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Estimating the weight of the Pleistocene marsupial lion, *Thylacoleo carnifex* (Thylacoleonidae : Marsupialia): implications for the ecomorphology of a marsupial super-predator and hypotheses of impoverishment of Australian marsupial carnivore faunas

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Abstract

Using demonstrated relationships between body mass and humeral and femoral circumferences, we calculate the weight of the only specimen of *Thylacoleo carnifex* known from a near-complete skeleton. Body weights of 112–143 kg were estimated for this individual, from Moree, north-western New South Wales. Extrapolating on the basis of geometric similitude, we further estimated the weight of the largest *T. carnifex* for which we had cranial data at 128–164 kg. Moreover, estimates for at least three of the thirteen available specimens exceeded 124–160 kg, suggesting that individuals of this size were common. Our estimates of average weight for the species range from 101 to 130 kg. These results clearly show that Pleistocene Australia had a 'large' cat equivalent and that 'large' terrestrial predator niches were not then occupied exclusively by reptiles. They may also diminish the argument that soil-nutrient deficiency constrained the evolution of large mammalian carnivores on this continent in the Pleistocene. Similarly, we posit that *prima facie* evidence for reptilian domination of terrestrial carnivore niches during the Miocene is wanting, although it is conceded that far more detailed investigation is required to comprehensively test these hypotheses. Earlier studies have drawn parallels between *T. carnifex* and sabre-toothed predators, thought to have specialised in hunting particularly large and powerful prey. Taken in the context of upwardly revised weight estimates, we argue that Pleistocene marsupial lions may have dispatched even *Diprotodon*-sized animals. But again, more comprehensive study, including thorough biomechanical design analysis of the post-cranial skeleton in particular, will be required to thoroughly illuminate the predatory habitus and general ecology of Australia's largest and most specialised marsupial carnivore.

Introduction

When he formally introduced *Thylacoleo carnifex* to the scientific community in 1859, Richard Owen, the eminent nineteenth century palaeontologist, described it as among the 'fellest and most destructive of predatory beasts'. It became popularly known as the marsupial lion. Owen's interpretation of dietary habitus sparked a controversy that would continue for decades. Many, but not all, later investigators favoured a herbivorous niche for *T. carnifex* (Flower 1868; Anderson 1929). The results of a detailed form–function analysis by Wells *et al.* (1982), strongly supportive of carnivory, appear to have ended this debate. Subsequent authors have accepted that, regarding diet, Owen was right from the start (Flannery 1997). However, another observation strongly implied by Owen (1859), i.e. that *T. carnifex* was of comparable size to *Panthera leo*, has also been challenged, evidently without dispute (see below). Arguments for herbivory in *T. carnifex* may have been founded on prejudice, i.e. because *T. carnifex* was a diprotodontian it couldn't be a carnivore (Broom 1898; Wells *et al.* 1982; Archer 1984; Wroe *et al.* 1998; Wroe 1999a). But, despite the dispatch of this central concern, much concerning the biology of *T. carnifex* remains

enigmatic, including its mode of locomotion and predatory behaviour (Archer 1984; Finch and Freedman 1988). The determination of body weight is important to the understanding of these issues. However, an extraordinary range of size estimates for *T. carnifex* have been presented in the literature. Many are not strictly quantitative, e.g. the size of '... a large wolf' (Rich and Hall 1984, p. 391), '... large Dog' (Case 1985, p. 47), or '... equivalent in size to a Leopard' (Wells *et al.* 1982, p. 584). But, some authors have forwarded actual weights. These estimates appear to be declining. Murray (1984) posits 75–100 kg, Flannery (1991) gives a range of 50–70 kg, Flannery (1997) places the limits at 40 and 60 kg, while Webb (1998) suggests that *T. carnifex* weighed 20 kg. Whether these estimates take the form of rough comparisons with living species or numerical values, a point worth noting is that none have been determined using any empirically based technique alluded to by the respective authors.

