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Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa

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We provide the first predictions of bite force (B_S) in a wide sample of living and fossil mammalian predators. To compare between taxa, we calculated an estimated bite force quotient (BFQ) as the residual of B_S regressed on body mass. Estimated B_S adjusted for body mass was higher for marsupials than placentals and the Tasmanian devil (*Sarcophilus harrisii*) had the highest relative B_S among extant taxa. The highest overall B_S was in two extinct marsupial lions. BFQ in hyaenas were similar to those of related, non-osteophagous taxa challenging the common assumption that osteophagy necessitates extreme jaw muscle forces. High BFQ in living carnivores was associated with greater maximal prey size and hypercarnivory. For fossil taxa anatomically similar to living relatives, BFQ can be directly compared, and high values in the dire wolf (*Canis dirus*) and thylacine (*Thylacinus cynocephalus*) suggest that they took relatively large prey. Direct inference may not be appropriate where morphologies depart widely from biomechanical models evident in living predators and must be considered together with evidence from other morphological indicators. Relatively low BFQ values in two extinct carnivores with morphologies not represented among extant species, the sabrecat, *Smilodon fatalis*, and marsupial sabretooth, *Thylacosmilus atrox*, support arguments that their killing techniques also differed from extant species and are consistent with 'canine-shear bite' and 'stabbing' models, respectively. Extremely high BFQ in the marsupial lion, *Thylacoleo carnifex*, indicates that it filled a large-prey hunting niche.

Keywords: bite force; prey size; osteophagy; Carnivora; Dasyuromorphia; Thylacoleonidae

1. INTRODUCTION

Bite force (B_S) is an important aspect of carnivore ecology, with the potential to shed light on the evolution of community structure and prey size in fossil taxa (Meers 2002; Vizcaíno & de Iuliis 2003; Rayfield 2004). However, empirical data are not easily obtained; B_S has been measured in only three mammalian carnivore species (Thomason 1991; Dessem & Druzinsky 1992; Binder & Van Valkenburgh 2000) and the comparative biology of B_S in mammals has remained largely unexplored. Important unanswered questions are: is bite force (i) allometrically related to body mass, (ii) phylogenetically constrained, (iii) more strongly influenced by skull length or skull width, (iv) relatively higher in bone-cracking specialists and (v) related to prey size in extant taxa? Answers will define the limits of using B_S estimate as a predictor of behaviour and prey size in fossil species.

2. MATERIAL AND METHODS

We calculated theoretical maximum bite forces using the 'dry skull' method (Thomason 1991; Electronic Appendices, sections A and B). Our sample comprised 49 specimens representing 39 taxa (31 extant and eight extinct). The dry skull method, derived from relationships between skull dimensions and jaw muscle cross-sectional areas, models the jaw as a simple lever. It is most applicable to the anterior-most portion of the jaw, where the caniniform teeth are located (Electronic Appendix, section A). Consequently, and because morphology of the canines has long been considered a significant predictor of predatory behaviour in mammalian carnivores (Wroe *et al.* 1998; Farlow & Pianka 2002), we have largely restricted our discussion to estimates of force for static bites at the canines (CB_S). However, analyses of B_S at the carnassial showed the same qualitative trends as for CB_S (Electronic Appendix, section C). A further advantage of the 'dry skull' method is that because results are derived solely from skull morphology, comparisons can be made between fossil and extant taxa.

The relationship between CB_S and body mass between species is allometric (figure 1; Meers 2002; $r^2 = 0.85$). To compare bite forces in taxa of greatly differing body masses an estimated bite force quotient (BFQ) was calculated using the residuals of regression (table 1; Electronic Appendix, section A). 'Average' BFQ was set at 100. Variance in allometry adjusted bite force is small relative to that for absolute B_S (Thomason 1991; Electronic Appendix, section D) and a second advantage of using BFQ is that it allows more meaningful comparisons based on small datasets. This quality is particularly valuable in analyses incorporating fossil taxa where sample sizes are limited.

