the Latin – *carnifex*), means “executioner”. In the same study, Owen (1859) identified *Thylacoleo* as “one of the fellest and most destructive of predatory beasts”. The marsupial lion is the

youngest species of the genus *Thylacoleo* (*T. crassidentatus* and *T. hilli* being known from the Pliocene), the largest member of all thylacoleonids (*ca.* 100-160 kg; Wroe et al. 1999; Wroe et al. 2003), and the most geographically dispersed of the three.

The family Thylacoleonidae belongs to the order Diprotodontia (Mammalia; Metatheria), which today comprises only omnivorous or herbivorous forms such as possums, koalas, wombats and kangaroos (e.g., Finch 1982; Wells et al. 1982, 2009; Case 1985; Wroe et al. 2000; Wroe 2003). There has been much debate and controversy about the probable diet of the marsupial lion. Since Owen (1859) initially characterized *Thylacoleo* as a carnivore based on its large and sectorial third lower and upper premolars (from now on referred to as carnassials), its canine-like incisors, and the extreme reduction of the other cheek teeth. In contrast, other contemporaneous researchers raised doubts about Owen's hypothesis (e.g., Dawkins 1864; Krefft 1866; Flower 1868; Cope 1882; De Vis 1883; Lydekker 1894), in particular because the angle, orientation and morphology of its caniniform incisors raised doubts about their use for killing prey (e.g., Anderson 1929; Gill 1954). However, all of the evidence obtained during the last few decades, from both adaptive (Finch 1982; Wells et al. 1982; Wroe et al. 2005; Wroe et al. 2008) and ecophysiological (Nedin 1991; Gröcke 1997; Wells et al. 1982) approaches, indicate that *Thylacoleo* was indeed a hypercarnivorous animal. *Thylacoleo* thus represents an extinct hypercarnivorous species without living analogs (Wroe 2000), as all living diprotodontids are omnivores or herbivores (e.g., Finch 1982; Wells et al. 1982, 2009; Case 1985; Wroe et al. 2000; Wroe 2003).

Despite the unequivocal evidence of carnivory, the specific way in which the marsupial lion killed its prey (i.e., its predatory behavior) remains more uncertain. This is probably because the morphology of its postcranial skeleton has received considerably less

attention than that of the skull and dentition. A detailed study of the postcranial morphology of *Thylacoleo* was lacking until Wells and Nichol (1977) presented a description of its manus and pes, concluding that *Thylacoleo* had a digitigrade posture in the manus and a plantigrade stance in the pes. Wells and Nichol (1977) also noted an efficient and powerful grasping mechanism of the forelimbs together with the possession of a short, very robust and pseudo-opposable thumb with a large hooded claw. Both Wells and Nichol (1977) and Wells et al. (2009) interpreted the morphology of the manus and pes of *Thylacoleo* as ideally adapted to a climbing grasp, inferring a scansorial habit (i.e., both terrestrial and capable of climbing). However, Finch (1982), in a study of limb proportions, concluded that *Thylacoleo* was not particularly climbing adapted. The difference of opinion between these authors may relate to the fact that the hands of generalized terrestrial carnivores and arboreal ones have some traits in common: a hand well-adapted to a climbing grasp could equally be well-adapted for holding prey (Wells and Nichol 1977), and both activities require a high degree of forearm maneuverability. A more extensive study on the potential abilities of *Thylacoleo* to either climb trees or manipulate prey would offer additional evidence on the predatory behavior deployed by the marsupial lion, and to the further understanding of its paleobiology.

In this paper we investigate the forearm anatomy of *Thylacoleo* to determine its probable predatory behavior. We use the shape of the elbow joint, a highly functional morphological trait considered an indicator of forearm maneuverability (Andersson and Werdelin 2003; Andersson 2004, 2005; Figueirido and Janis 2011; Figueirido et al. 2015), and we employ landmark-based methods of geometric morphometrics to compare the elbow of *Thylacoleo* with the elbow of extant mammals.

Material and Methods

The sample of *Thylacoleo carnifex* (Metatheria; Diprotodontia) includes three specimens collected from James' Quarry cave, Naracoorte, South Australia (collectively SAM-P12384) and housed at the South Australian Museum in Adelaide (South Australia) (Fig. 1A). The photographs of isolated humeri were taken by CMJ.

We also collected data on the humeri of 190 specimens belonging to 78 extant species, from the placental orders Carnivora, Primates, and Pilosa, and the marsupial orders Diprotodontia, Dasyuromorphia and Peramelemorphia (Table 1). Although it may appear that our sample size is unbalanced in favor of placentals, we note that marsupials only represent 4% of the species diversity of mammals (Nowak 1999).

We included a wide sample of placentals with various degrees of forearm maneuverability. Taxa with a high degree of forearm maneuverability (i.e., with a great ability for forearm pronation and supination), including predominantly arboreal or scansorial forms, either for climbing trees, holding onto branches (e.g., the American black bear, *Ursus americanus*; the orangutan, *Pongo pygmaeus*; the brown-throated three-toed sloth, *Bradypus variegatus*), or for manipulating food (e.g., the kinkajou, *Potos flavus*). Taxa with a moderate degree of forelimb maneuverability include generalized terrestrial forms (e.g., the tiger, *Panthera tigris*, which can use its forelimbs to grapple with its prey). Taxa with the most restricted capacity to pronate and supinate the forearm include cursorially adapted forms (e.g., the African hunting dog, *Lycaon pictus*).

For the marsupials, we collected data from arboreal and terrestrial Diprotodontia: these included Vombatiformes (e.g., the koala, *Phascolarctos cinereus*; and the wombat, *Vombatus ursinus*), and Phalangeriformes (possums, and Macropodiformes such as tree kangaroos *Dendrolagus* spp., and the swamp wallaby, *Wallabia bicolor*). Other terrestrial

forms included Peremelemorphia (the greater bilby, *Macrotis lagotis*) and Dasyuromorphia (carnivorous marsupials, including the Tasmanian devil, *Sarcophilus harrisi*; the recently extinct thylacine *Thylacinus cynocephalus*; and the spotted quoll, *Dasyurus maculatus*). Some examples are shown in Figure 1B. These data were obtained from the American Museum of Natural History (New York) and the Museum of Comparative Zoology of Harvard University (Cambridge, Massachusetts).

We used the approach of Andersson and Werdelin (2003) and Andersson (2004) to capture the shape of the elbow joint (Fig. 2A), collecting digital pictures on the anterior surface of the humerus distal epiphysis with a scale bar and at an appropriate distance. We digitized six homologous landmarks in two dimensions (Fig. 2B) with TPSdigv.2 (Rohlf 2008) and we used the measure tool of this software to incorporate a measure of size.

All the specimens were aligned using Procrustes superimposition (Dryden and Mardia 1998) to remove the effects of rotation, translation and scaling. We used Centroid size (Cs; the square root of the sum of the Euclidean distances between each of the landmarks and the centroid; Bookstein 1991) and Procrustes coordinates (i.e, aligned x,y landmark coordinates) as proxies for size and shape, respectively. The Procrustes superimposition method was performed with MorphoJ (Klingenberg 2011).

We assembled a phylogeny following various published sources (see Fig. 3) with Mesquite (Maddison and Maddison 2011). We then quantified the phylogenetic signal in elbow shape and size using a permutation test developed by Laurin (2004) for univariate traits, and extended for multivariate analyses by Klingenberg and Gidaszewski (2010), to simulate the null hypothesis of complete independence (e.g., Gidaszewski et al. 2009; Figueirido et al. 2010, 2013; Klingenberg and Marugán-Lobón 2013; Martín-Serra et al. 2014a, 2014b, 2015) using MorphoJ (Klingenberg 2011).

Additionally, a multivariate regression analysis (Monteiro 1999) of shape on size was performed to test the influence of allometry. The statistical significance was tested with a permutation test against the null hypothesis of complete independence of shape on size (Drake and Klingenberg 2008). However, as species are not independent data points, we also applied independent contrasts analysis (IC; Felsenstein 1985) to take phylogenetic effects into account. The statistical significance was again tested with a permutation test against the null hypothesis of complete independence of shape on size (Drake and Klingenberg 2008). The independent contrast analyses and the permutation tests were performed with MorphoJ (Klingenberg 2011).

To control for the possibility that larger species might require a less flexible elbow simply to brace their body weight, or that small terrestrial species might encounter more situations that require them to climb more often simply because of their small size, and so require a more flexible elbow, we eliminated the predicted component of shape due to size differences by computing the residuals from the evolutionary regression analyses following Klingenberg and Marugán-Lobón (2013) and Martín-Serra et al. (2014a, 2014b, 2015). These residuals were used in all subsequent multivariate analyses as size-free data. Here we show the results including body size (i.e., those results obtained from Procrustes coordinates), but the results omitting body size (i.e., residuals) are shown in the supplementary material. The results omitting body size should be interpreted with caution, because body size is a variable that influences the degree of substrate use in living taxa and it is a strong limiting factor for arboreal species (e.g., Taylor 1974; Van Valkenburgh 1987). If size-related shape changes (allometric effects) are removed, it is possible that the “substrate-signal” in elbow-shape would be also erased.

We reconstructed the hypothetical morphology of the ancestral nodes in the phylogenetic tree shown in Figure 3 (e.g. McArdle and Rodrigo 1994; Martins and Hansen 1997; Garland et al. 1999; Polly 2001; Rohlf 2001; Finarelli and Flynn 2006; Astúa 2009; Figueirido et al. 2010; Almécija et al. 2013; Figueirido et al. 2013; Martín-Serra et al. 2014a,b) using the square-changed parsimony method of Maddison (1991) with MorphoJ (Klingenberg 2011). We used this approach to specifically compare the elbow of *Thylacoleo* with the ancestral states of other mammalian groups and with other tips of the phylogeny.

To investigate the ordination of the taxa in the phenotypic space, we performed a Principal Components Analysis (PCA) from the covariance matrix of the Procrustes coordinates. The hypothetical ancestral shapes were then plotted onto the phenotypic space and the branches were later connected to create elbow phylomorphospaces (see, e.g., Klingenberg and Ekau 1996; Rohlf 2002; Gidaszweski et al. 2009; Figueirido et al. 2010, 2013; Klingenberg and Gidaszewski 2010; Klingenberg et al. 2012; Martín-Serra 2014a, 2014b; Sherratt et al. 2014) using MorphoJ (Klingenberg 2011). To explore the influence of phylogeny on the first two PCs, we mapped the scores of the species on these eigenvectors onto the phylogeny shown in Figure 3 using squared-changed parsimony, assuming a Brownian motion model of evolution, with the PDAPtree module of Mesquite (Midford et al. 2002).

We also conducted a Canonical Variates Analysis (CVA) to determine the features distinguishing among taxa with different degrees of forearm mobility (Table 1). The extant taxa were classified according to degree of object manipulation with their forelimbs (low, medium and high). Species with high forelimb mobility are those that are capable of putting food into their mouths using their forearms, or which have a wide angle of forearm rotation

measured in vivo (mainly in primates). Species with low forearm mobility are those with limited capacity for forearm supination due to cursorial adaptations. Those species with moderate forearm mobility still are able to perform some forearm movements for grappling with prey or for grasping food, but they usually do not use their forearms to put food in their mouths, because they do not have the same freedom of movement.

These criteria to quantify “elbow mobility” were appropriate for all the taxa except for the more terrestrial primates such as the rhesus macaque (*Macaca mulatta*): like all primates, this taxon can put food into its mouth, but has a mean range of radio-ulnar pronation and supination much lower (79°) than the orangutan (*Pongo*, 150°) and gibbons (*Hylobates*, 163°), as seen in experimental studies (O’Connor and Rarey 1979).

Furthermore, this macaque is clearly more terrestrial than any other primate included in our sample (Table 1), and for this reason we classified it as having moderate elbow mobility.

The statistical significance of the pairwise differences in mean shapes among the three groups was assessed with a permutation test using both the Mahalanobis distances (MDs) and the Procrustes distances (PDs) between groups using MorphoJ (Klingenberg 2011). The test operates by randomly reassigning the specimens into the groups compared 10,000 times. The means of all random groups are then calculated and the pairwise distances among them are computed. The test provides a *P*-value, which is the proportion of permutations that result in a pairwise distance between groups equal to or less than the observed one. Therefore, if our groups are significantly different according to the morphology of the elbow, the pairwise distances obtained in each permutation should be lower than the one obtained with the original data.

To assess how much of the variation is due to phylogenetic relationships of the species under study, we performed phylogenetic MANOVAs from the species scores on

both canonical axes. To do this, we used the ‘aov.phylo’ function included in the ‘Geiger’ package (Harmon et al. 2008) for R. We used Brownian motion as a model for evolutionary change, and ran 1,000 simulations to create an empirical null distribution of F -values to compare with our sample.

Both of the functions obtained from the sample of living taxa in CVA were later applied to the Procrustes coordinates of all thylacoleonid elbow shapes. The percentage of probability of living species to belong to any of the groups was assessed using the direct method of leave-one out cross-validation procedure (e.g., Timm 2002) with SPSS v.19. The *Thylacoleo* specimens were classified according to their proximity to group centroids.

As shown in the results, we determined that the morphology of the elbow joint of *Thylacoleo* was indicative of a highly mobile forelimb. Because there is little anatomical difference between the forelimbs of terrestrial carnivores that usually manipulate prey and those of arboreal mammals because both require highly mobile forelimbs (Wells and Nichol 1977; Fabre et al. 2013), we also performed a Linear Discriminant Analysis (LDA) to separate the living arboreal and terrestrial taxa (Table 1). Again, the statistical significance of pairwise differences in mean shapes between the two groups was assessed with a permutation test using both the Mahalanobis distances (MDs) and the Procrustes distances between groups after 10,000 permutations. The reliability of the discrimination was assessed by the “leave-one-out” cross-validation method (e.g., Timm 2002) and the classification of thylacoleonids into one of the two groups was determined according to their proximity to group centroids.

Results

Allometry and phylogeny in elbow-joint shape. –The permutation test indicated a strong phylogenetic signal in both distal humerus size and shape (LogCs: tree length = 7.642, $P < 0.0001$; Procrustes coordinates: tree length = 0.555, $P < 0.0001$). The presence of a phylogenetic signal does not invalidate this structure as a functional trait, as it mainly reflects forearm motion and body weight support. Rather, this simply means that this structure has an evolutionary history, as few cases exhibit a homoplastic degree high enough to mask the presence of phylogenetic signal.