Accepting that *T. carnifex* was wolf- or leopard-sized, a number of investigators have argued that Pleistocene Australia had no 'large' mammalian carnivores or no 'large' felid analogues (Hecht 1975; Hunt 1996; Flannery 1997; Webb 1998). In doing so, these authors implicitly or explicitly impose a somewhat restricted definition on the concept of 'large' mammalian carnivore or cat. Only four extant felids (the lion, tiger, jaguar and cougar) ever exceed the maximum attained by leopards (Seidensticker and Lumpkin 1991). Even if we accept this definition of 'large' the conclusion rests on the premise that *T. carnifex* was, in fact, leopard-sized, a judgment thus far founded on the observation of skeletal proportions only.

Moreover, extrapolating on the conclusion that *T. carnifex* was not a large felid equivalent, Hecht (1975) suggested that the 'large' terrestrial carnivore niche in Pleistocene Australia was then occupied only by the giant varanid, *Megalania prisca*. Hecht's research preceded that of Wells *et al.* (1982), which firmly established *Thylacoleo* as a carnivore. Rich and Hall (1984) express some skepticism regarding the significance of *M. prisca* in the ecology of Pleistocene Australia, because of its rarity. But, effectively accepting and further developing Hecht's (1975) hypothesis, Flannery (1991, 1997) posited that the alleged domination of large terrestrial carnivore niches by reptiles in Australia may have harked back to at least early Miocene times and was the product of long-standing soil-nutrient deficiency and erratic climate.

With a view toward shedding light on the biology of *T. carnifex*, as well as broader palaeoecological issues, the following estimates of body weight in the Pleistocene marsupial lion are presented.

Materials and Methods

Anderson *et al.* (1985) demonstrated that combined femoral and humeral minimum mid-shaft circumferences closely correlated with body weight in quadrupedal mammals. The method developed by these authors has been widely employed by palaeontologists and constitutes a demonstrably more accurate means of estimating weight than others using data from long bone lengths (Gingerich 1990). Using the equation provided by Anderson *et al.* (1985) (i.e. weight in grams = $0.78C_{h+f}^{2.73\pm 0.09}$, where C_{h+f} is the combined mid-shaft circumference of the femur and humerus), we estimated the weight on the basis of the only near-complete skeleton of *T. carnifex* (Table 1). The result was then corrected for logarithmic transformation bias using the equation given by Smith (1993), i.e. $CF = 1/n \sum \exp(\log r_2)$, giving a result of 1.132282. In addition, we calculated body weights using equations determined by Anyonge (1993) for the estimation of body weight in carnivores (Table 1). Anyonge's equations give estimates based on femoral and humeral circumference data independently, i.e. weight in grams = $10^{(2.88 \times \log(f)) - 3.4}$ (where f = the femoral circumference taken at the midpoint on the long axis) and $10^{(2.47 \times \log(h)) - 2.72}$ (where h = humeral circumference taken at a point 35% back from the distal end of the bone). Corrections for logarithmic transformation bias could not be performed on these results because Anyonge (1993) did not present necessary raw data, i.e. femoral and humeral circumference values for the specimens included in his analysis. Consequently, these are likely to represent underestimates, as the logarithmic transformation bias value can not be less than 1.0 (Smith 1993).

On the basis of skull length, AM F52398-1 was of intermediate size. Assuming geometric similarity, i.e. $L \propto M^{0.33}$, we then calculated the weight of other available *T. carnifex* specimens (Table 2). The hypothesis of geometric similitude has been supported by analysis incorporating a wide variety of plant and animal taxa (Niklas 1994). Skull length was taken as the distance from the posteriormost tip of the occipital condyle to the anteriormost tip of the premaxillary suture.