3. RESULTS

The highest B_S estimate adjusted for body mass were

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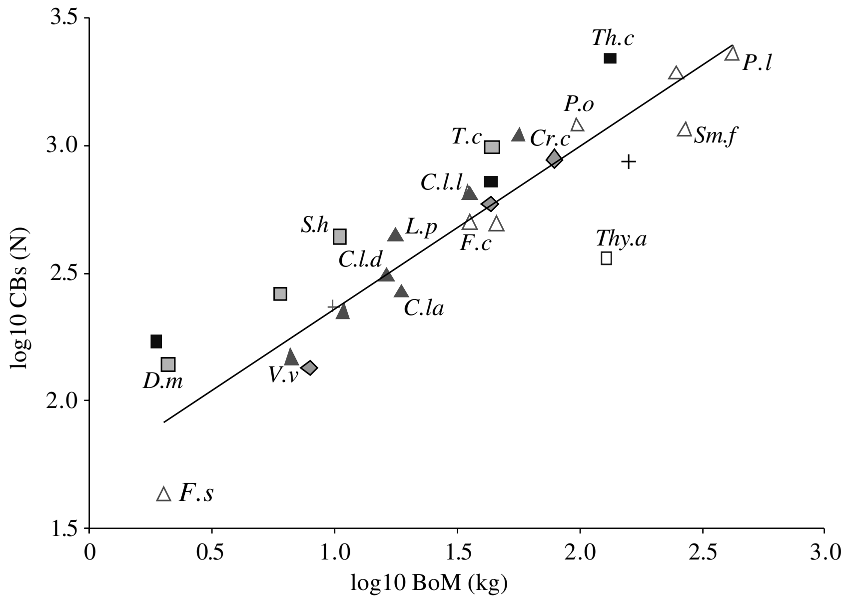

Figure 1. Log predicted canine bite force (CB_S) plotted against log body mass (BoM). Regression for all extant taxa = solid black line. Individual data points are: for felids (open triangles), canids (grey filled triangles), dasyuromorphians, grey filled squares, thylacoleonids (black filled squares), hyaenids (grey filled diamonds), ursids, a mustelid and a viverrid (grey crosses), and a thylacosmilid (open squares). Species abbreviations as in table 1.

in two extinct marsupial lions, *Thylacoleo carnifex* (194) and *Priscileo roskellyae* (196). The lowest was also in a fossil marsupial, *Thylacosmilus atrox* (41). Among extant carnivorous mammals the highest BFQ was in the Tasmanian devil, *Sarcophilus harrisii* (181). For placentals, BFQ was greatest in the Pleistocene dire wolf, *Canis dirus* (163). Another canid, the African hunting dog, *Lycaon pictus*, had the highest BFQ for living Carnivora (142).

Mean BFQ was higher in marsupials than placentals (158 versus 98), although marsupials do not have larger heads—relationships between head lengths and body masses in dasyuromorphians were similar to those of canids, and thylacoleonids were similar to felids (figure 2). However, relative to body mass, CB_S was significantly higher in dasyuromorphians than in canids ($F_{1,13}=33.51$, $p<0.01$) and significantly higher in thylacoleonids than in cats ($F_{1,11}=11.84$, $p<0.01$).

The average BFQ for Felidae (104) was slightly less than in Canidae (110) and dogs had greater head to body size (figure 2), but the difference in this instance was not significant. Across all taxa, skull width was a better predictor of CB_S than skull length ($r^2=0.92$ and 0.78, respectively; Thomason 1991).

CB_S was considerable for specialist bone-crackers included in our study, the spotted and brown hyaenas (*Crocuta crocuta* and *Hyaena hyaena*) and the Tasmanian devil (*S. harrisii*). However, in the two hyaenids, BFQ at the canine was exceeded by several non-osteophagous carnivorans (figure 1; table 1) and BFQ for the Tasmanian devil was not much above average for dasyuromorphians and less than in two marsupial lions. BFQ at the carnassial teeth followed a similar pattern (Electronic Appendix, section C), an expected result because the position of the carnassial varies little among mammalian predators (Greaves 1983).