Although the multivariate regression of Procrustes coordinates on LogCs (species averages) was not statistically significant ($n = 81$; $P = 0.0967$), the multivariate regression of both contrasted variables yielded a clear significant association ($n = 79$; $P = 0.0030$) (see Fig. 4). This result indicates that placentals and marsupials follow different allometric trends, and this is the reason why the interspecific regression was not significant. However, when phylogeny was taken into account, the association between the contrasts of size and the contrast of shape was significant, which means that changes in elbow size between nodes are accompanied by changes in elbow shape. In any event, our results indicate that evolutionary allometry is a significant source of elbow shape variation.

Functional anatomy of the elbow joint. –The reconstructed shapes at the internal nodes and some of the tips of the phylogeny are depicted in Figure 5. Relative to other marsupials such as the wombat, other diprotodonts or dasyuromorphians, or even other thylacoleonids such as the Miocene *Priscileo* (personal observation of *Priscileo pitikantensis* SAM P37720), both the trochlea and the capitulum of *Thylacoleo* are large (Fig. 5). The articular surface of the trochlea is less proximo-distally extended than in the wombat (Fig. 5B), the ancestral state for dasyuromorphians (Fig. 5D), all carnivorans (Fig.

5G), and pantherine felids (i.e., the large felids) (Fig. 5H). In contrast, the trochlea of *Thylacoleo* is more proximo-distally extended than in the koala (Fig. 5A), and the ancestral shape for xenarthrans (Fig. 5E). The extension of the capitulum of *Thylacoleo* is similar to the capitulum of dasyuromorphians (Fig. 5D), xenarthrans (Fig. 5E), and pantherine felids (Fig. 5H). The capitulum is less latero-proximally extended than in the koala (Fig. 5A) or the ancestral state for diprotodontids (Fig. 5C), but more so than in the wombat (Fig. 5B) and primates (Fig. 5F).

The articular surface of the *Thylacoleo* humeral distal epiphysis is not as shallow as in the koala (Fig. 5A), xenarthrans (Fig. 5E) or primates (Fig. 5F), due to the trochlea being extended medially, resulting in a large distal trochlear crest. In contrast, the articular surface of *Thylacoleo* is more shallow than that of the wombat (Fig. 5B), the ancestral state for dasyuromorphians (Fig. 5D), all carnivorans (Fig. 5G), and pantherine felids (Fig. 5H). Although the elbow shape of *Thylacoleo* is similar to that of the ancestor for all diprotodontids (Fig. 5C), the trochlea is more medio-distally extended and the capitulum is less proximally extended, rendering it less shallow.

A large trochlea and a rounded condyle-like capitulum allow for a high ability to supinate the forearm (Taylor 1974; Argot 2001), and thus we can deduce that the forearm of *Thylacoleo* was well able to perform this movement.. The articular surface of the *Thylacoleo* elbow is also characterized by a large trochlear crest, which increases stabilization of the forearm (Jenkins 1973; Figueirido and Janis 2011; Janis and Figueirido 2014; Figueirido et al. 2015). Our results thus indicate that *Thylacoleo* was able to stabilize the forearm to a greater degree than the koala but less so than other more terrestrial taxa (excluding the wombat, see discussion below). This anatomy is probably indicative of the ability to stabilize the forearm on the ground, the typical condition of terrestrial species.

Thus the elbow-joint anatomy of *Thylacoleo* indicates that while it was able to lock the arm into a prone position, as in living terrestrial species, it also retained the ability to supinate the forearm as seen in living arboreal species.

The phenotypic space of the mammalian elbow joint. – As the first two PCs explained *ca.* 75% of the original variance, we show here only these components because they provide a reasonable approximation for the total shape variation. The third component explained less than 10% of the original shape variance and the inspection of this eigenvector did not reveal any relevant morphological pattern. The morphospace depicted from the scores of the taxa on the first two PCs is shown in Figure 6A, with their associated shape changes in Figure 6B, and the respective phylomorphospace in Figure 6C. The PCA performed from size-corrected data yielded very similar results (Fig. S1), indicating that the main axis of shape variation of our data does not reflect size differences.

The first PC explains 64.32% of the original variance and ordines the taxa according to forearm mobility: taxa with positive scores have mobile forearms, with a high capacity for supination, while those with negative scores have forearms with more restricted mobility, more locked into a prone position (Fig. 6A, C). Taxa with positive scores on PC1 have distal humeri of a rectangular shape, with the trochlea and capitulum of subequal size, while taxa with negative scores have distal humeri that are more square and box-shaped, with a capitulum that is larger than the trochlea (see Fig 6B, upper).

While it appears that PC1 separates placentals (with more negative scores) from marsupials (with more positive scores), this is because canids occupy the negative portion of this axis. Although there are very few marsupials that resemble carnivoran placentals (i.e., quadrupedal and at least somewhat more terrestrial), note that both the thylacine (*Thylacinus cynocephalus*) and the quoll (*Dasyurus maculatus*) fall close to the “placental

space” along PC1 as does, to a lesser extent, the Tasmanian devil (*Sarcophilus harrisi*). The other terrestrial quadrupedal marsupials in this plot, the bilby (*Macrotis lagotis*) and the wombat (*Vombatus ursinus*), also plot with less negative scores than most other marsupials, falling in a similar portion of the morphospace to small carnivores with relatively mobile forelimbs (e.g., the African palm civet, *Nandinia binotata*; the fisher, *Martes pennant*; and the binturong, *Arctictis binturong*) (Fig. 6A). More arboreal carnivorans (e.g., the kinkajou, *Potos flavus*, and the small-toothed palm civet, *Arctogalidia trivirgata*) have more negative scores on PC1, as do the American and Asiatic black bears (*Ursus americanus* and *Ursus tibethanus*, respectively).

The second PC explains 11.4% of the original variance, and appears, at least in part, to separate arboreal marsupials (positive scores) from arboreal placentals (negative scores), along the positive side of the first axis (although along the negative side of the first axis marsupials tend to have lower scores than placentals – see for example the placement of the quoll, *Dasyurus maculatus*) (see Fig. 6A, C). Taxa with positive scores on PC2 have a distal humerus characterized by a pronounced trochlear groove (or a large trochlear crest), while those with negative scores have a less pronounced groove (see Fig. 6B, lower). Why arboreal marsupials and placentals should be characterized by this difference is not clear, but we note that some of the xenarthrans (the silky anteater, *Cyclopes didactylus*; the two-toed sloth, *Choloepus hoffmanni*; and the Northern tamandua, *Tamandua mexicana*) cluster with the arboreal marsupials, as do some of the South American primates (e.g., the spider monkey, *Ateles geoffroyi*, and the mantled howler, *Alouatta palliata*).

Mapping the PC scores on the phylogeny shown in Figure 3 using squared-changed parsimony corroborates these results, as neither placentals nor marsupials exhibit a specific range of scores on both eigenvectors (Fig. S2). Note, however, that marsupials differ from

placentals in their ontogeny (Kelly and Sears 2011): marsupials are born in a highly altricial state and require well-developed forelimbs to climb to the mother's teat (Sears 2004). This difference in developmental timing between the fore- and hind limbs in marsupials in comparison with placentals (Weisbecker et al. 2008; Sears 2009; Geiger et al. 2014) might explain why no marsupial has evolved the more restrictive type of elbow joint seen in canids. The supposedly canid-like thylacine does not have a forelimb anatomy in general indicative of canid-like cursorial locomotion (Janis and Figueirido 2014).

The elbow shape of *Thylacoleo* clusters in an intermediate position between that of highly arboreal placentals (i.e., primates and pilosans) and marsupials (i.e., phalangeroids and tree kangaroos). Note, however, that *Thylacoleo* does not cluster with the arboreal marsupials: its scores on PC1 are similar to the wombat (*Vombatus ursinus*), the only terrestrial quadrupedal diprotodontid marsupial, and its scores on PC2 are more negative than any marsupial except the mountain cuscus (*Phalanger carmelitae*). In addition, *Thylacoleo* is the only hypercarnivorous taxon with this type of elbow morphology: pantherine felids, other hypercarnivorous carnivorans (e.g., the African wild dog, *Lycaon pictus*, and the grey wolf, *Canis lupus*), and dasyuromorphians score more positively on both eigenvectors (Fig. 6A,C).

Thylacoleo: a terrestrial hypercarnivore with extreme forearm maneuverability. –

The CVA performed from the Procrustes coordinates to distinguish among the three groups compared (Table 1) yielded two canonical functions: (CF I: $\lambda = 3.954$, Variance (%) = 77.60; CF II: $\lambda = 1.142$, Variance (%) = 22.40). As indicated by the permutation test, both functions allowed a significant separation ($p < 0.0001$) between the three pairs of groups using both MD and PD among groups (Table 2). Furthermore, 87.7% of all the specimens were correctly assigned to their own groups by using the leave-one out cross validation

procedure. The result of the phylogenetic MANOVA of the specimens scores on both canonical axis was significant for forearm mobility (Wilks = 0.17582, $F = 51.932$, $P_{\text{phyl}} < 0.001$), indicating that the difference between the three mobility groups is significant even after accounting for phylogenetic relationships.

The pairwise plot depicted from the scores of the specimens on both canonical axes is shown in Figure 7A. The first function mainly separates those taxa with high forearm mobility (scoring positively) from the other two groups (Fig. 7A). Taxa with positive scores have distal humeri that are narrow and rectangular-shaped, with trochlea and capitulum of similar length (Fig. 7B, upper left corner). In contrast, taxa with negative scores have a more square and more box-shaped trochleae (Fig. 7B, upper right corner). All thylacoleonids plot within the range of the scores of taxa possessing a highly mobile forearm on the first function, although they do not cluster with them on this plot due to their different scores on the second axis. One specimen of *T. carnifex* (SAMP-12384c) has scores within the range of taxa with moderate forearm mobility (Fig. 7A), falling close to one of the wombat individuals; but note that a few extant forms, such as bears, with highly mobile elbows also have similar scores on this axis.

The second canonical axis separates those taxa with highly restricted, with positive scores, and moderately restricted mobility, with negative scores (Fig. 7A). Taxa with moderate forearm mobility have a larger trochlea with marked grooves and also a longer capitulum (Fig. 7B, lower left corner) than those taxa with low forearm mobility (Fig. 7B, lower right corner). Note, however, that the shape variance accounted for by this second axis is influenced by the position of the wombat specimens, which fall outside of the range of the defined groups with extremely negative scores on the second axis (Fig. 7A).

This unexpected position of the wombat specimens on the second canonical axis reflects the fact that wombats have a relatively long and rectangular-shaped distal humerus articular surface, but with an extremely well developed trochlea crest. The combination of these traits reflects moderate forearm mobility combined with the ability to stabilize the forelimbs on the ground. In contrast, other terrestrially adapted marsupials (i.e., dasyuromorphians such as the thylacine, *T. cynocephalus*) with moderate forearm mobility plot close to pantherine felids (Felidae), and they do not behave as outliers. This is because they have not developed a wombat-like deep trochlea crest: dasyuromorphians resemble placental carnivores in having a trochlea that is relatively shorter than their capitulum, and a large and square capitulum, a condition that confers forearm stabilization in a different fashion.

The usual elbow-joint morphology of terrestrial mammals for stabilizing the forelimb on the ground is for a large capitulum, transferring the weight of the animal through the radius to the carpus. However, the retention of the rounded capitulum typical of arboreal taxa in the wombat (allowing the rotation of the radius around the ulna) necessitates an alternative means of stabilizing the forelimb for terrestrial activity, achieved in the wombat via the ulna by means of a large trochlear crest. This, along with other aspects of the forelimb anatomy, results in a secondary restriction of the ability to supinate (Grand and Barboza 2001). Although the retention of a rounded capitulum reflects phylogenetic inheritance from the ancestral arboreal condition in both the wombat and *Thylacoleo*, the marsupial lion has not secondarily restricted its forearm mobility in this fashion: the greater degree of forelimb stabilization in the wombat may relate to its digging adaptations.

All of the thylacoleonids fall within the range of taxa with moderate forearm mobility on this axis, closest to the wombats among extant taxa, although both of these marsupials plot outside of the 95% of confidence ellipses, occupying an empty part of the morphospace. The thylacoleonid individuals occupy an intermediate position between the wombats and those taxa with high forearm mobility such as primates, pilosans and koalas. This result is also supported when the CVA is performed with size-corrected data (Fig. S3), which indicates that the main axis of shape variation of our data is not strongly influenced by size differences. The main difference between both analyses is that in the size-corrected CVA morphospace, the specimens of *Thylacoleo* score less negatively on the second axis. As in the PCA, *Thylacoleo* does not cluster with other hypercarnivorous species such as pantherine felids.

As previously discussed, the forelimb development of marsupials is different from that of placentals (Weisbecker et al 2008; Sears 2009; Geiger et al. 2014), and so we made a more direct comparison of *Thylacoleo* with marsupials alone. We performed a Linear Discriminant Analysis (LDA) to determine whether *Thylacoleo* clustered with extant arboreal or terrestrial forms. The LDA yielded a function ($\lambda = 4.564$), which allowed the discrimination of the 85.7% of the taxa (MD=4.248 [$p < 0.001$]; PD=0.257 [$p < 0.001$]). In this first analysis, we included the wombats as unknowns along with the *Thylacoleo* specimens because wombats were also outliers in CVA and we were curious to see how they would be classified. All of the specimens of wombats and *Thylacoleo* cluster with terrestrial taxa (Fig. 8A). Repeating the analysis, but now including the wombats as a known terrestrial forms, provided similar results ($\lambda = 4.564$; 90.1% of the taxa correctly classified; MD=3.9179 [$p < 0.001$]; PD=0.207 [$p < 0.001$]). The shape of the distal humerus of arboreal marsupials has a long and very shallow trochlea and a “condyle-like” capitulum

(Fig. 8C, right). In contrast, the distal humerus of terrestrial marsupials is characterized by a trochlea and capitulum of similar length, and a trochlea with a large crest (Fig. 8C, left). Although the specimens of *Thylacoleo* cluster in an intermediate region between arboreal and terrestrial species in the latter analysis (Fig. 8B), all individuals were classified as terrestrial. Therefore, we can deduce that *Thylacoleo* was mainly a terrestrial animal but probably with some abilities for climbing, as revealed by the intermediate position between both ecological groups along the discriminant function. Our results are in accord with those of Wells et al. (2009), who suggested a scansorial habit for the marsupial lion, despite its large body size.

The LDAs performed from size-corrected data yielded similar results for the living species (Fig. S4), which indicates that the main axes of shape variation are not strongly influenced by allometric effects. However, the specimens of *Thylacoleo* and some of the wombat individuals now plot with the arboreal taxa (Fig. S4). Removing the effects of allometry may also erase important ecomorphological information, as body size is a strong limiting factor for arboreal behavior (e.g., Taylor 1974; Van Valkenburgh 1987). In fact, although *Thylacoleo* is not outside the body size boundaries of arboreal mammals because it was smaller than large extant apes and many extant bears, it is nevertheless a rather large animal in this respect. Furthermore, the fact that some of the wombat individuals also plot as arboreal forms, if entered as unknowns, underscores the fact that terrestrially adapted mammals may be assigned as arboreal ones if the allometric effects of body size on shape are not taken into account.