Table 1. Dimensions and body weight estimates for a near-complete *Thylacoleo carnifex* individual (AM F52398-1)

Estimates are derived from equations provided by Anderson *et al.* (1985) and Anyonge (1993). Linear measurements in millimetres. Body weight in kilograms

F	Minimum femoral mid-shaft circumferences	84
<i>f</i>	Femoral circumference as measured at the bone's midpoint on the long axis	85
H	Minimum humeral mid-shaft circumferences	88
<i>h</i>	Humeral circumference as measured at a point 35% from the distal extremity	86
SKL	Skull length from posterior of occipital condyle to anterior tip of premaxillary suture	245
W ₁	Estimated body weight following method of Anderson <i>et al.</i> (1985), i.e. using F+H	111.95 ^A
W ₂	Estimated body weight using methodology of Anyonge (1993), i.e. using <i>h</i>	114.34
W ₃	Estimated body weight using methodology of Anyonge (1993), i.e. using <i>f</i>	143.46

^ACorrected for logarithmic transformation bias (see Smith 1993).

Table 2. Body weight estimates for additional specimens of *Thylacoleo carnifex*

Estimates are based on the assumption of geometric similarity ($L \propto M^{0.33}$). TWS = tooth wear stage (follows Archer and Dawson 1982). SKL = skull length from posterior of occipital condyle to anteriormost tip of premaxillary suture. W₁, W₂ and W₃ were calculated assuming weights of 111.95, 114.34, and 143.46 kg, respectively, for AM F52398-1 (see Table 1). LC = Lake Colongulac, Victoria; DD = Darling Downs, Queensland; WC = Wellington Caves, New South Wales; N = Naracoorte, South Australia. Linear dimension in millimetres. Body weight in kilograms

Specimen No.	Locality	TWS	SKL	W ₁	W ₂	W ₃
AM F4662	DD	IV	256	127.72	130.45	163.66
BM M16591 ^A	LC	II	254	124.75	127.41	159.86
AM F 4659	WC	III	240	105.24	107.48	134.85
AM F18666	WC	I	240	105.24	107.48	134.85
AM F9	WC	II	182	45.89	46.87	58.81
SAM P16720	N	III	229	91.42	93.37	117.15
SAM P16732	N	IV	236	100.06	102.20	128.22
SAM P28942	N	III	250	118.95	121.49	152.42
SAM P20804	N	IV	245	111.95	114.43	143.46
SAM P16730	N	II	213	73.56	75.14	94.27
SAM P16723	N	IV	255	126.23	128.92	161.75
SAM P20805	N	IV	215	75.66	77.27	96.95
Average ^B				101.43	103.60	129.98

^AMeasurement from Gill (1973)

^BInclusive of Moree specimen (AM F52398-1)

Because of the unique pattern of tooth replacement in *T. carnifex* (Archer 1984), it is difficult to accurately assess the age of *T. carnifex* individuals. However, tooth wear stage, as determined by Archer and Dawson (1982), can be taken as an approximation. On this basis it is probable that at least four of the thirteen individuals included in the present study were juveniles or sub-adults and had yet to attain maximum size (i.e. tooth wear stages of I or II). As well as showing Stage IV tooth wear, the epiphyses of the leg bones were fully fused in the Moree specimen. We thus concluded that it was a fully grown adult.

Institutional abbreviations: AM = Australian Museum; BM = British Museum; SAM = South Australian Museum.

Results

From the results presented in Table 1, it can be seen that the body weight estimates for the Moree individual (112–143 kg) greatly exceed the average body weights of males and females of five of the seven largest extant felid species (Table 3). Only averages for male and female *Panthera leo* and *Panthera tigris* are higher than the lower of these figures. The higher figure is greater than the averages given for female *P. tigris*. Recorded minimum weights for these two pantherines vary. For *P. leo*, Seidensticker and Lumpkin (1991) give a figure of 120 kg, but Turner and Anton (1997) cite 120 kg as an average weight for southern African lionesses, implying that some are smaller still. For *P. tigris* the minimum is 65 kg (J. Gittleman, personal communication). For three of the thirteen specimens of *Thylacoleo* available for analysis (i.e. BM M16591, AM F4662, SAM P16723), calculations assuming geometric similitude produced estimates exceeding at least 124–160 kg, suggesting that *T. carnifex* of such dimensions were common. Such individuals would have approached, or exceeded, the average weights of female *P. tigris* (132 kg) and *P. leo* (151 kg). The highest estimated weight for any individual was 164 kg for the Darling Downs specimen (AM F4662). Our lower estimate of average body weight for *T. carnifex* (101 kg) is close to double, or more than double, those of both males and females of all extant felids excepting male and female *P. leo* and *P. tigris*. The higher average is very close to that of female *P. tigris*.