As an upper restriction on niche, a predator's maximal prey size is an important component of its ecology and is likely to be strongly influenced by its biomechanical limits. Predator body mass has been shown to correlate with maximal prey size in mammals (Meers 2002). Among extant canids, the four hypercarnivores that often prey on animals larger than themselves, the grey wolf (*Canis lupus lupus*), dingo (*C. l. dingo*), African hunting dog (*L. pictus*) and the dhole (*Canis alpinus*), have the highest BFQ (108–142). BFQ was consistently lower in the five more solitary, omnivorous foxes, jackals and coyote characterized by relatively low maximal prey sizes (80–97). Thus, although the ability to bring down large prey in canids is related to cooperative hunting, it is still reflected in a higher BFQ. Within living Felidae, BFQ values were 57 and 75 for the two species that specialize in relatively small prey, while BFQ was 94 or greater for the seven known to take relatively large prey (table 2). B_S adjusted for body mass was also low in bears (44–78), which are restricted to relatively small prey (Meers 2002). BFQ was higher in extant dasyuromorphian marsupials, but the same trends were evident. The lowest BFQ was in the eastern quoll (*Dasyurus viverrinus*), which takes comparatively smaller prey and is less carnivorous than the other marsupials considered (see below). Overall, BFQ was 100 or higher in 15 of the 16 extant placental and marsupial carnivores sampled that take prey larger than their own maximal body masses. In 12 of the 14 extant species where maximal prey size was less than the species' mean body mass, BFQ was less than 100 (table 2). The difference between large and small prey specialists was significant ($t(28)=-4.92$, $p<0.01$) and hypercarnivores had significantly higher values for BFQ than more omnivorous species ($t(28)=-3.33$, $p<0.02$; table 2).

4. DISCUSSION

(a) *Comparisons between extant taxa*

Results suggest that, relative to body mass, calculated canine B_S is considerably higher in marsupials than in

Table 1. Measurements of basal skull length (BSL) and maximum skull width at the zygoma (SWZ); and estimates of body mass (BoM), canine bite force (CB_S), and bite force quotient (BFQ), for 39 taxa of recent and fossil mammals.
(Measurements and calculations were taken from prepared skulls. Methods for body mass estimations given in Electronic Appendix, section A. Fossil taxa indicated with †.)

species	family	BSL (cm)	SWZ (cm)	BoM (kg)	CB_S (N)	BFQ
Alopex lagopus	Canidae	13.86	8.05	8.2	178	97
Canis alpinus	Canidae	17.69	10.78	16.5	314	112
Canis aureus	Canidae	13.53	8.12	7.7	165	94
Canis lupus dingo (*C l.d*)	Canidae	18.04	9.97	17.5	313	108
Canis lupus hallstromi	Canidae	15.95	9.41	12.3	235	100
Lycaon pictus (*L.p*)	Canidae	18.52	13.18	18.9	428	142
Vulpes vulpes (*V.v*)	Canidae	13.79	7.35	8.1	164	92
Urocyon cineroargentus	Canidae	11.91	6.14	5.3	114	80
Canis latrans (*C.la*)	Canidae	18.85	9.86	19.8	275	88
Canis lupus lupus (*C.l.l*)	Canidae	22.92	13.22	34.7	593	136
Canis dirus †	Canidae	26.19	17.58	50.8	893	163
Ursus americanus	Ursidae	24.39	17.2	105.2	541	64
Ursus arctos	Ursidae	26.96	16.28	128.8	751	78
Ursus thibetanus	Ursidae	20.92	11.07	77.2	312	44
Meles meles	Mustelidae	12.31	8.05	11.4	244	109
Gennetta tigrinus	Viverridae	10.93	5.19	6.2	73	48
Crocuta crocuta (*Cr.c*)	Hyaenidae	23.64	16.73	69.1	773	117
Hyaena hyaena	Hyaenidae	19.98	15.18	40.8	545	113
Proteles cristatus	Hyaenidae	12.46	7.22	9.3	151	77
Panthera onca (*P.o*)	Felidae	22.25	18.63	83.2	1014	137
Panthera tigris	Felidae	28.86	22.73	186.9	1525	127
Acinonyx jubatus	Felidae	15.93	12.30	29.5	472	119
Felis yagouaroundi	Felidae	10.09	6.94	7.1	127	75
Lynx rufus	Felidae	7.58	5.93	2.9	98	100
Felis concolor (*F.c*)	Felidae	16.77	12.92	34.5	472	108
Felis sylvestris (*F.s*)	Felidae	7.51	5.39	2.8	56	58
Neofelis nebulosa	Felidae	16.74	11.88	34.4	595	137
Panthera leo (*P.l*)	Felidae	33.41	24.81	294.6	1768	112
Panthera pardus	Felidae	18.01	13.02	43.1	467	94
Smilodon fatalis † (*Sm.f*)	Felidae	29.48	19.53	199.6	976	78
Dasyurus maculatus (*D.m*)	Dasyuridae	10.09	6.01	3.0	153	179
Dasyurus viverrinus	Dasyuridae	7.27	4.15	0.87	65	137
Sarcophilus harrisii (*S.h*)	Dasyuridae	13.96	11.17	12.0	418	181
Nimbacinus dicksoni †	Thylacinidae	13.24	8.08	5.3	267	189
Thylacinus cynocephalus (*T.c*)	Thylacinidae	25.04	14.83	41.7	808	166
Priscileo roskellyae †	Thylacoleonidae	8.34	6.34	2.7	184	196
Wakaleo vanderleurei †	Thylacoleonidae	18.53	12.58	41.4	673	139
Thylacoleo carnifex † (*Th.c*)	Thylacoleonidae	24.04	20.15	109.4	1692	194
Thylacosmilus atrox † (*Thy.a*)	Thylacosmilidae	257.71	139.65	106	353	41