We consider that the “arboreal signal” in the elbows of both *Thylacoleo* and wombats reflects their evolutionary history rather than their actual behavior. Note also that

neither taxon plots close to the related, definitively arboreal, koala on either the PCA or the CVA.

Discussion

The results of the comparison of the elbow joint of *Thylacoleo* with other mammals lead to an interesting paleobiological question: if this animal was mostly terrestrial, then why did it retain the degree of forearm maneuverability characteristic of more arboreal forms? Wells and Nichol (1977) concluded that the manus of *Thylacoleo* had an efficient and powerful grasping mechanism, with the pseudo-opposability of digit I against the pisiform combined with a slight capacity for divergence of digit V. Case (1985) also raised the idea of the huge, clawed and possibly opposable pollex of *Thylacoleo* was related to the ability for food manipulation (Fig. 9).

We propose here that *Thylacoleo* used its high forearm maneuverability for dispatching prey, with a predatory behavior opposite to the placental carnivores with which it is usually compared. That is, while large felids use their forelimbs to grapple with prey, and use their canines to hold and kill it, we propose that *Thylacoleo* used its large, and retractable claw on the semi-opposable thumb to kill the prey, and may have used its supposedly caniniform incisors to subdue it.

Pantherine felids usually kill their prey by suffocation or neural distress, using their canines to exert a prolonged and efficient bite onto the prey's throat, snout or neck (Ewer 1973; Biknevicius and Van Valkenburgh 1996). However, there are a number of reasons to doubt that *Thylacoleo* used its "caniniform" incisors in a similar fashion.

Firstly: In felids, as in all mammals, the lower canines meet the uppers by occluding along the entire length of the anterior margin exerting a powerful piercing bite. But such piercing would be difficult with the incisors of *Thylacoleo*, as they meet tip to tip and at an

entirely different angle (see Fig. 10A). In addition, the upper incisors of *Thylacoleo* become blunt with wear, at least in old individuals (Anderson 1929; Wells et al. 1982: see Fig. 10C).

Secondly: Recent biomechanical studies of the skull of *Thylacoleo* demonstrate a weaker rostrum than in the lion (*Panthera leo*) under simulated intrinsic forces (Wroe 2008). This was interpreted as reflecting a different style of predatory behavior in *Thylacoleo* than the “clamp and hold” technique deployed by pantherine felids, although *Thylacoleo* would be able to employ its massive carnassial-like premolars to scissor through hide and flesh (Wroe 2008). However, this evidence could also support our hypothesis that the incisors were not used to administer a killing bite.

Thirdly: Extant large felids possess transversely oriented incisor rows that form protruding arcades, isolating them from the rest of the dentition to enable them to tear the flesh of their prey (Biknevicius and Van Valkenburgh 1996). It is obvious that one of these incisors functions is lacking in the marsupial lion: if the incisors were “canine-like”, then how was *Thylacoleo* able to tear the flesh and the skin of its prey? And if the incisors were not as “canine-like” as previously thought, then how did *Thylacoleo* kill its prey?

A qualitative comparison between the skulls of *Thylacoleo* and the aye-aye (*Daubentonia madagascarensis*; Fig. 10D) may provide some insights to these questions. Sir Richard Owen (1871) compared the skulls of both taxa, as their external morphological resemblance is exceptional, despite the obvious difference in size. Both mammals share, among other traits, an extreme development of the median incisors meeting at a similar occlusal angle (Owen 1871). In the aye-aye these incisors are used for gnawing holes in wood at specific points along the tree bark when the grubs that they feed on are detected (Erickson 1991), although the aye-aye has ever-growing incisors and lacks the dental

specialization towards flesh eating seen in *Thylacoleo*. The incisors of *Thylacoleo* may have been used to tear skin and flesh, rather than tree bark, a behavior leading to craniodental similarity with the aye-aye, at least in some respects.

The blunting of the incisors of *Thylacoleo* might have resulted because the skin or the flesh of its preferred prey was very hard and/or very abrasive. Fossil remains of the marsupial lion have been found associated with remains of large macropodids of the genera *Macropus* and *Sthenurus* (Horton and Wright 1981), and the exceptionally tough skin of kangaroos may have posed particular problems for their predators. Note that the leather of the large macropodine kangaroos (*Macropus giganteus* and *Macropus rufus*) is unique because it offers high strength while remaining lightweight and flexible. For this reason kangaroo leather is used for high performance sporting products (Looney et al. 2002). Thus a carnivore specialized for killing kangaroos might face different challenges in removing the skin to one specialized for killing ungulates.

All of these evidences indicate that the “caniniform” incisors of *Thylacoleo* were not adapted to administering a killing bite, although they may have been used to hold and/or subdue the prey, as well as to bite through hide and flesh. However, the angle and position of these incisors have been interpreted as precluding their use for holding (Gill 1954: see Fig. 10B). If the incisors could not be used to subdue the prey, the flexibility of the forearm may have also been important in use for grappling, as well as administering a killing slash with the claw on the pollux.

Conclusions

The determination of the behavior of an extinct animal is always a challenge for paleobiologists, especially when living relatives and/or ecological analogs are absent. This

is the case for the Australian “marsupial lion”, *Thylacoleo carnifex*, whose behavior and ecology has been a matter of debate since Richard Owen’s 1871 description, and it is often assumed to have had felid-like behavior. The skull of *Thylacoleo* is superficially cat-like, and large “carnassial” teeth indicate a carnivorous diet: but the marsupial lion lacks large canines, and the proposed “caniniform” incisors seem to be not well equipped to administer a killing bite. *Thylacoleo* also possessed a greatly enlarged claw on the pollux (Wells and Nichol 1977; Finch and Freedman 1988) and wrist anatomy (Weisbecker and Archer 2008) on a highly mobile forelimb. How, then, did *Thylacoleo* kill its prey?

The osteological design of *Thylacoleo* is unique among mammals, and predatory behavior is an ecological aspect that cannot be inferred from other ecophysiological methods. Our ecomorphological analysis of the elbow-joint morphology of *Thylacoleo* sheds light on how it may have dispatched its prey. We show here that *Thylacoleo* could perform a much greater degree of supination of the manus than seen in extant carnivorous mammals, permitted by a distal humeral articular surface with a large and very shallow trochlea and a “condyle-like” rounded capitulum. This exceptional maneuverability of the *Thylacoleo* forearm, in combination with the possession of an extremely large hooded and retractable claw on the semi-opposable thumb (Wells and Nichol 1977), is suggestive of a “prey-killing arsenal” (Meachen-Samuels 2012) very different to any other known hypercarnivore, extant or extinct. We propose that the robust, powerfully built and “claw equipped” forelimb of *Thylacoleo* (Wroe et al. 2008) played a more active role for dispatching large prey than in living predators (Cox and Jefferson 1988; Londei 2000; Weisbecker and Archer 2008). The extensive use of the forelimb most probably evolved because its canine-like incisors were not as efficient for prey killing as the true canines of pantherine felids (e.g., Anderson 1929; Gregory 1951; Gill 1954; Wells et al. 1982).

Perhaps with the possession of this claw, the inherited mobile forelimb from a vombatiform arboreal ancestor (Weisbecker and Archer 2008), and the presence of prominent carnassial teeth (Wroe 2008), it was not necessary to develop large canines.

While the predatory behavior of *Thylacoleo* will never be known for certain, the use of morphometric techniques allows us to infer the probable ecomorphology of this enigmatic predator. Our main conclusion is that *Thylacoleo* did not have the predatory behavior of an extant large felid as has been traditionally suggested (Owen 1859, and many subsequent authors). Our results demonstrate that the forelimb mobility of this animal was unlike that of any known terrestrial mammal: the documented ability for supinating the hand, in combination with the enormous sheathed claw on a semi-opposable pollux, raises the distinct possibility that this claw was deployed as the mode of killing the prey. In addition, despite the evidence for a powerful bite, the mode of occlusion and the wear on the “caniniform” incisors make it unlikely that the incisors were deployed for a killing bite, although they may well have been involved in subduing the prey and/or tearing into the carcass. Thus it is apparent that *Thylacoleo*, despite being called the marsupial “lion” probably represent a unique type of predator ecomorph.

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Figure 1. Anterior surface of the humerus distal epiphysis (proxy for elbow-joint shape). A, elbow joints (distal humeri) of the three specimens of *Thylacoleo carnifex* sampled. From left to right: SAMP-12384a (reversed), SAMP-12384b, SAMP-12384c (reversed). Scale bar equals 3cm. B, elbow joints of different species of placental and marsupials used for comparison. First line (from left to right): koala (*Phascolarctos cinereus*), wombat (*Vombatus ursinus*) and Tasmanian devil (*Sarcophilus harrisi*). Second line (from left to right): Tasmanian tiger (*Thylacinus cynocephalus*), F, Hoffmann's two-toed sloth (*Choloepus hoffmanni*) and placental tiger (*Panthera tigris*). The area of the trochlea is represented in light grey (in blue in the on-line version) and the area of the capitulum is represented in dark grey (in pink in the on-line version). Scale bar equals 1cm.

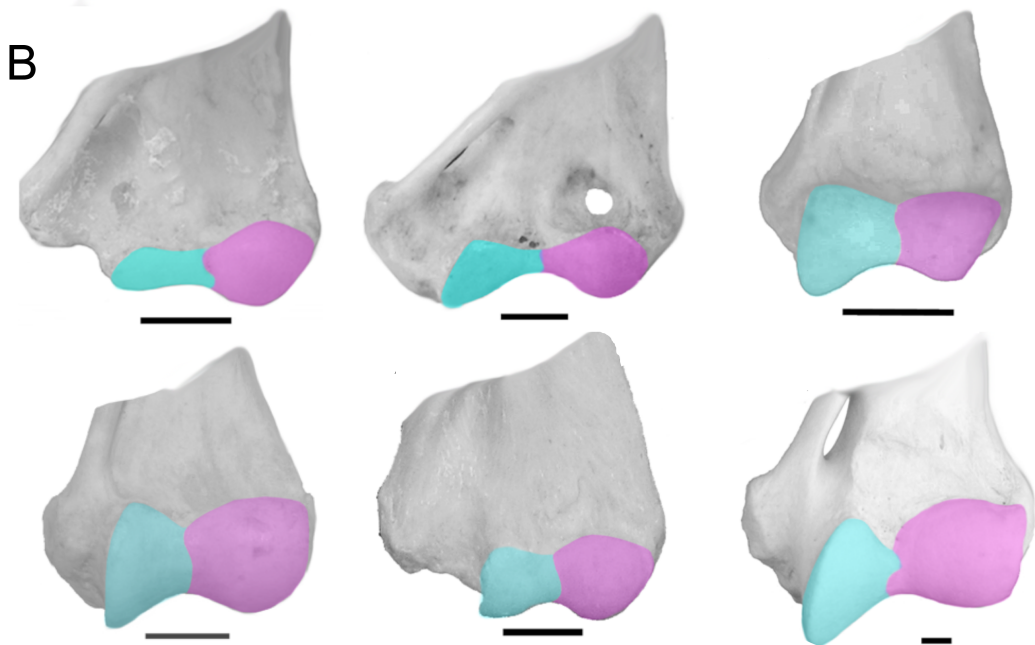


Figure 2. Morphometric data collected for analysis. A, elbow-joint shape of the marsupial lion (*Thylacoleo*) showing anatomical features. B, six landmarks digitized on the high-resolution digital images to recover the shape of the elbow joint. The area of the trochlea is represented in light grey (in blue in the on-line version) and the area of the capitulum is represented in dark grey (in pink in the on-line version). Scale bar equals 3cm.

Abbreviations: *ca*, capitulum; *ef*, entepicondylar foramen; *le*, lateral epicondyle; *me*, medial epicondyle; *rf*, radial fossa; *tr*, trochlea; *trc*, trochlea crest (or groove).

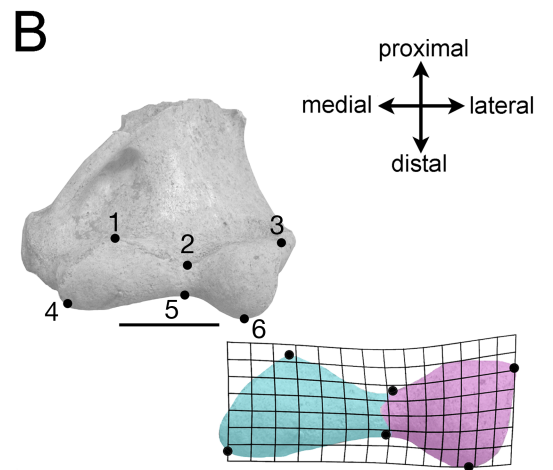
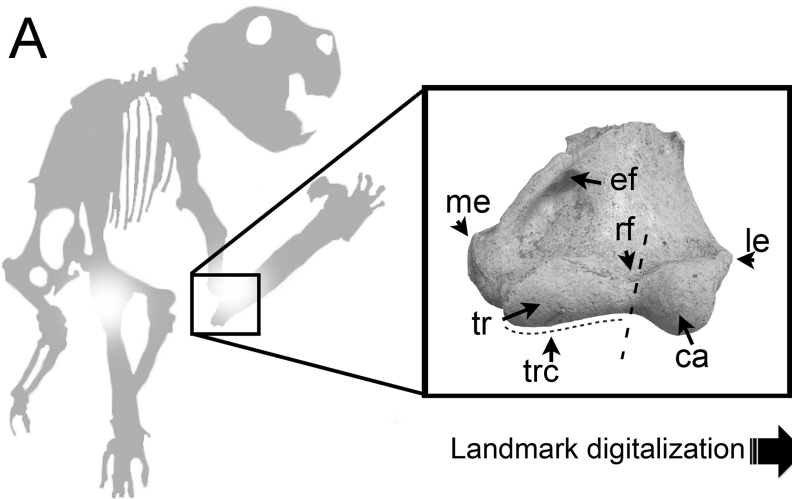


Figure 3. Phylogeny used in this study. The main tree topology is based on Bininda Emonds et al. (2007). The phylogenetic relationships for the Carnivora are based on Nyakatura and Bininda-Emonds (2012) and for the Primates on the updated consensus 10 kTree Website (ver.3; <http://10ktrees.fas.harvard.edu/>) (Arnold et al. 2010). The phylogenetic relationships for marsupials were taken from Johnson (2014). Node numbers refer to the ancestral shapes reconstructed in Figure 4.