These findings suggest that *T. carnifex* commonly grew to well within the weight range of the two largest living cat species. Moreover, relatively few hypercarnivorous terrestrial mammals are thought to have ever exceeded the body weights proposed here for Australia's largest carnivorous marsupial. Van Valkenburgh (1991) lists only four specialist meat-eating carnivoran taxa, with estimated average body weights of over 100 kg, for the last 37 million years in North America (*Amphicyon longiramus*, *Barbourofelis lovei*, *Smilodon populator*, *Homotherium serum*). Indeed, our estimates of average body weight significantly exceed that given by Van Valkenburgh (1991) for the smallest species of sabre-toothed 'tiger', *Smilodon gracilis* (i.e. 80 kg). Furthermore, we posit that *T. carnifex* was, on average, larger than South America's most formidable late-Tertiary marsupial predator, *Thylacosmilus atrox*. Three *Thylacosmilus* crania are known. Riggs (1934) gives a skull length of 260 mm for the holotype (FM P14531), while the two remaining specimens (FM P14344, FM P14474) are much smaller. A skull length of 197 mm is given for FM P14344. The third specimen (FM P14474), is incomplete, but Riggs (1934, p. 9) observes that it is '... about the same size as the paratype [FM P14344]'. For the holotype, Riggs (1934) provides a dimension for the maximum mid-shaft diameter of the femur (i.e. 25 mm). Assuming a circular cross-section for the femur at this point, we calculate a circumference of 79 mm (i.e. $C = \pi d$). Following the methodology of Anyonge (1993), we estimate a body weight of 116 kg for this, the

Table 3. Average body weights and maximum recorded weight of the seven largest extant felid taxa

Average weights are from Van Valkenburgh (1990). Maximum weights are from Seidensticker and Lumpkin (1991)

Taxon	Average weight		Maximum weight
	Females	Males	
<i>Puma concolor</i>	55.0	68.0	103.0
<i>Panthera onca</i>	45.0	55.0	136.0
<i>Panthera leo</i>	151.0	172.2	250.0
<i>Panthera tigris</i>	132.1	190.1	320.0
<i>Panthera pardus</i>	41.1	45.5	90.0
<i>Acinonyx jubatus</i>	59.7	61.2	65.0
<i>Uncia uncia</i>	32.0	32.0	75.0

largest known specimen of *Thylacosmilus*. Using the same method, the estimated body weight of the Moree *T. carnifex* is 143 kg (i.e. maximum mid-shaft diameter = 27 mm, circumference = 85). This is the same result for the Moree individual as determined using direct measurement of the mid-shaft femoral circumference (see Table 1, W₃).

Discussion

Palaeoecological implications

These first empirically determined estimates of body weight in *Thylacoleo carnifex* may challenge Hecht's (1975) and Flannery's (1991, 1997) arguments regarding reptilian dominance of the large carnivore niche in Pleistocene Australia. Regarding the specific contention that *Megalania prisca* was the only, or even principle, predator of Australia's Pleistocene megafauna, we note that, while *T. carnifex* has been implicated with the butchery of very large Pleistocene taxa (Horton and Wright 1981; Runnegar 1983), *M. prisca* has not (B. Mackness, personal communication). We also reiterate the observation of Rich and Hall (1984), i.e. that fossils of *M. prisca* are extremely uncommon. Contrastingly, *Thylacoleo carnifex* constitutes a widely distributed and regular find among Australia's Pleistocene deposits (Archer and Dawson 1982). Moreover, being ectothermic, *M. prisca* required far less food in relation to its body weight (Flannery 1997). Hecht (1975) estimated *M. prisca* to be around 5.5 m long and 620 kg. Unless *M. prisca* was more numerous than the fossil record indicates, we tender that it was a less significant predator of large mammals.