placentals and this cannot simply be explained by differences in head size. The presence of the superfast myosin isoform in both carnivorans and dasyuromorphians suggests that their muscle microphysiology is similar (Hoh *et al.* 2001). Differences between these two groups may relate to brain volumes, which, in carnivorans, are around two and a half times that of marsupial carnivores (Wroe *et al.* 2003). Within the temporal region of the skull, cross-sectional area places limits on the maximal force that can be generated by muscle (Thomason 1991), and expansion of brain volume impinges on available muscle area within the zygoma. Consequently, within a skull of given length and width, greater brain size impinges on maximal B_S. Extant carnivorans may have more precisely targeted killing behaviours than marsupial counterparts (Ewer 1969) and through greater efficiency may be able to accomplish similar results with less B_S. Because mean BFQ in marsupials is much higher than in placentals, our finding that the relatively omnivorous *D. viverrinus* has a BFQ well within the range of hypercarnivorous placentals is consistent with this interpretation. If *in vivo* testing shows that placentals produce bite forces that are similar, after adjustment for body mass, to marsupials, it will probably be a result of differences in jaw muscle anatomy, such as muscle pennation or microphysiology, although none have been clearly identified to date.

Mean BFQ was lower in cats than canids, reflecting the smaller head size of cats relative to body mass, but relative to skull length, CB_S in felids was greater, possibly because of their greater skull width relative to length (Electronic Appendices, sections E and F). Although extant canids and dasyuromorphians have higher mean BFQ than felids, the shorter skull of cats may confer greater resistance to forces produced by struggling prey. Cats also have more powerful, flexible forelimbs, of critical utility in violent, close quarter interactions and may recruit ventral cervical

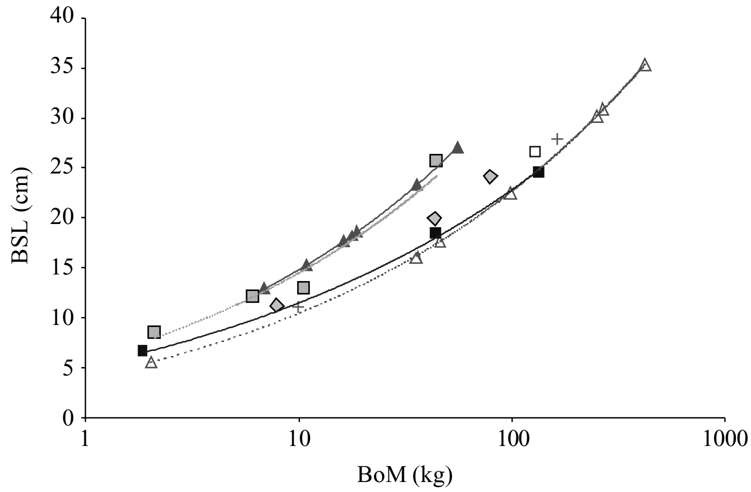

Figure 2. Basal skull length (BSL) plotted against body mass (BoM). Power regressions are shown for felids (black dashed line), canids (grey solid line), dasyuromorphians (grey dashed line), thylacoleonids (black solid line). Symbols as in figure 1.