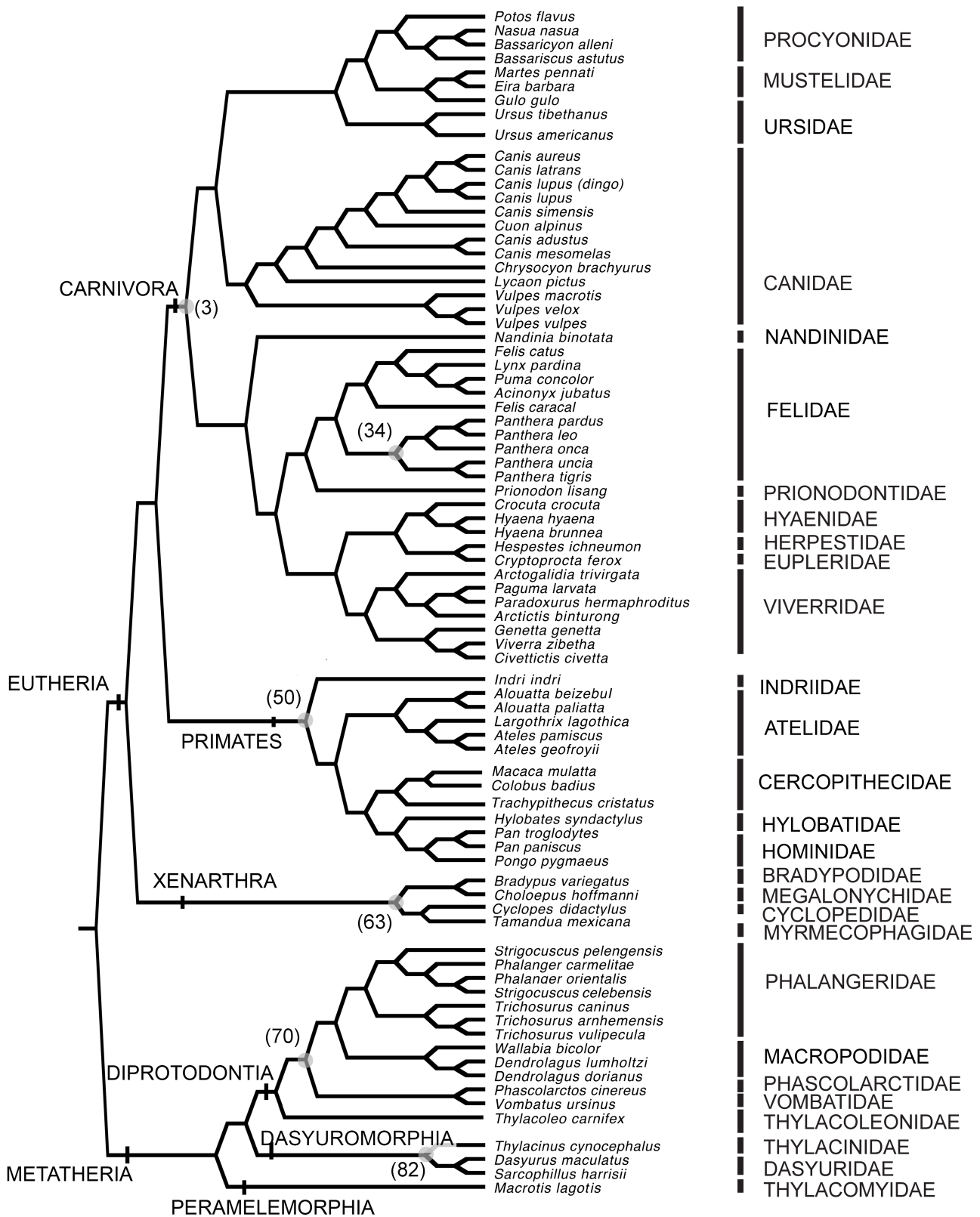


Figure 4. Multivariate regression of elbow shape on size. A, interspecific allometry regression analysis of the 81 species analyzed in this study. The 95% confidence ellipses for placentals and marsupials are also shown. B, evolutionary allometry regression analysis of the contrast of elbow shape on the contrast of size. In both cases the thin plate spline diagrams represent size-related shape changes accounted for each regression vector shown as deviations from the average shape (grey dots) to the predicted shape change over one unit of centroid size (black dots); the lollipops indicate the corresponding landmark shift.

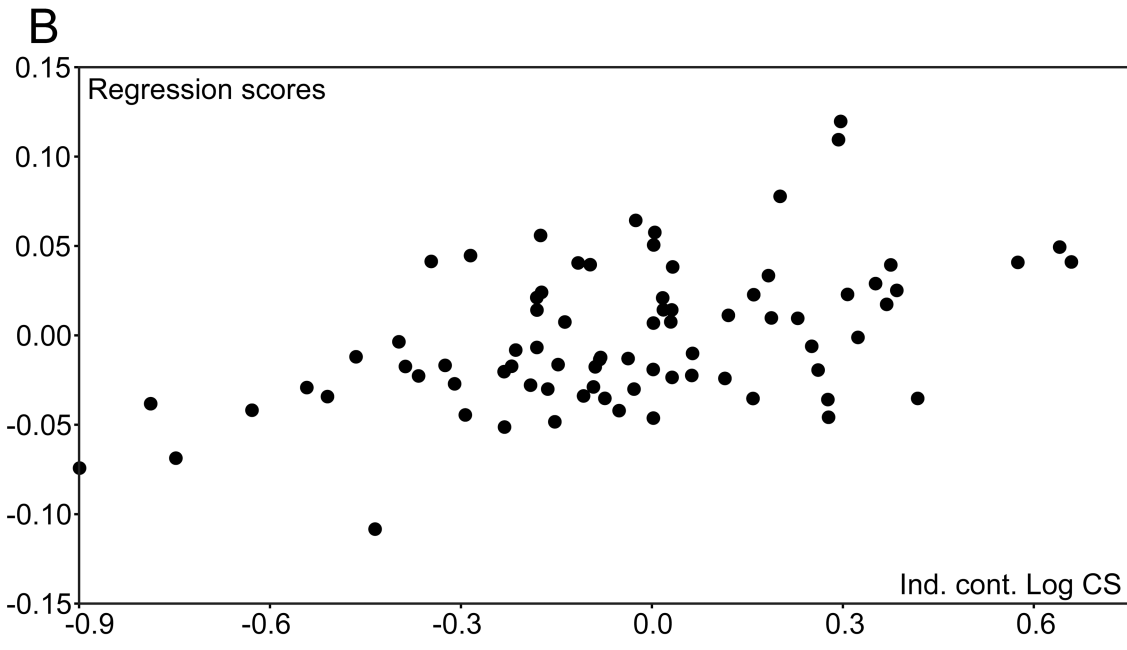
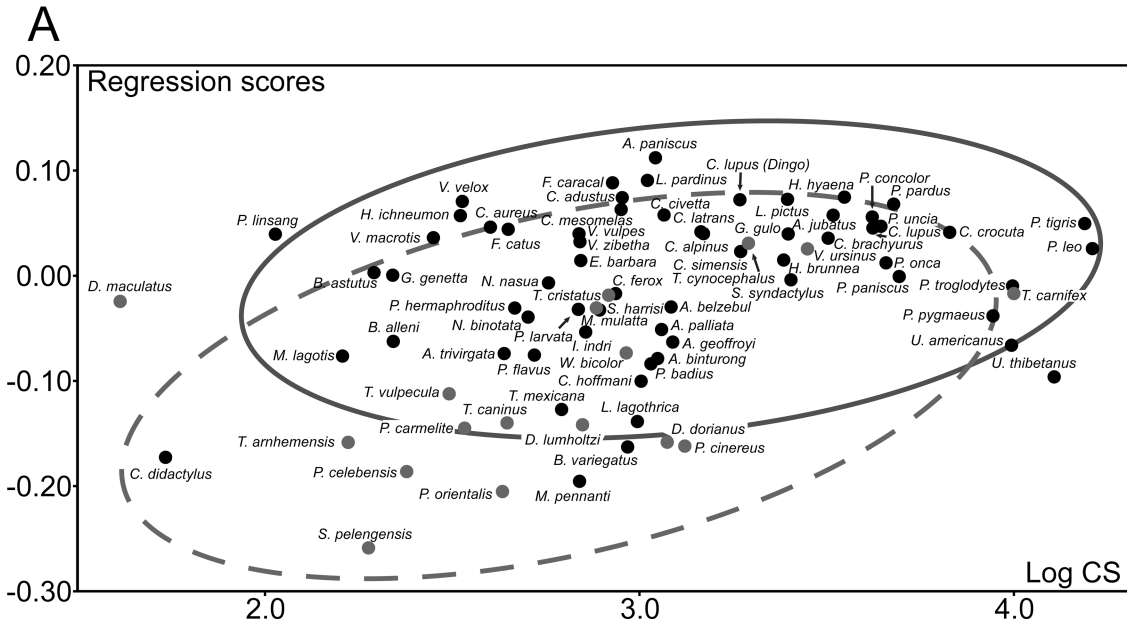


Figure 5. Morphometric comparison of the elbow-joint anatomy of *Thylacoleo* with other taxa and hypothetical shapes. The diagrams represent deformation grids showing the morphological change obtained from the elbow of *Thylacoleo* (black outline) to the elbow of: A, the koala (*Phascolarctos cinereus*). B, The wombat (*Vombatus ursinus*); C, The ancestral state for extant diprotodontians (Node 70, Fig. 3); D, The ancestral state for dasyuromorphians (Node 82, Fig. 3); E, The ancestral state for xenarthrans (Node 70, Fig. 63); F, The ancestral state for primates (Node 50, Fig. 3); G, The ancestral state for all carnivorans (Node 3, Fig. 3); and H, The ancestral state for pantherine felids (Node 34, Fig. 3). The ancestral states (shapes of the internal nodes) were inferred using squared-change parsimony (see text for details). Note that as the branch lengths were not included, the reconstructed ancestral shapes could be considered as an average or a consensus shape for the group.

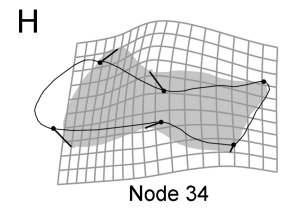
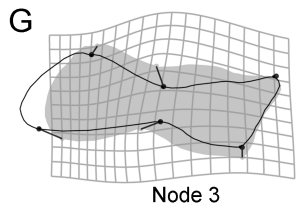
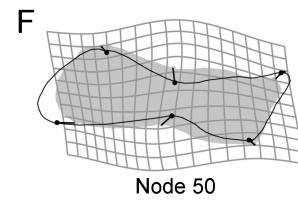
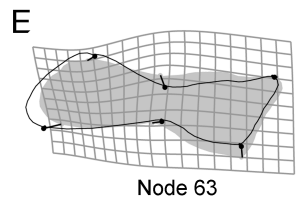
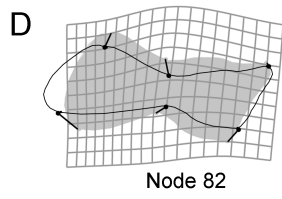
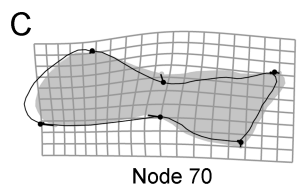
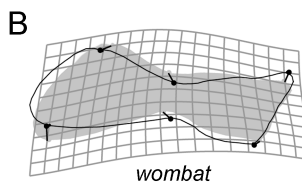
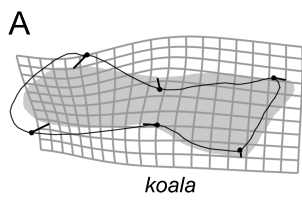


Figure 6. Principal Components Analysis (PCA) performed on the shape of the elbow of living mammals and *Thylacoleo*. A, Morphospace depicted from the scores of the species on the first two eigenvectors. The 95% confidence ellipses for placentals and marsupials are also shown. B, The thin plate spline diagrams representing the shape changes accounted for each PC are shown as deviations from the average or consensus shape (0.0) in each PC (grey straight lines) to the target shapes (black dots). The warping outline of each reconstructed elbow shape is shown for clarity. C, Projection of the phylogenetic tree topology of Figure 3 onto the phenotypic space depicted from the first two principal components (PCs) of elbow shape.