We also contend that a rapidly growing body of fossil data from Riversleigh, north-western Queensland, may undermine the assertion that mammalian carnivore faunas were impoverished during Miocene times (Flannery 1997). Only one terrestrial crocodile exceeding even 1.0 m in length, *Quinkana* sp. (maximum of 1.5–2.0 m), is known from Miocene-aged Riversleigh local faunas (Willis 1997, and personal communication). Although two large snake taxa, *Yurlunggur* sp. (up to 6 m) and '*Montypythonoides*' *riversleighensis* (about 4 m) are known from this locality, it is likely that the larger of these was not terrestrial, but aquatic (J. D. Scanlon, personal communication). On the other hand, recent discoveries have revealed an unexpected diversity of large marsupial carnivore taxa from Riversleigh (Wroe 1997, 1999a, 1999b). Formally described taxa include six thylacinids, a thylacoleonid, two propleopines and a 'bone-cracking' dasyurid (Table 4). At least six further species represent large carnivorous taxa that are either new or previously unreported from Riversleigh deposits: three thylacinids (Wroe 1999a; Wroe and Muirhead 1999) and three thylacoleonids (Gillespie 1999). On the basis of the length of the upper molar tooth-row (20.3 mm for the single upper dentition known, QM F5427), the smallest of these,

Table 4. Carnivorous marsupial taxa, of the size of *Dasyurus maculatus* or greater, from pre-Pliocene mammal-bearing deposits of Riversleigh, north-western Queensland

Note: does not include at least five species yet to be described

Species	Family	Author
<i>Nimbacinus dicksoni</i>	Thylacinidae	Muirhead and Archer (1990)
<i>Thylacinus macknessi</i>	Thylacinidae	Muirhead (1992)
<i>Muribacinus gadiyuli</i>	Thylacinidae	Wroe (1996a)
<i>Ngamalacinus timmulvaneyi</i>	Thylacinidae	Muirhead (1997)
<i>Wabulacinus ridei</i>	Thylacinidae	Muirhead (1997)
<i>Badjcinus turnbulli</i>	Thylacinidae	Muirhead and Wroe (1998)
<i>Ganbulanyi djadjinguli</i>	Dasyuridae	Wroe (1998)
<i>Priscileo roskellyae</i>	Thylacoleonidae	Gillespie (1997)
<i>Wakaleo</i> sp. (QM F36453)	Thylacoleonidae	Gillespie (1999)
<i>Ekaltadeta ima</i>	Hypsiprymmodontidae	Archer and Flannery (1985)
<i>Ekaltadeta jamiemulvaneyi</i>	Hypsiprymmodontidae	Wroe (1996b)

Muribacinus gadiyuli, was well within the size range of adult *Dasyurus maculatus* [from the Australian Museum collection a randomly selected female (AM 12481) measured 20.2 mm, while a randomly selected male (AM 9069) was 21.9 mm, on the same dimension]. The largest marsupial carnivore from these Miocene deposits is an undescribed, leopard-sized species of *Wakaleo* (Gillespie 1999). This specimen, known from a partial dentary (QM F36453), is of similar morphology to *W. vanderleueri*. Its P₃ is 14.3 mm long. The holotype of *W. vanderleueri* (CPC 13527) comprises a complete skull 179 mm in length and partial dentary. Murray and Megirian (1990) estimate the range of the length of P₃ in *W. vanderleueri* at 14.2–14.5 mm. Following the methodology outlined above for *T. carnifex*, we have calculated the body weight of the holotype of *W. vanderleueri* at 44–56 kg. This is near-average to large size for a male leopard (Table 3). Thus, we argue that there is, as yet, no clear-cut case suggestive of relative impoverishment for Australia's Miocene marsupial carnivore faunas. However, it is accepted that more rigorous evaluation will be needed to fully test the complex issues underlying Flannery's (1997) hypothesis. An additional, potentially confounding factor, is the possibility that vertebrate carcasses contributed significantly to the diet of giant dromornithid birds (Wroe 1999a, 1999c), although this interpretation is not universally accepted.