Table 2. Bite force adjusted for body mass allometry (BFQ), maximal prey size and feeding category in 31 extant mammalian carnivores.
(RMPS, maximal prey size (1, greater than maximal body mass of predator; 2, less than maximal body mass of predator); FC, feeding category (1, hypercarnivore; 2, other); '—', insufficient data. Maximal body mass data largely from Meers (2002). For additional data see Electronic Appendix, section A.)

species	common name	family	BFQ	RMPS	FC
Alopex lagopus	Arctic fox	Canidae	97	2	2
Canis alpinus	Dhole	Canidae	112	1	1
Canis aureus	golden jackal	Canidae	94	2	2
Urocyon cineroargentus	grey fox	Canidae	80	2	2
Canis lupus dingo	Dingo	Canidae	108	1	2
Canis lupus hallstromi	singing dog	Canidae	100	—	—
Lycaon pictus	African hunting dog	Canidae	142	1	1
Vulpes vulpes	red fox	Canidae	92	2	2
Canis latrans	Coyote	Canidae	88	2	2
Canis lupus lupus	grey wolf	Canidae	136	1	1
Ursus americanus	black bear	Ursidae	64	2	2
Ursus arctos	brown bear	Ursidae	78	2	2
Ursus thibetanus	Asiatic bear	Ursidae	44	2	2
Gennetta tigrinus	striped genet	Viverridae	48	2	2
Meles meles	European badger	Mustelidae	109	2	2
Crocuta crocuta	spotted hyaena	Hyaenidae	117	1	1
Hyaena hyaena	brown hyaena	Hyaenidae	113	1	1
Proteles cristatus	Aardwolf	Hyaenidae	77	2	2
Panthera onca	jaguar	Felidae	137	1	1
Panthera tigris	tiger	Felidae	127	1	1
Felis concolor	cougar	Felidae	108	1	1
Acinonyx jubatus	cheetah	Felidae	119	1	1
Felis yagouaroundi	jaguarundi	Felidae	75	2	1
Lynx rufus	bobcat	Felidae	100	1	1
Felis sylvestris catus	cat	Felidae	58	2	1
Neofelis nebulosa	clouded leopard	Felidae	137	1	1
Panthera leo	lion	Felidae	112	1	1
Panthera pardus	leopard	Felidae	94	1	1
Dasyurus maculatus	spotted-tailed quoll	Dasyuridae	179	1	1
Dasyurus viverrinus	eastern quoll	Dasyuridae	137	2	2
Sarcophilus harrisii	Tasmanian devil	Dasyuridae	181	1	1

musculature to assist in jaw closure (Van Valkenburgh *et al.* 2003; Antón *et al.* 2004).

(b) ***Bite force and osteophagy***

Our finding that BFQ at both the canine and carnassial in osteophages were often comparable to, and sometimes less than, many non-osteophagous relatives was unexpected. This may have important implications regarding the biomechanics of osteophagy.

In most carnivores, maximal bite forces are used in the killing bite at the canines where maximal loads will be distributed between adjacent teeth in the anterior region of the jaw. In contrast, osteophagy requires the concentration of high loads on a limited part of the food item in order to produce material failure. The highest bite forces are typically achievable in carnassial biting, which is restricted to one side of the mandible rather than distributed between left and right jaws (Greaves 1983). In hyaenids, maximum forces may be generated immediately anterior to the carnassial (Werdelin 1989). Moreover, from observation, osteophages may use kinetic, rather than static bites to crack bones, further increasing loads. Consequently, theoretical forces that can be achieved are far greater than those experienced during a canine bite. The application of maximal bite forces at post-canine teeth on hard materials requires very robust dentitions, as evidenced in specialized bone-crackers such *C. crocuta*, *H. hyaena* and *S. harrisii*. Our results suggest that although the capacity of teeth (and probably crania) to resist high stresses on hard substances in the cheek–tooth row is an essential adaptation to specialized osteophagy in mammals, particularly high bite strength relative to body size is not. The flipside of this argument is that many felids and canids could theoretically apply relatively greater bite forces at a single point in the cheek–tooth row than could a same-sized hyaenid. However, we posit that in practice, non-osteophageous taxa will not voluntarily develop maximal bite forces in a post-canine bite because neither their dentitia nor their crania are optimized to resist such high stresses in this region. Unused capacity at the carnassial in non-osteophages may be an incidental product of the requirement for high B_S at the canines as part of their killing strategy.