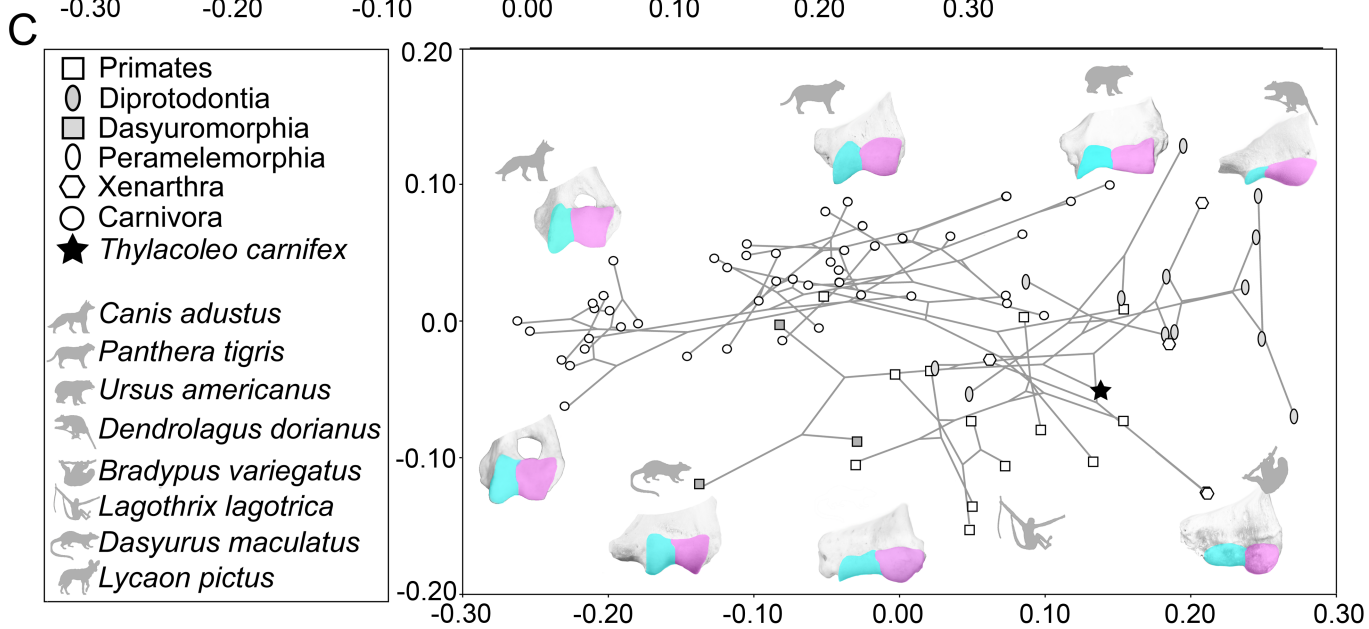
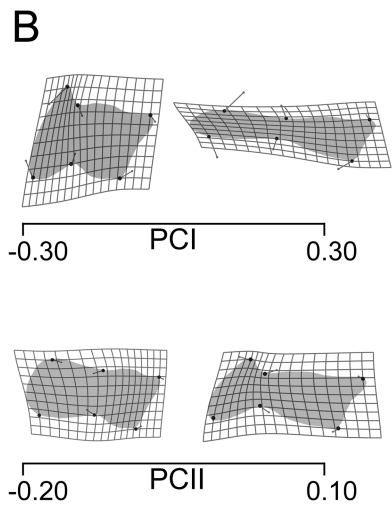
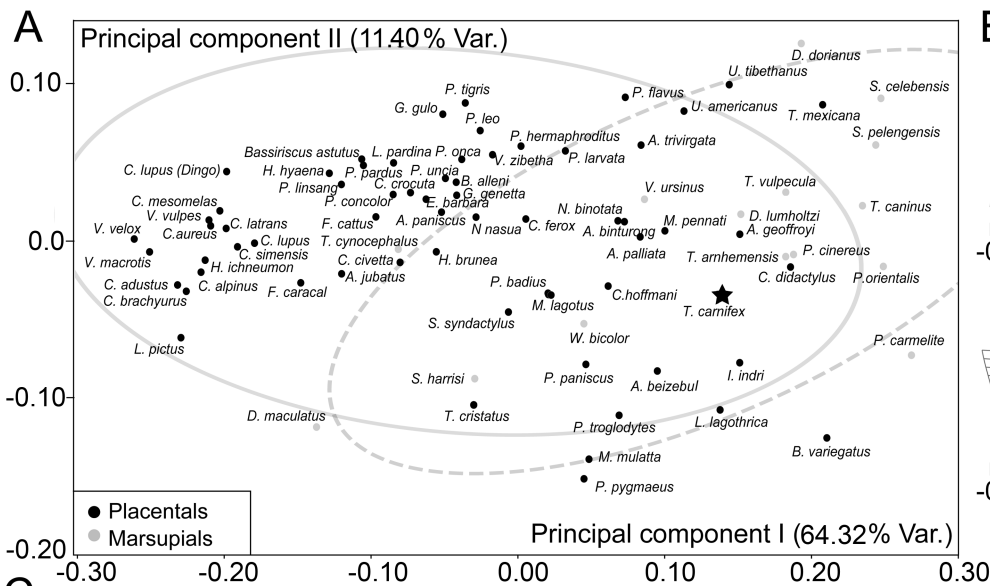


Figure 7. Canonical variates analysis (CVA) performed to determine elbow shape features that best distinguish mammals with high mobility of the forearm from those with medium mobility and low mobility. A, Pairwise plot depicted from the scores on both canonical axes obtained for the CVA. B, The thin plate spline diagrams for each canonical function are shown as deviations from the average or consensus shape (0.0) in each discriminant function (grey straight lines) to the target shapes (black dots). The warping outline of each reconstructed elbow shape is also shown for clarity.

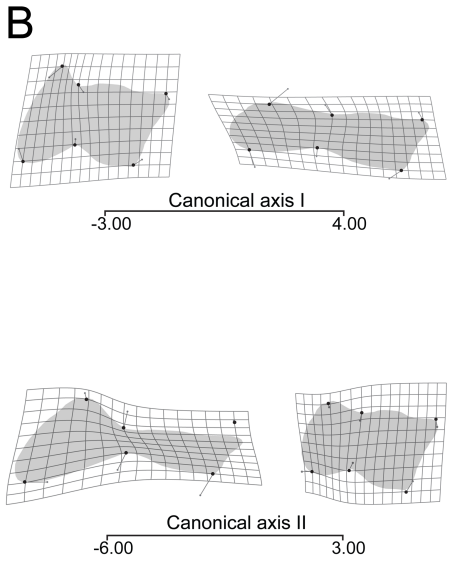
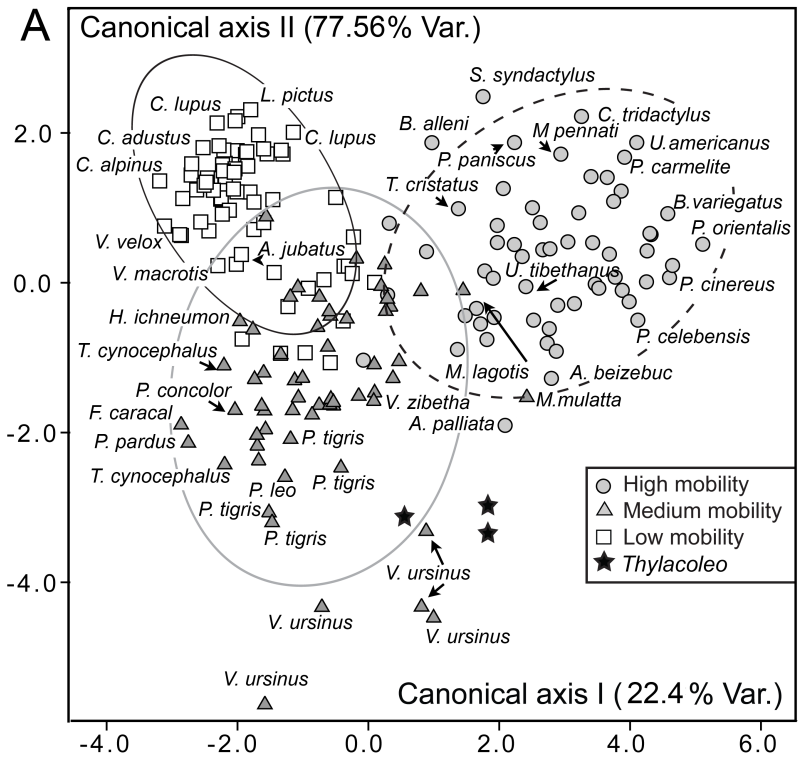


Figure 8. Linear Discriminant Analyses (LDA) performed from the shape of the elbow joint of marsupials and placentals to investigate the most probable substrate use of *T. carnifex*. A, Discriminant function obtained from the LDA performed from the elbow shape of marsupials only, excluding the wombats from the function, and included in the analysis as unknowns, to discriminate between arboreal and terrestrial forms. B, Discriminant function obtained from the LDA performed from the elbow shape of marsupials, now including the wombats as known terrestrial species into the function, to discriminate between arboreal and terrestrial forms. C, Thin plate spline diagrams for arboreal and terrestrial forms shown as deviations from the consensus shape (grey dots) to the target shapes (black dots) obtained from the analysis of B. The warping outline of each reconstructed elbow shape is also shown for clarity.

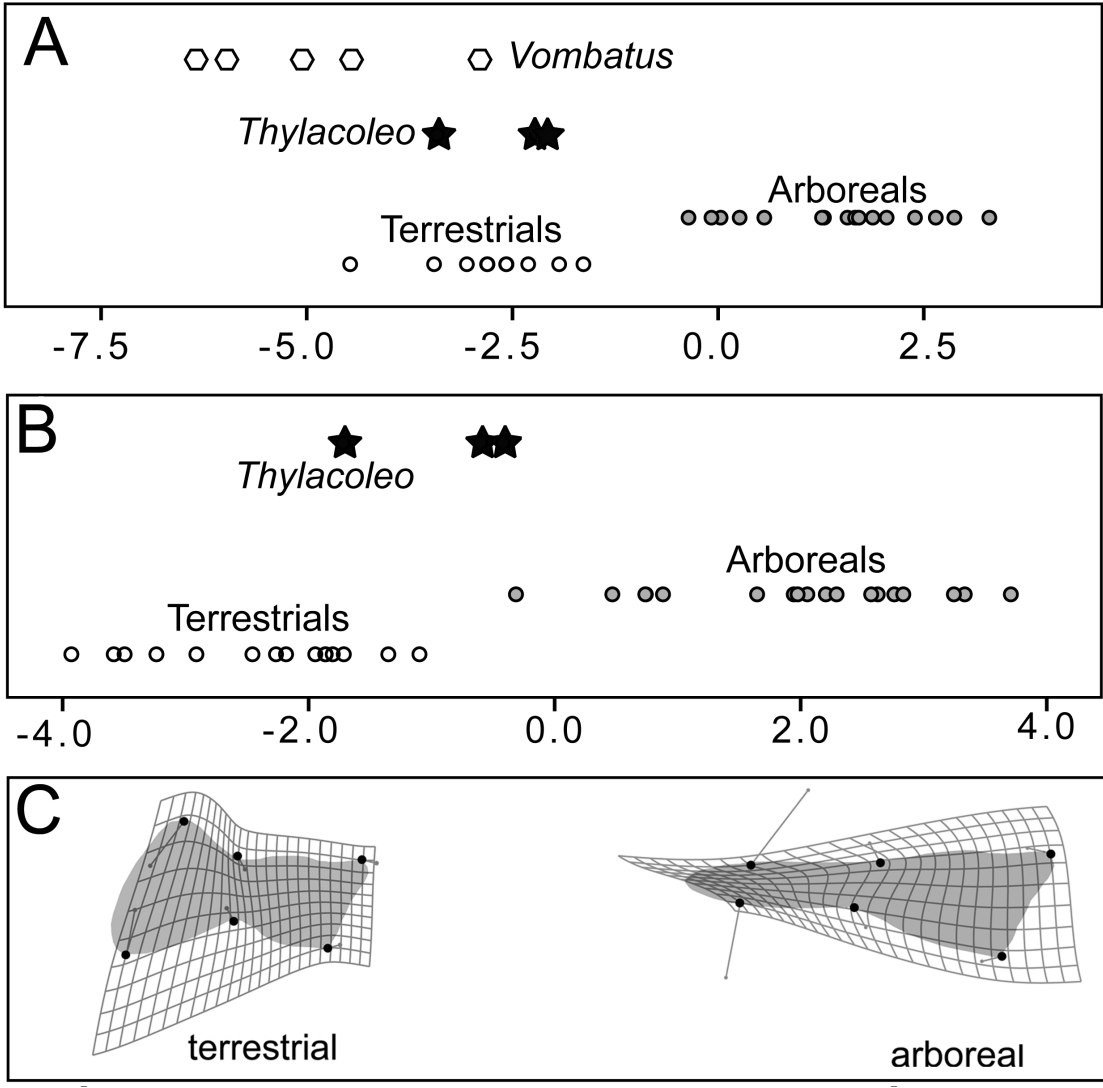


Figure 9. The manus of *Thylacoleo* showing hypothesized movements of the pollex. A, Right manus with digits II to V flexed and digit I showing the flexion-extension movement in medial (A) and dorsal views (B). Redrawn and modified from Wells and Nichol (1977). Medial (C) and dorsal (D) views of the right manus. Specimen P16679 from Victoria Fossil cave.

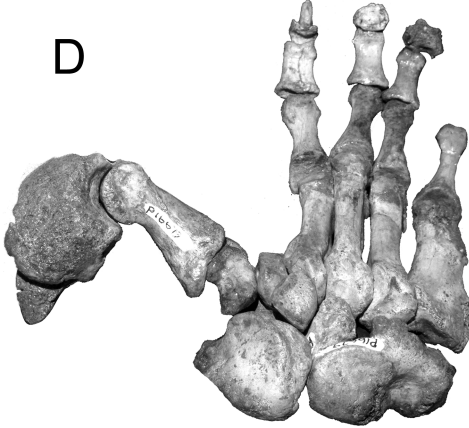
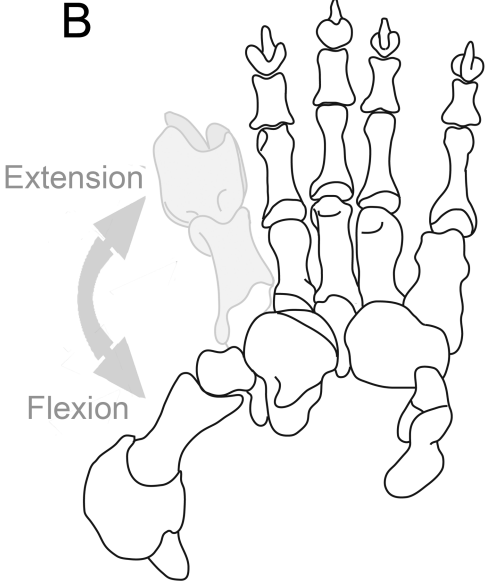
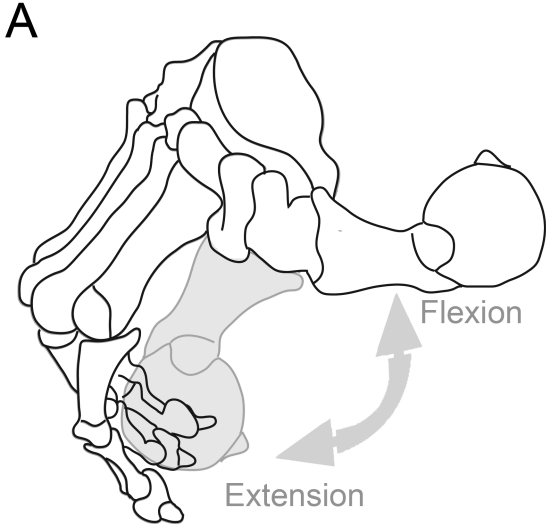


Figure 10. Aspects of the craniodental anatomy of *Thylacoleo*. A, Schematic drawing showing the hypothesis of Anderson (1929): the non-parallel, convergent nature of the incisors of *Thylacoleo* (left) would preclude them meeting as in a placental carnivore such as a lion (right). B, Schematic drawing showing the hypothesis of Gill (1954): the angle and position of the incisors of *Thylacoleo* may preclude their use for holding prey. The arrows indicate points for holding a hypothetical prey item (rectangle). C, Ventral view of the skull of *Thylacoleo* (specimen AMNH 19251 from Queensland) illustrating the heavy wear in the upper incisors. Scale bar 1 cm. D, Skull anatomy of *Daubentonia* (MCZ 45946). Scale bar = 3 cm.