Ecomorphology of Thylacoleo carnifex

Thylacoleo carnifex has often been described as powerfully built (Wells *et al.* 1982; Archer 1984; Case 1985). Our results suggest that this observation might be interpreted as understatement. Recent inclination to understate the weight of *T. carnifex* may have been founded, at least in part, on the acceptance of linear dimensions as a reasonable basis for estimation. However, differences in body shape can produce vastly different weights for animals of similar head–body length. For example, from data supplied by Viranta (1996), *Panthera pardus* has a maximum head–body length greater than that of *Ursus americanus*, yet the ursid can be three times as heavy as the largest leopard (i.e. 270 v. 90 kg). A possibly even more extreme example is that of the Miocene amphicyonid *Amphicyon major*. Legendre and Roth (1988) give a maximum weight estimate of 630 kg for this taxon, also of leopard-like dimensions with respect to head–body length. Similar disparity has been suggested within the Felidae. Historically, *Smilodon fatalis* and *Panthera leo* have been judged as of roughly equivalent body weight on the basis of linear dimensions, but results given by Anyonge (1993) suggest that *S. fatalis* may have been the heavier by a factor of two.

From data tabulated by Finch and Freedman (1988), it is clear that, with respect to body length, the Moree specimen (AM F52398-1) was not much longer than *Thylacinus cynocephalus* (marsupial wolf). Respective presacral vertebral column lengths were 676.0 mm and 644.6 mm. However, our body weight estimate for AM F52398-1 exceeds that of even the largest *T. cynocephalus*, i.e. 35 kg (Smith 1982), by a factor greater than 3.5. Our results also suggest that *T. carnifex* was considerably more robust than extant felids. That *T. carnifex* is closer, in terms of head–body length, to *P. pardus* than *P. leo*, is not disputed. Finch and Freedman (1986) give a head–sacrum length of 991 mm for the Moree individual, compared with 1330 mm for a specimen of *Panthera leo*, while a specimen of *P. pardus* (M 34318) measures 1021 mm on this dimension. But, if our results are correct, then with respect to body weight, the Moree *Thylacoleo* was probably closer to the lion than the leopard. We suggest that, rather than extant felids, more appropriate analogues for body shape in *T. carnifex* might be found among the extinct felid species of *Smilodon* (and see below for further comparisons), or ursids among extant carnivores. With respect to comparisons between the marsupial lion and placental carnivores, another factor that may have been overlooked is tail morphology. On the basis of analysis of the proximal portions known, Finch and Freedman (1986) argue that the tail of *T. carnifex* was long, thick and muscular, unlike those of placental carnivores.

Upward revision of the maximum weight of *T. carnifex* clearly impacts on interpretation of the taxon's biology. The high weight estimates obtained in the present study lend tacit support to the

contention of Finch and Freedman (1988) that *T. carnifex* did not regularly climb trees, unlike the leopard to which it has been compared (Wells *et al.* 1982). Finch and Freedman (1988) note that conflicting evidence complicates the interpretation of locomotor mode in *T. carnifex*, but tentatively posit that it was a cursor of medium speed, that its powerful hind limbs enabled leaping and that its massive forearms were adapted to securing and manipulating prey. The great weight suggested in the present analysis might require downward estimation of the cursorial abilities of *T. carnifex*. While quite possibly capable of an explosive burst, it seems unlikely that an animal of such robustness could sustain high speed for long.