(c) *Bite force and the prediction of feeding ecology*

(i) *Extant carnivores*

Our results demonstrate that among living mammalian carnivores, BFQ is a broad indicator of relative prey size and feeding ecology. However, considered in isolation, B_S adjusted for body mass is not an infallible predictor. In the aardwolf (*Proteles cristatus*), BFQ is low (77), but higher than in some bears, a viverrid and two small cat species (table 2). Although this finding is consistent in that all take relatively small prey, it does not reflect the fact that *P. cristatus* subsists largely on termites. Interestingly, the unusual, hypotrophied post-canine morphology of the aardwolf unambiguously suggests that vertebrates are rarely taken, but the canines are quite well developed. Together with moderate BFQ, this indicates that it is physically capable of killing much larger prey than it does. The retention of functional canines and moderate BFQ in *P. cristatus* may be related to intra and/or interspecific defence. Either way, the aardwolf clearly lies outside generalized biomechanical subcategories, such as the cat and dog types, which themselves differ in details including head shape, canine cross-sectional morphologies and killing behaviour. This example demonstrates well that BFQ may not directly reflect feeding ecology for morphologically atypical taxa that do not fit within generalized biomechanical models. Consequently, in the reconstruction of ecology for fossil carnivores, BFQ must be qualified against the type and extent of morphological departure from biomechanical subcategories observable in living species. For example, predictions incorporating BFQ for fossil cats, or taxa with cat-like morphologies, are best made on the basis of comparisons with extant felids.

(ii) *Extinct taxa with morphologically similar extant relatives*

Neither cranial, nor post-cranial morphology of the thylacine, *Thylacinus cynocephalus*, differ greatly from those of living dasyuromorphians (Wroe 2003). Based on low rates of canine tooth breakage and snout morphology, it has been argued that thylacines may have been restricted to small or medium sized prey (Jones 2003; Johnson & Wroe 2003). Our finding that BFQ was comparable to extant dasyuromorphians known to take relatively large prey is *contra* these interpretations (table 1). Similarly, high BFQ in the Miocene thylacinid, *Nimbacinus dicksoni*, suggests that relatively large prey were accessible to this anatomically conservative species.

Likewise, among fossil placentals, morphology of the dire wolf (*C. dirus*) is similar to that of living relatives. If *C. dirus* was a social hunter, then its high BFQ (163) relative to extant canids suggests that it preyed on relatively large animals.

(iii) *Extinct taxa without morphologically similar living relatives*

Some fossil taxa included in our analyses clearly fell well outside extant morphotypes. Major differences between the sabrecat *Smilodon fatalis* and all extant felids, including extreme hypertrophy of the canines, very powerful forelimbs, lengthening of the neck and shortening of the lumbar region, leave little doubt that it used killing techniques not represented among living carnivores and regularly took large prey (Janis 1994; Antón & Galobart 1999; Antón *et al.* 2004; Argot 2004). Notwithstanding its high absolute CB_S compared with large living felids, BFQ in *S. fatalis* was low (78). Having secured large prey with its muscular forelimbs, *S. fatalis* used its hypertrophied canines to effect fatal trauma (Antón *et al.* 2004; Argot 2004). The reduced cross-sectional area of the canines in sabrecats may require relatively less bite force than that used by living *Panthera* (M. Meers, personal communication). In the marsupial sabretooth, *T. atrox*, both BFQ (41) and absolute B_S were extremely low, but as with *S. fatalis*, post-cranial adaptations and canine morphology indicate a killing technique without present day analogy and systematic predation on relatively large taxa (Argot 2004).