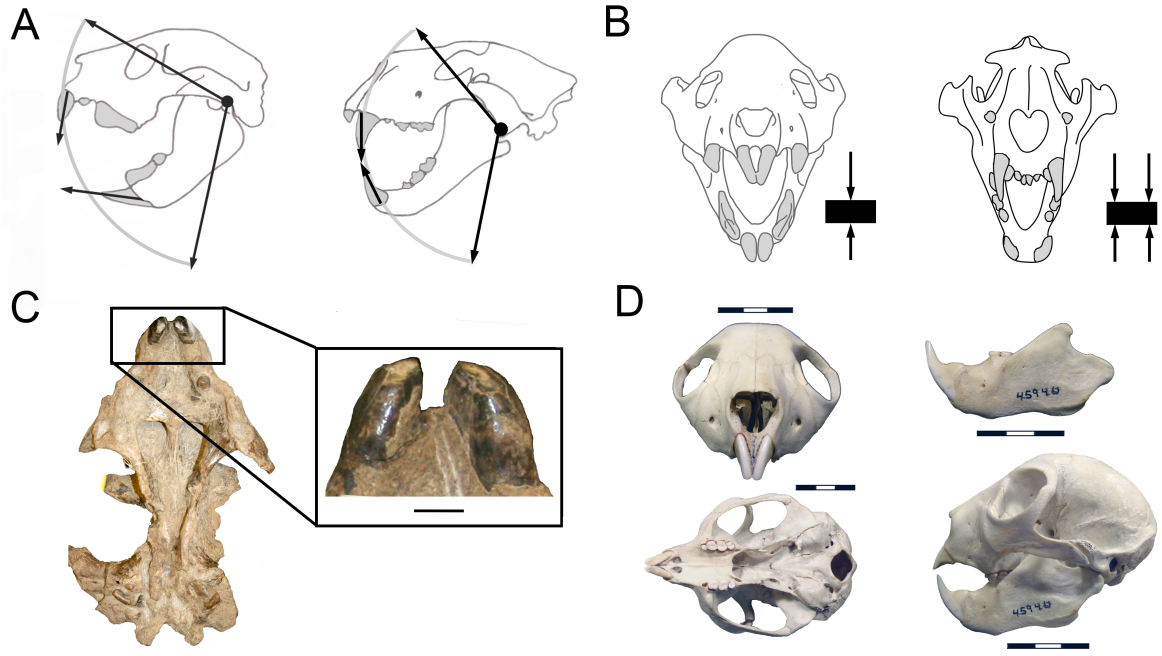


Table 1. Sample size used in this study. The ecological categories used in CVA and LDA are also shown. Bibliographic sources: 1, Samuels et al. (2013); 2, McDonald (1984); 3, Nowak (1999); 4, Gompper and Decker (1998); 5, Meachen-Samuels and Van Valkenburgh (2009); 6, Hayssen (2010); 7, Quinn and Wilson (2002); 8, Jones et al. (1996); 9, Groves (1971); 10, Jones et al. (2001); 11, Jones (2003); 12 Jones and Stoddart (1998); 13, Procter-Gray and Ganslosser (1986); 14, Lindenmayer et al. (1999); 15, Johnson and Johnson (1983); 16, Iwaniuk et al. (2000); 17, Wilson and Mittermeier (2009); 18, Poglajen-Neuwall and Toweill (1988); 19, Andersson and Werdelin (2003); 20, Sillero-Zubiri and Marino (2004); 21, Powell (1981); 22, Taylor (1974); 23, Gebo and Rose (1993); 24, Ford and Hoffmann (1988); 25, Mendel (1985); 26, Mendel (1981); 27, White (1993); 28, Taylor (1978); 29, Youlatos (1996); 30, O'Connor and Rarey (1979); 31, Figueirido and Janis (2011); 32, Warburton et al. (2011); 33, Grand and Barboza (2001). For the museum numbers see Table S1. Daggers denotate extinct taxa.

SPECIES	COMMON NAME	N	ORDER	FAMILY	ECOLOGY	FOREARM MOBILITY
<i>Acinonyx jubatus</i>	Cheetah	6	Carnivora	Felidae	Terrestrial ¹	Low ¹⁶
<i>Alouatta beizebul</i>	Red-handed howler monkey	1	Primates	Atelidae	Arboreal ³	High ²⁹
<i>Alouatta palliata</i>	Mantled howler monkey	1	Primates	Atelidae	Arboreal ³	High ²⁹
<i>Arctictis binturong</i>	Binturong (bearcat)	2	Carnivora	Viverridae	Arboreal ¹	High ¹⁶
<i>Arctogalidia trivirgata</i>	Small-toothed palm civet	3	Carnivora	Viverridae	Arboreal ^{2,3}	High ¹⁷
<i>Ateles geoffroyi</i>	Geoffroy's spider monkey	1	Primates	Atelidae	Arboreal ³	High ²⁹
<i>Ateles paniscus</i>	Black spider monkey	1	Primates	Atelidae	Arboreal ³	High ²⁹
<i>Bassaricyon alleni</i>	Allen's oligo	1	Carnivora	Procyonidae	Arboreal ³	High ³
<i>Bassariscus astutus</i>	Ringtail "cat"	1	Carnivora	Procyonidae	Arboreal ¹	High ¹⁸
<i>Bradypus variegatus</i>	Brown-throated three-toed sloth	1	Pilosa	Bradypodidae	Arboreal ⁶	High ²⁵
<i>Canis adustus</i>	Side-striped jackel	5	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Canis aureus</i>	Golden jackel	3	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Canis latrans</i>	Coyote	4	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Canis lupus</i>	Wolf	10	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Canis lupus (dingo)</i>	Dingo	2	Carnivora	Canidae	Terrestrial ¹	Low ¹⁶
<i>Canis mesomelas</i>	Black-backed jackel	5	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Canis simensis</i>	Ethiopian wolf	1	Carnivora	Canidae	Terrestrial ¹	Low ²⁰
<i>Choloepus hoffmani</i>	Hoffman's two-toed sloth	1	Pilosa	Megalonychidae	Arboreal ³	High ²⁶
<i>Chrysosyon brachyurus</i>	Maned wolf	2	Carnivora	Canidae	Terrestrial ¹	Low ¹⁶
<i>Civettictis civetta</i>	African civet	1	Carnivora	Viverridae	Terrestrial ¹	Medium ¹⁷
<i>Crocuta crocuta</i>	Spotted hyena	9	Carnivora	Hyaenidae	Terrestrial ¹	Low ¹⁹
<i>Cryptoprocta ferox</i>	Fossa	1	Carnivora	Eupleridae	Arboreal ¹	High ¹⁶
<i>Cuon alpinus</i>	Dhole	3	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Cyclopes didactylus</i>	Pygmy anteater	1	Pilosa	Cyclopedidae	Arboreal ³	High ²⁷
<i>Dasyurus maculatus</i>	Spotted quoll	1	Dasyuromorphia	Dasyuridae	Arboreal ¹⁰	Medium ³
<i>Dendrolagus dorianus</i>	Doria's tree-kangaroo	1	Diprotodontia	Macropodidae	Arboreal ¹³	High ³²

<i>Dendrolagus lumholtzi</i>	Lumholtz's tree-kangaroo	2	Diprotodontia	Macropodidae	Arboreal ¹³	High ³²
<i>Eira barbara</i>	Tayra	3	Carnivora	Mustelidae	Arboreal ¹	Medium ¹⁶
<i>Felis caracal</i>	Caracal	3	Carnivora	Felidae	Terrestrial ¹	Medium ¹⁶
<i>Felis catus</i>	Domestic cat	1	Carnivora	Felidae	Arboreal ¹	Medium ¹⁷
<i>Genetta genetta</i>	Common genet	3	Carnivora	Viverridae	Arboreal ¹	Medium ¹⁶
<i>Gulo gulo</i>	Wolverine	3	Carnivora	Mustelidae	Terrestrial ¹	Medium ¹⁶
<i>Herpestes ichneumon</i>	Egyptian mongoos	1	Carnivora	Herpestidae	Terrestrial ¹	Medium ¹⁷
<i>Hyaena brunea</i>	Brown hyena	1	Carnivora	Hyenidae	Terrestrial ¹	Low ¹⁹
<i>Hyaena hyaena</i>	Striped hyena	3	Carnivora	Hyaenidae	Terrestrial ¹	Low ¹⁹
<i>Indri indri</i>	Indri	1	Primates	Indriidae	Arboreal ⁷	High ⁷
<i>Lagothrix lagothrica</i>	Brown woolly monkey	3	Primates	Atelidae	Arboreal ³	High ³¹
<i>Lycaon pictus</i>	Hunting dog	5	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Lynx pardina</i>	Iberian lynx	1	Carnivora	Felidae	Terrestrial ¹	Medium ¹⁹
<i>Macaca mulatta</i>	Rhesus macaque	1	Primates	Cercopithecidae	Arboreal ³	Medium ³⁰
<i>Macrotis lagotis</i>	Greater bilby	1	Peramelemorphia	Thylacomyidae	Terrestrial ¹⁵	High ³
<i>Martes pennanti</i>	Fisher	1	Carnivora	Mustelidae	Arboreal ¹	High ²¹
<i>Nandinia binotata</i>	African palm civet	1	Carnivora	Nandinidae	Arboreal ³	High ²²
<i>Nasua nasua</i>	South American coati	1	Carnivora	Procyonidae	Arboreal ⁴	Medium ⁴
<i>Paguma larvata</i>	Masked palm civet	2	Carnivora	Viverridae	Arboreal ¹	High ²³
<i>Pan paniscus</i>	Bonobo	1	Primates	Hominidae	Arboreal ³	High ³⁰
<i>Pan troglodytes</i>	Chimpanzee	4	Primates	Hominidae	Arboreal ⁸	High ³⁰
<i>Panthera leo</i>	Lion	3	Carnivora	Felidae	Terrestrial ¹	Medium ¹⁶
<i>Panthera onca</i>	Jaguar	4	Carnivora	Felidae	Arboreal ⁵	Medium ¹⁶
<i>Panthera pardus</i>	Leopard	2	Carnivora	Felidae	Arboreal ⁵	Medium ¹⁶
<i>Panthera tigris</i>	Tiger	7	Carnivora	Felidae	Terrestrial ⁵	Medium ¹⁶
<i>Panthera uncia</i>	Snow leopard	4	Carnivora	Felidae	Arboreal ¹	Medium ¹⁶
<i>Paradoxurus hermaphroditus</i>	Asian palm civet	1	Carnivora	Viverridae	Arboreal ¹	Medium ¹⁷
<i>Phalanger carmelite</i>	Mountain cuscus	1	Diprotodontia	Phalangeridae	Arboreal ³	High ³

<i>Strigocuscus celebensis</i>	Small Sulawesi cuscus	1	Diprotodontia	Phalangeridae	Arboreal ³	High ³
<i>Phalanger orientalis</i>	Northern common cuscus	2	Diprotodontia	Phalangeridae	Arboreal ³	High ³
<i>Phascolarctos cinereus</i>	Koala	4	Diprotodontia	Phascolarctidae	Arboreal ³	High ³³
<i>Pongo pygmaeus</i>	Orangutan	2	Primates	Hominidae	Arboreal ⁹	High ³⁰
<i>Potos flavus</i>	Kinkajou	1	Carnivora	Procyonidae	Arboreal ¹	High ²⁴
<i>Prionodon linsang</i>	Banded linsang	1	Carnivora	Prionodontinae	Arboreal ¹	Medium ¹⁷
<i>Procolobus badius</i>	Western red colobus	1	Primates	Cercopithecidae	Arboreal ³	High ³⁰
<i>Puma concolor</i>	Puma	4	Carnivora	Felidae	Terrestrial ¹	Medium ¹⁶
<i>Sarcophilus harrisii</i>	Tasmanian devil	1	Dasyuromorphia	Dasyuridae	Terrestrial ¹¹	Medium ³
<i>Strigocuscus pelengensis</i>	Banggai cuscus	1	Diprotodontia	Phalangeridae	Arboreal ³	High ³
<i>Symphalangus syndactylus</i>	Siamang	1	Primates	Hylobatidae	Arboreal ³	High ³⁰
<i>Trachypithecus cristatus</i>	Silvery langur	1	Primates	Cercopithecidae	Arboreal ³	High ³⁰
<i>Tamandua mexicana</i>	Northern tamandua	1	Pilosa	Myrmecophagidae	Arboreal ³	High ²⁸
<i>Thylacinus cynocephalus</i>	Thylacine or Tasmanian tiger	8	Dasyuromorphia	Thylacinidae	Terrestrial ¹²	Medium ³¹
<i>Thylacoleo carnifex</i> †	Marsupial lion	3	Diprotodontia	Thylacoleonidae	Unknown	Unknown
<i>Trichosurus arnhemensis</i>	Northern brushtail possum	1	Diprotodontia	Phalangeridae	Arboreal ³	High ³
<i>Trichosurus caninus</i>	Short-eared possum	2	Diprotodontia	Phalangeridae	Arboreal ³	High ³
<i>Trichosurus vulpecula</i>	Common brushtail possum	1	Diprotodontia	Phalangeridae	Arboreal ¹⁴	High ³
<i>Ursus americanus</i>	American black bear	4	Carnivora	Ursidae	Arboreal ¹	High ¹⁶
<i>Ursus tibethanus</i>	Asiatic black bear	3	Carnivora	Ursidae	Arboreal ¹	High ¹⁶
<i>Viverra zibetha</i>	Large Indian civet	1	Carnivora	Viverridae	Terrestrial ¹	Medium ¹⁷
<i>Vombatus ursinus</i>	Common wombat	5	Diprotodontia	Vombatidae	Terrestrial ³	Medium ³³
<i>Vulpes macrotis</i>	Kit fox	1	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Vulpes velox</i>	Swift fox	2	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Vulpes vulpes</i>	Red fox	5	Carnivora	Canidae	Terrestrial ¹	Low ¹⁹
<i>Wallabia bicolor</i>	Swamp wallaby	1	Diprotodontia	Macropodidae	Terrestrial ³	High ²

Table 2. Results of the Canonical Variates Analyses (CVA) performed from the Procrustes coordinates describing elbow shape to separate among high, medium and low elbow mobility groups. Numbers in bold type indicate Mahalanobis distances among pairs of groups (and the associated p -values) and in thin type Procrustes distances (and the associated p -values).

	High	Medium
Medium	2.74 ($p < 0.0001$) 0.15 ($p < 0.0001$)	
Low	4.68 ($p < 0.0001$) 0.29 ($p < 0.0001$)	3.98 ($p < 0.0001$) 0.18 ($p < 0.0001$)

SUPPLEMENTARY MATERIAL

Table S1. Sample used in this study.