Case (1985) argued that *T. carnifex* was of similar size to *T. cynocephalus*, but that direct competition was avoided because the marsupial lion selected larger prey (although he concluded that it was probably too small to take *Diprotodon*). He founded this inference on the presence of features in *T. carnifex* shared with felids, known to take relatively large prey. Furthermore, a number of investigators have specifically compared *T. carnifex* with sabre-toothed carnivores (Horton and Wright 1981; Finch 1982; Wells *et al.* 1982; Case 1985). Morphological similarities alluded to by these authors include extreme hypertrophy of the 'carnassial', reduction of premolars anterior to this vertical shearing blade, absence of interlocking canines and powerful fore limbs. Horton and Wright (1981) further support the contention of niche correspondence for *T. carnifex* and sabre-tooths, on the basis of analysis of tooth marks found on herbivores from Lancefield Swamp, including *Diprotodon*. The high proportion of marks on ribs observed by Horton and Wright (1981) led them to conclude that, like sabre-tooths, *T. carnifex* concentrated on eating internal organs. Tooth marks on *Diprotodon* material from Reddestone Creek have also been attributed to *T. carnifex* by Runnegar (1983), and Case (1989) presents an analysis of taphonomic data, showing that the association of *T. carnifex* remains with those of large-gigantic marsupials is not independent.

Additional features are common to *T. carnifex* and the species of *Smilodon* in particular (believed to have concentrated on particularly large and/or powerful prey with respect to their own body weights: Gonyea 1976; Van Valkenburgh 1990; Anyonge 1996). Shared characteristics include extreme brachycephalisation, a relatively short back, lumbar vertebrae with vertical to posteriorly directed neural spines, and hypertrophy of the claw on the first digit of the manus – all traits that have been correlated with high body weight and/or dispatching very large prey (M. Anton, personal communication).

It may be argued that *T. carnifex*, even at an average weight of 101–130 kg, would not have been capable of dispatching Australia's largest Pleistocene herbivore, *Diprotodon australis* (up to 2000 kg: Flannery 1997). With respect to this we suggest the following: the only obvious defensive 'card' in the repertoire of *D. australis* that might have deterred *T. carnifex* was size. On the other hand, Pleistocene–Recent predators of large-to-gigantic placental herbivores, were, and continue to be, faced by potentially lethal 'defensive' weapons, in the form of sharp horns, tusks and hooves (an additional obstacle faced or faces would-be predators of proboscideans and rhinoceroids – extremely thick skin). Jaguars, *P. onca*, are capable of killing bulls of up to 500 kg in weight (Turner and Anton 1997). Given a maximum of 2000 kg for *D. australis*, the average was presumably much lower. We tender that if *P. onca*, around half the size of *T. carnifex* by our estimates, can dispatch an animal as formidably 'armed' and aggressive as a half-tonne bull, then the claim that *T. carnifex* might kill *D. australis* of up to at least average size is not unreasonable.

Having submitted the case for re-instatement of *T. carnifex* to 'super predator' status, some qualification is called for. Thus far, parallels with sabre-tooth carnivores remain strongly suggestive of niche correspondence only. We concede that far more detailed investigation is required before precise delineation of the predatory habitus of *T. carnifex* can be presented. In particular, thorough biomechanical design analyses of the postcranial skeleton would be of great benefit. It is hoped that issues raised in the present study might stimulate research along such lines. Nonetheless, we reassert, on the basis of this and preceding studies, that *T. carnifex* was most probably a 'big game' specialist.

Conclusion

It is likely that body weight in *T. carnifex* has been seriously underestimated and that the Pleistocene marsupial lion was a mammalian super-predator by any reasonable standard. Moreover, we posit that these new size estimates, functionally correlated features shared with *Smilodon*, and taphonomic data, collectively constitute evidence that *T. carnifex* may have preyed on even the biggest of Australian megafaunal taxa, *Diprotodon*. These findings undermine the hypothesis that large mammalian predator niches were dominated by reptiles and that soil-nutrient deficiency prohibited the evolution of specialist marsupial carnivores comparable in size to large felids in Pleistocene Australia. At present *prima facie* evidence for reptilian 'domination' of terrestrial carnivore niches in Miocene Australia is even less compelling.

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