Current functional models of sabretooth killing behaviour include: (i) the 'stabbing' model in which the force applied to the canines is primarily neck-driven (Antón & Galobart 1999; Argot 2004) and (ii) a 'canine-shear bite', in which significant absolute force is required of the jaw adductors in conjunction with input from neck muscles (Akersten 1985). Because absolute CB_S in *S. fatalis* is high, and BFQ is considerably higher than in *T. atrox*, our results are consistent with the 'canine shear-bite' model for the sabrecat, with significant force required of the jaw adductors in conjunction with cervical musculature. From estimates of bending strength in the mandibular corpus, Bicknevicus & Van Valkenburgh (1996) posit that *S. fatalis* may have applied a sustained throat clamping bite. Our results do not rule out this possibility, but are *contra* the conclusion that bite force in *S. fatalis* was comparable to that of similar sized pantherines. However, in the marsupial sabretooth, CB_S and BFQ are both so low that we consider our result supportive of a primarily neck-driven use of the canines and strongly *contra* the possibility that *T. atrox* applied a sustained throat bite to dispatch large prey.

For the marsupial lion, *T. carnifex*, BFQ was the highest of any large predator and its CB_S approached that of a lion (*Panthera leo*) more than twice its size (table 1). If the killing mechanism of *T. carnifex* was functionally equivalent to that of extant felids, our results suggest that it could take prey much larger than itself. However, although cat-like in many respects, its dentition is unusual and interpretation of feeding ecology in the marsupial lion has long attracted controversy (Wells *et al*. 1982; Wroe *et al*. 2004*a*). Our findings confirm that short outlever arms and anteriorly placed muscle resultants conferred high mechanical efficiency (Wells *et al*. 1982). The marsupial lion's vertical shearing 'carnassial' cheek–teeth are relatively larger than in any other mammalian carnivore (Wells *et al*. 1982; Werdelin 1988). Brought together with a very high B_S, these carnassials may have enabled *T. carnifex* to rapidly slice through tracheas or vital blood vessels and quickly dispatch large, potentially dangerous prey, although mechanical simulation will be required to confirm this. When CB_S and BFQ are considered together with forelimb, cervical and lumbar morphology that converges on that of marsupial and placental sabretooths, as well as taphonomic data (Janis 1994; Wroe 2003; Argot 2004), the marsupial lion may have been capable of taking sub-adults of the heaviest available prey (Wroe *et al*. 2004*b*).

5. CONCLUSIONS

The dry skull method, because it takes into account subtle changes in the shape of the skull and jaws, provides estimates of B_S that can be applied across unrelated taxa and thus allows quantitative comparisons of this important component of a predator's biomechanical performance. Adjusted for body mass, our estimates of B_S (i) show variations that are broadly consistent with patterns of predatory behaviour and diet observed in extant carnivores, (ii) provide a basis for predicting maximal prey size in extinct mammalian predators that are morphologically similar to extant predators, (iii) allow quantifiable comparisons of biomechanics within ecomorphs, where there are no living analogues, such as sabretooths and (iv) challenge the widely held assumption that osteophagy requires relatively higher B_S than that seen in non-osteophagous relatives. Mechanical simulations and further investigations of jaw muscle anatomies and the mechanics of the skull, using FEA modelling (Daniel & McHenry 2001; Snively & Russell 2002; Rayfield 2004) and *in vivo* force measurement, will further clarify these patterns and permit examination of the following predictions inferred from our analyses: (i) the biomechanics of osteophagy are more tightly constrained by the structural properties of the carnivore's skull and dentition than by muscle force, (ii) non-osteophagous large prey specialists should be reluctant to apply all available muscle force in a post-canine bite, because of the threat of material failure (moreover, their crania will be optimized to resist stress at the canines, while in specialist bone-crackers skulls will be optimized to resist stress near the carnassial) and (iii) if *in vivo* testing shows that placentals produce bite forces that are similar after allometric adjustment to marsupials, it will be because of differences in muscle anatomy and organization.

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