	SPECIES	NUMBER	ORDER	FAMILY
1	<i>Acinonyx jubatus</i>	AMNH 119656	Carnivora	Felidae
2	<i>Acinonyx jubatus</i>	AMNH 119682	Carnivora	Felidae
3	<i>Acinonyx jubatus</i>	AMNH 119655	Carnivora	Felidae
4	<i>Acinonyx jubatus</i>	AMNH 80172	Carnivora	Felidae
5	<i>Acinonyx jubatus</i>	MCZ 13667	Carnivora	Felidae
6	<i>Acinonyx jubatus</i>	MCZ 59279	Carnivora	Felidae
7	<i>Alouatta beizebuc</i>	AMNH 133544	Primates	Atelidae
8	<i>Alouatta palliata</i>	MCZ 47261	Primates	Atelidae
9	<i>Arctictis binturong</i>	MCZ 35594	Carnivora	Viverridae
10	<i>Arctictis binturong</i>	MCZ 5107	Carnivora	Viverridae
11	<i>Arctogalidia trivirgata</i>	MCZ 35899	Carnivora	Viverridae
12	<i>Arctogalidia trivirgata</i>	MCZ 35915	Carnivora	Viverridae
13	<i>Arctogalidia trivirgata</i>	MCZ 35927	Carnivora	Viverridae
14	<i>Ateles geoffroyi</i>	MCZ 45145	Primates	Atelidae
15	<i>Ateles paniscus</i>	AMNH 35709	Primates	Atelidae
16	<i>Bassaricyon alleni</i>	MCZ 37922	Carnivora	Procyonidae
17	<i>Bassiriscus astutus</i>	MCZ 42161	Carnivora	Procyonidae
18	<i>Bradypus variegatus</i>	MCZ 5015	Pilosa	Bradypodidae
19	<i>Canis adustus</i>	AMNH 114174	Carnivora	Canidae
20	<i>Canis adustus</i>	AMNH 216334	Carnivora	Canidae
21	<i>Canis adustus</i>	AMNH 33322	Carnivora	Canidae
22	<i>Canis adustus</i>	AMNH 52049	Carnivora	Canidae
23	<i>Canis adustus</i>	AMNH 80662	Carnivora	Canidae
24	<i>Canis aureus</i>	AMNH 187144	Carnivora	Canidae
25	<i>Canis aureus</i>	AMNH 27741	Carnivora	Canidae
26	<i>Canis aureus</i>	AMNH 54516	Carnivora	Canidae
27	<i>Canis latrans</i>	AMNH 123036	Carnivora	Canidae
28	<i>Canis latrans</i>	AMNH 131833	Carnivora	Canidae
29	<i>Canis latrans</i>	AMNH 136419	Carnivora	Canidae
30	<i>Canis latrans</i>	AMNH 99653	Carnivora	Canidae
31	<i>Canis lupus</i>	MCZ 62196	Carnivora	Canidae
32	<i>Canis lupus</i>	AMNH 134940	Carnivora	Canidae
33	<i>Canis lupus</i>	AMNH 244144	Carnivora	Canidae
34	<i>Canis lupus</i>	AMNH 98225	Carnivora	Canidae
35	<i>Canis lupus</i>	AMNH 98226	Carnivora	Canidae
36	<i>Canis lupus</i>	AMNH 98230	Carnivora	Canidae
37	<i>Canis lupus</i>	MCZ 56612	Carnivora	Canidae
38	<i>Canis lupus</i>	MCZ 50518	Carnivora	Canidae
39	<i>Canis lupus</i>	MCZ 56610	Carnivora	Canidae
40	<i>Canis lupus</i>	MCZ 62506	Carnivora	Canidae

41	<i>Canis lupus (Dingo)</i>	MCZ 21591	Carnivora	Canidae
42	<i>Canis lupus (Dingo)</i>	MCZ 21590	Carnivora	Canidae
43	<i>Canis mesomelas</i>	AMNH 187711	Carnivora	Canidae
44	<i>Canis mesomelas</i>	AMNH 114228	Carnivora	Canidae
45	<i>Canis mesomelas</i>	AMNH 34731	Carnivora	Canidae
46	<i>Canis mesomelas</i>	AMNH 34732	Carnivora	Canidae
47	<i>Canis mesomelas</i>	AMNH 54209	Carnivora	Canidae
48	<i>Canis simensis</i>	AMNH 214799	Carnivora	Canidae
49	<i>Choloepus hoffmani</i>	MCZ 12348	Pilosa	Megalonychidae
50	<i>Chrysosyon brachyurus</i>	AMNH 120999	Carnivora	Canidae
51	<i>Chrysosyon brachyurus</i>	AMNH 133940	Carnivora	Canidae
52	<i>Civettictis civetta</i>	MCZ 37950	Carnivora	Viverridae
53	<i>Crocuta crocuta</i>	AMNH 187781	Carnivora	Hayenidae
54	<i>Crocuta crocuta</i>	AMNH 114227	Carnivora	Hayenidae
55	<i>Crocuta crocuta</i>	AMNH 27765	Carnivora	Hayenidae
56	<i>Crocuta crocuta</i>	AMNH 27767	Carnivora	Hayenidae
57	<i>Crocuta crocuta</i>	AMNH 52097	Carnivora	Hayenidae
58	<i>Crocuta crocuta</i>	MCZ 13232	Carnivora	Hyaenidae
59	<i>Crocuta crocuta</i>	MCZ 20968	Carnivora	Hyaenidae
60	<i>Crocuta crocuta</i>	MCZ 5227	Carnivora	Hyaenidae
61	<i>Crocuta crocuta</i>	MCZ No N°	Carnivora	Hyaenidae
62	<i>Cryptoprocta ferox</i>	AMNH 10046	Carnivora	Eupleridae
63	<i>Cuon alpinus</i>	AMNH 102083	Carnivora	Canidae
64	<i>Cuon alpinus</i>	AMNH 54842	Carnivora	Canidae
65	<i>Cuon alpinus</i>	AMNH 54976	Carnivora	Canidae
66	<i>Cyclopes tridactylus</i>	MCZ 7287	Pilosa	Cyclopedidae
67	<i>Dasyurus maculatus</i>	AMNH 66162	Dasyuromorphia	Dasyuridae
68	<i>Dendrolagus dorianus</i>	AMNH 192143	Diprotodontia	Macropodidae
69	<i>Dendrolagus lumholtzi</i>	AMNH 65248	Diprotodontia	Macropodidae
70	<i>Dendrolagus lumholtzi</i>	AMNH 65261	Diprotodontia	Macropodidae
71	<i>Eira barbara</i>	MCZ 15915	Carnivora	Mustelidae
72	<i>Eira barbara</i>	MCZ 30492	Carnivora	Mustelidae
73	<i>Eira barbara</i>	MCZ 485	Carnivora	Mustelidae
74	<i>Felis caracal</i>	AMNH 113794	Carnivora	Felidae
75	<i>Felis caracal</i>	AMNH 90105	Carnivora	Felidae
76	<i>Felis caracal</i>	AMNH 187788	Carnivora	Felidae
77	<i>Felis catus</i>	AMNH 244096	Carnivora	Felidae
78	<i>Genetta genetta</i>	MCZ 14537	Carnivora	Viverridae
79	<i>Genetta genetta</i>	MCZ 38068	Carnivora	Viverridae
80	<i>Genetta genetta</i>	MCZ 8555	Carnivora	Viverridae
81	<i>Gulo gulo</i>	MCZ 52977	Carnivora	Mustelidae
82	<i>Gulo gulo</i>	MCZ 48566	Carnivora	Mustelidae
83	<i>Gulo gulo</i>	MCZ 5131	Carnivora	Mustelidae
84	<i>Hyaena hyaena</i>	AMNH 05	Carnivora	Hyaenidae
85	<i>Hyaena hyaena</i>	AMNH 24436	Carnivora	Hyaenidae
86	<i>Hyaena hyaena</i>	AMNH 54512	Carnivora	Hyaenidae

87	<i>Herpestes ichneumon</i>	MCZ 60113	Carnivora	Herpestidae
88	<i>Hyaena brunea</i>	MCZ 57136	Carnivora	Hayenidae
89	<i>Indri indri</i>	AMNH 100504	Primates	Indriidae
90	<i>Lagothrix lagothricia</i>	AMNH 188153	Primates	Atelidae
91	<i>Lagothrix lagothricia</i>	AMNH 70404	Primates	Atelidae
92	<i>Lycaon pictus</i>	AMNH 82085	Carnivora	Canidae
93	<i>Lycaon pictus</i>	AMNH 82086	Carnivora	Canidae
94	<i>Lycaon pictus</i>	AMNH 82087	Carnivora	Canidae
95	<i>Lycaon pictus</i>	AMNH 82088	Carnivora	Canidae
96	<i>Lycaon pictus</i>	AMNH 85154	Carnivora	Canidae
97	<i>Lynx pardina</i>	AMNH 169492	Carnivora	Felidae
98	<i>Macaca Mulatta</i>	AMNH 41999	Primates	Cercopithecidae
99	<i>Macrotis lagotus</i>	MCZ 31095	Peramelemorphia	Thylacomyidae
100	<i>Martes pennati</i>	MCZ 64713	Carnivora	Mustelidae
101	<i>Nandinia binotata</i>	AMNH 51469	Carnivora	Nandinidae
102	<i>Nasua nasua</i>	MCZ 999	Carnivora	Procyonidae
103	<i>Paguma larvata</i>	MCZ 36767	Carnivora	Viverridae
104	<i>Paguma larvata</i>	MCZ 36769	Carnivora	Viverridae
105	<i>Pan paniscus</i>	AMNH 86857	Primates	Hominidae
106	<i>Pan troglodytes</i>	MCZ 20041	Primates	Hominidae
107	<i>Pan troglodytes</i>	AMNH 201658	Primates	Hominidae
108	<i>Pan troglodytes</i>	AMNH 51278	Primates	Hominidae
109	<i>Pan troglodytes</i>	AMNH 51377	Primates	Hominidae
110	<i>Panthera leo</i>	AMNH 54995	Carnivora	Felidae
111	<i>Panthera leo</i>	AMNH 54996	Carnivora	Felidae
112	<i>Panthera leo</i>	AMNH 52078	Carnivora	Felidae
113	<i>Panthera onca</i>	AMNH 135928	Carnivora	Felidae
114	<i>Panthera onca</i>	AMNH 135929	Carnivora	Felidae
115	<i>Panthera onca</i>	AMNH 139959	Carnivora	Felidae
116	<i>Panthera onca</i>	AMNH 22919	Carnivora	Felidae
117	<i>Panthera pardus</i>	AMNH 34946	Carnivora	Felidae
118	<i>Panthera pardus</i>	AMNH 34475	Carnivora	Felidae
119	<i>Panthera tigris</i>	AMNH 100024	Carnivora	Felidae
120	<i>Panthera tigris</i>	AMNH 113743	Carnivora	Felidae
121	<i>Panthera tigris</i>	AMNH 113744	Carnivora	Felidae
122	<i>Panthera tigris</i>	AMNH 113748	Carnivora	Felidae
123	<i>Panthera tigris</i>	AMNH 135846	Carnivora	Felidae
124	<i>Panthera tigris</i>	AMNH 54605	Carnivora	Felidae
125	<i>Panthera tigris</i>	AMNH 135847	Carnivora	Felidae
126	<i>Panthera uncia</i>	AMNH 100110	Carnivora	Felidae
127	<i>Panthera uncia</i>	AMNH 166952	Carnivora	Felidae
128	<i>Panthera uncia</i>	AMNH 207704	Carnivora	Felidae
129	<i>Panthera uncia</i>	AMNH 35476	Carnivora	Felidae
130	<i>Papio hamadryas</i>	AMNH 82096	Primates	Cercopithecidae
131	<i>Paradoxurus hermaphroditus</i>	MCZ 5017	Carnivora	Viverridae
132	<i>Phalanger carmelitae</i>	MCZ 61727	Diprotodontia	Phalangeridae

133	<i>Phalanger celebensis</i>	AMNH 146805	Diprotodontia	Phalangeridae
134	<i>Phalanger orientalis</i>	AMNH 80933	Diprotodontia	Phalangeridae
135	<i>Phalanger orientalis</i>	AMNH 80934	Diprotodontia	Phalangeridae
136	<i>Phascolarctos cinereus</i>	AMNH 42903	Diprotodontia	Phascolarctidae
137	<i>Phascolarctos cinereus</i>	AMNH 107805	Diprotodontia	Phascolarctidae
138	<i>Phascolarctos cinereus</i>	AMNH 65607	Diprotodontia	Phascolarctidae
139	<i>Phascolarctos cinereus</i>	AMNH 65609	Diprotodontia	Phascolarctidae
140	<i>Pongo pygmaeus</i>	AMNH 200898CA	Primates	Hominidae
141	<i>Pongo pygmaeus</i>	MCZ 50960	Primates	Hominidae
142	<i>Potos flavus</i>	MCZ 62043	Carnivora	Procyonidae
143	<i>Prionodon linsang</i>	MCZ 36576	Carnivora	Prionodontinae
144	<i>Procolobus badius</i>	MCZ 37932	Primates	Cercopithecidae
145	<i>Puma concolor</i>	AMNH 183357	Carnivora	Felidae
146	<i>Puma concolor</i>	AMNH 244616	Carnivora	Felidae
147	<i>Puma concolor</i>	AMNH 80451	Carnivora	Felidae
148	<i>Puma concolor</i>	AMNH 87803	Carnivora	Felidae
149	<i>Sarcophilus harrisi</i>	MCZ 6342	Dasyuromorphia	Dasyuridae
150	<i>Strigocuscus pelengensis</i>	AMNH 108000	Diprotodontia	Phalangeridae
151	<i>Symphalangus syndactylus</i>	AMNH 106581	Primates	Hylobatidae
152	<i>Tachypithecus cristatus</i>	MCZ 35636	Primates	Cercopithecidae
153	<i>Tamandua mexicana</i>	MCZ 28014	Pilosa	Myrmecophagidae
154	<i>Thylacinus cynocephalus</i>	NHM 1963.8.30.1	Dasyuromorphia	Thylacinidae
155	<i>Thylacinus cynocephalus</i>	NHM 72.666	Dasyuromorphia	Thylacinidae
156	<i>Thylacinus cynocephalus</i>	NHM 83.8.22.1	Dasyuromorphia	Thylacinidae
157	<i>Thylacinus cynocephalus</i>	MCZ 36797	Dasyuromorphia	Thylacinidae
158	<i>Thylacinus cynocephalus</i>	AMNH 42259	Dasyuromorphia	Thylacinidae
159	<i>Thylacinus cynocephalus</i>	AMNH 35244	Dasyuromorphia	Thylacinidae
160	<i>Thylacinus cynocephalus</i>	AMNH 35504	Dasyuromorphia	Thylacinidae
161	<i>Thylacinus cynocephalus</i>	AMNH 35866	Dasyuromorphia	Thylacinidae
162	<i>Trichosurus arnhemensis</i>	AMNH 197668	Diprotodontia	Phalangeridae
163	<i>Trichosurus caninus</i>	AMNH 65535	Diprotodontia	Phalangeridae
164	<i>Trichosurus caninus</i>	AMNH 65537	Diprotodontia	Phalangeridae
165	<i>Trichosurus vulpecula</i>	MCZ 5106	Diprotodontia	Phalangeridae
166	<i>Ursus americanus</i>	AMNH 45149	Carnivora	Ursidae
167	<i>Ursus americanus</i>	AMNH 70357	Carnivora	Ursidae
168	<i>Ursus americanus</i>	AMNH 90334	Carnivora	Ursidae
169	<i>Ursus americanus</i>	AMNH 99655	Carnivora	Ursidae
170	<i>Ursus tibethanus</i>	AMNH 15578	Carnivora	Ursidae
171	<i>Ursus tibethanus</i>	AMNH 35496	Carnivora	Ursidae
172	<i>Ursus tibethanus</i>	AMNH 57076	Carnivora	Ursidae
173	<i>Viverra zibetha</i>	MCZ 35916	Carnivora	Viverridae
174	<i>Vombatus ursinus</i>	MCZ 24974	Diprotodontia	Vombatidae
175	<i>Vombatus ursinus</i>	AMNH 146850	Diprotodontia	Vombatidae
176	<i>Vombatus ursinus</i>	AMNH 35512	Diprotodontia	Vombatidae
177	<i>Vombatus ursinus</i>	AMNH 35701	Diprotodontia	Vombatidae
178	<i>Vombatus ursinus</i>	AMNH 35798	Diprotodontia	Vombatidae

179	<i>Vulpes macrotis</i>	AMNH 131834	Carnivora	Canidae
180	<i>Vulpes velox</i>	AMNH 100190	Carnivora	Canidae
181	<i>Vulpes velox</i>	AMNH 100215	Carnivora	Canidae
182	<i>Vulpes vulpes</i>	AMNH 128486	Carnivora	Canidae
183	<i>Vulpes vulpes</i>	AMNH 128488	Carnivora	Canidae
184	<i>Vulpes vulpes</i>	AMNH 128490	Carnivora	Canidae
185	<i>Vulpes vulpes</i>	AMNH 166938	Carnivora	Canidae
186	<i>Vulpes vulpes</i>	AMNH 98163	Carnivora	Canidae
187	<i>Wallabia bicolor</i>	AMNH 65125	Diprotodontia	Macropodidae
188	<i>Thylacoleo carnifex</i>	SAMP 12384a	Diprotodontia	Thylacoleonidae
189	<i>Thylacoleo carnifex</i>	SAM 12384b	Diprotodontia	Thylacoleonidae
190	<i>Thylacoleo carnifex</i>	SAM 12384c	Diprotodontia	Thylacoleonidae

Figure S1. Principal Components Analysis (PCA) performed on the residuals extracted from the multivariate regression analysis of shape on size (Fig.4B) of the distal humerus (the proximal portion of the elbow joint) of living mammals and Thylacoleo. A, Morphospace depicted from the scores of the species on the first two eigenvectors. The 95% confidence ellipses for placentals and marsupials are also shown. B, Projection of the phylogenetic tree topology of Figure 3 onto the phenotypic space depicted from the first two principal components (PCs) of elbow shape. C, Thin plate spline diagrams representing the shape changes accounted for each PC are shown as deviations from the average or consensus shape (0.0) in each PC (grey straight lines) to the target shapes (black dots). The warping outline of each reconstructed elbow shape is also shown for clarity.

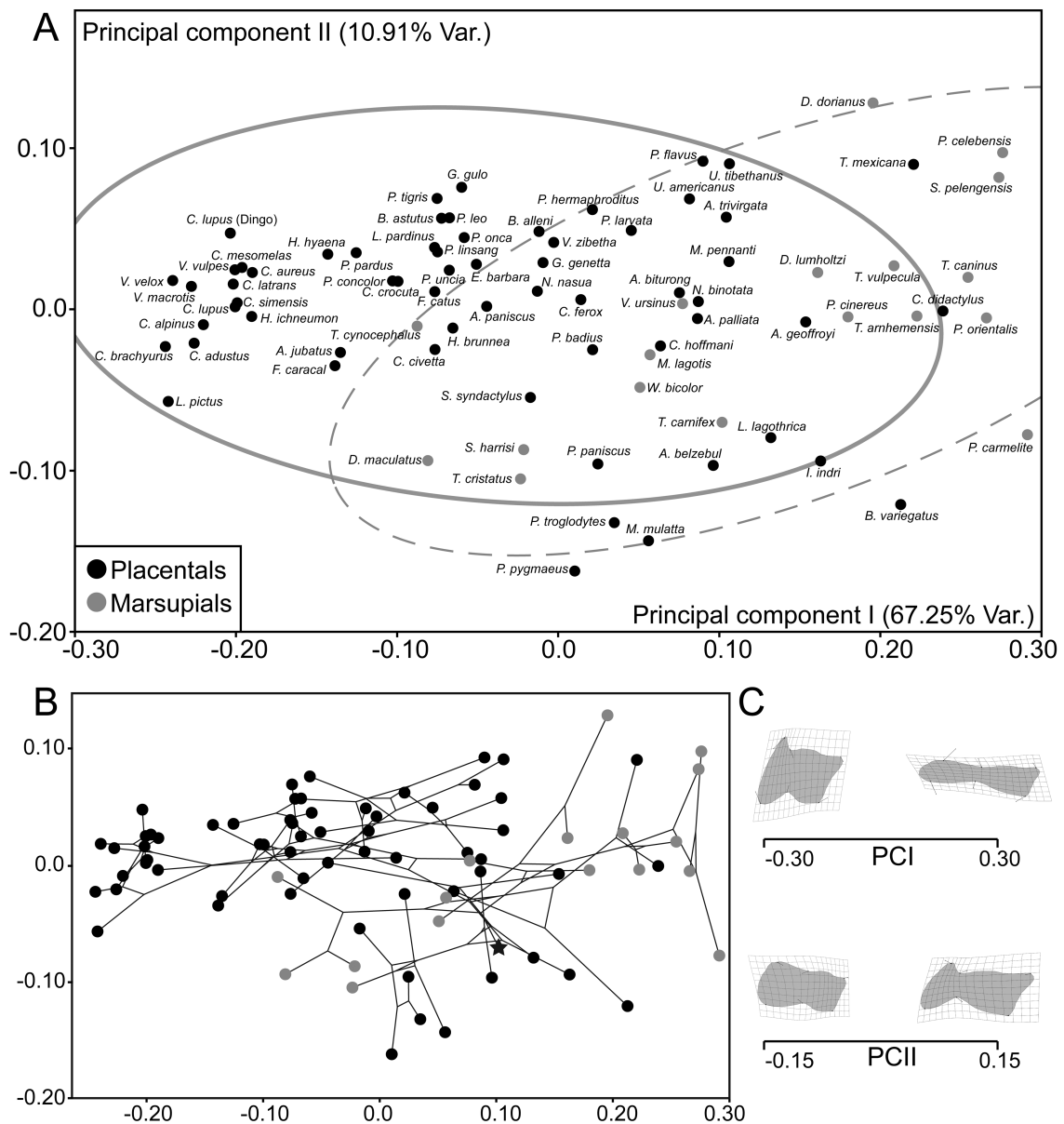


Figure S2. Principal components scores of the species on the first two eigenvectors mapped onto the phylogeny shown in Figure 3 using squared-changed parsimony and assuming Brownian motion.

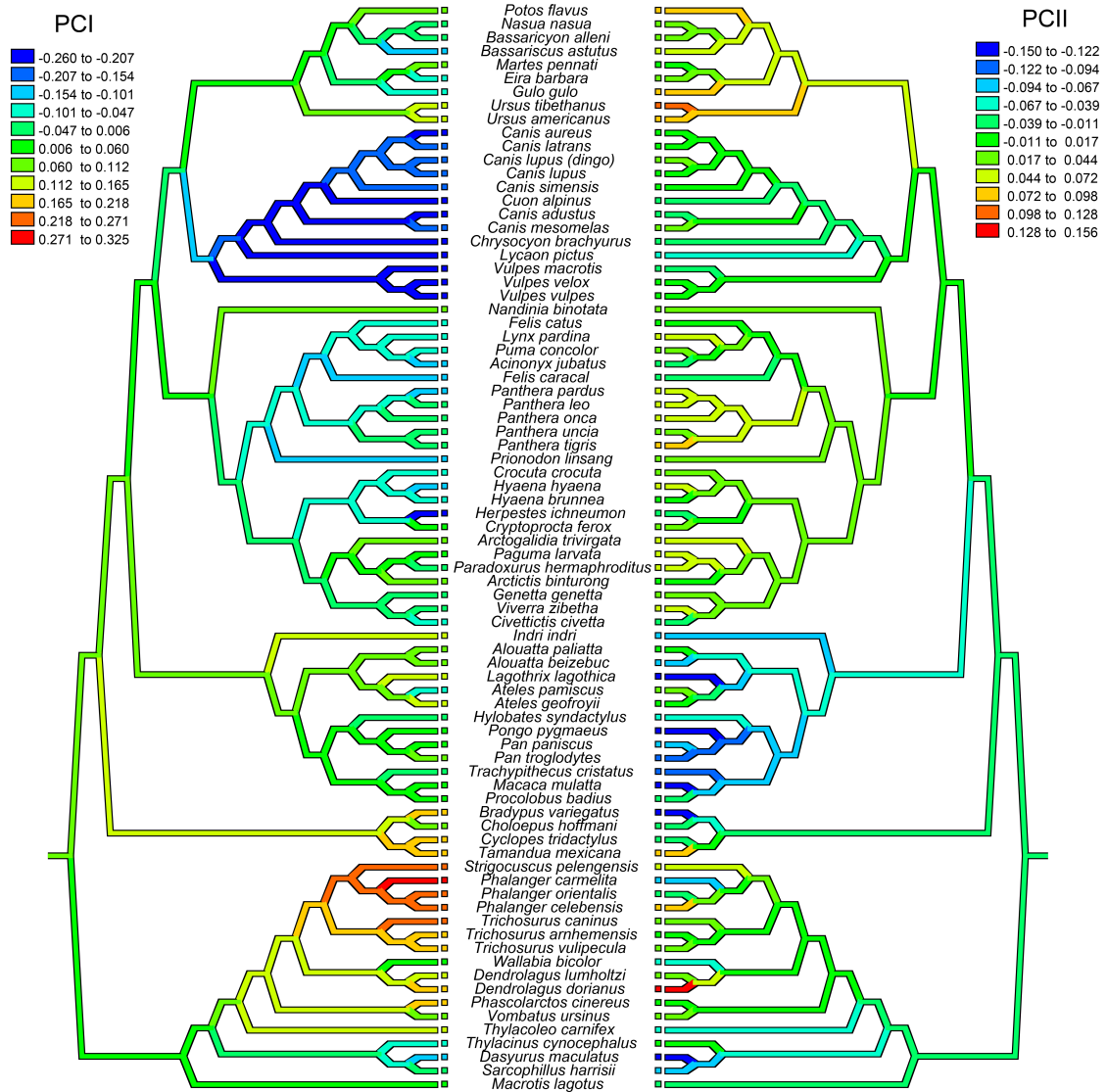


Figure S3. Canonical variates analysis (CVA) performed from the residuals extracted from the evolutionary allometry regression analysis of elbow shape on size to determine shape features of the distal humerus that best distinguish mammals with high mobility of the forearm from those with medium mobility and low mobility. A, Pairwise plot depicted from the scores on both canonical axes obtained for the CVA. B, The thin plate spline diagrams for each canonical function are shown as deviations from the average or consensus shape (0.0) in each discriminant function (grey straight lines) to the target shapes (black dots). The warping outline of each reconstructed elbow shape is also shown for clarity.

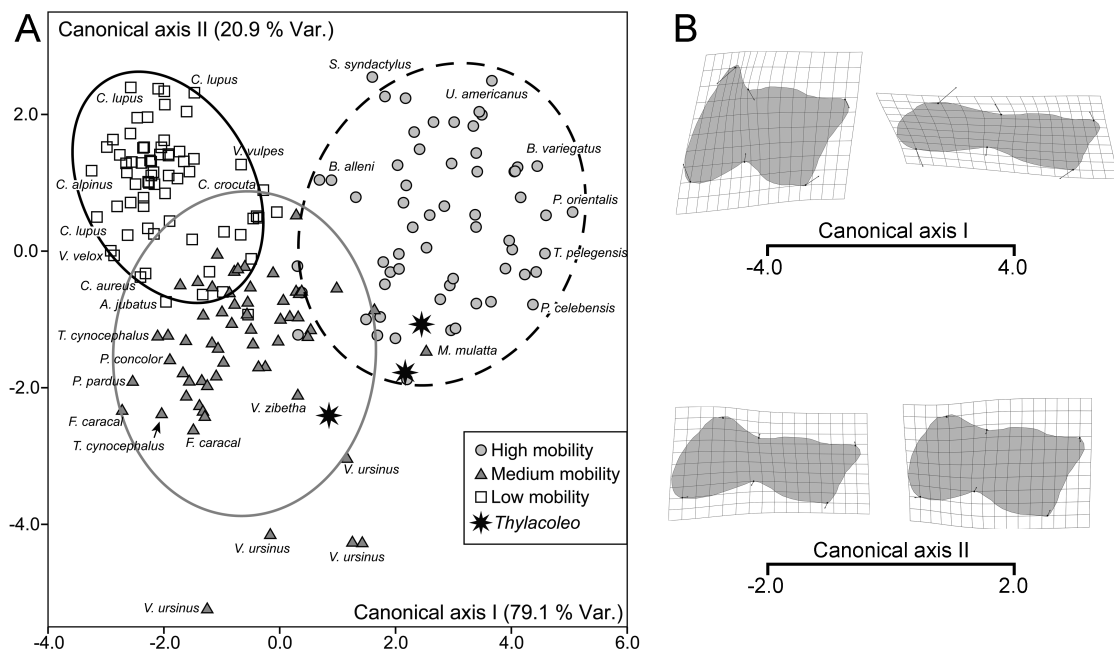


Figure S4. Linear Discriminant Analyses (LDA) performed from the residuals extracted from the evolutionary allometry regression analysis of elbow shape on size to investigate the most probably substrate use of *T. carnifex*. A, Discriminant function obtained from the LDA performed from the elbow shape of marsupials only, excluding the wombats from the analysis (included as unknowns), to discriminate between arboreal and terrestrial forms. B, Discriminant function obtained from the LDA performed from the elbow shape of marsupials including the wombats as known terrestrial species into the function to discriminate between arboreal and terrestrial forms. C, Thin plate spline diagrams for arboreal and terrestrial forms shown as deviations from the consensus shape (grey dots) to the target shapes (black dots) obtained from the analysis of B. The warping outline of each reconstructed elbow shape is also shown for clarity.

