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Three-dimensional biomechanics reveals distinct predatory behaviors in scimitar- and dirk-toothed sabertooth cats

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SUMMARY

Over the Cenozoic, large cat-like forms have convergently evolved into specialized killers of 'megaherbivores' that relied on their large, and laterally-compressed (saber-like) canines to rapidly subdue their prey [1-5]. Scimitar- and dirk-toothed sabertooths are distinct ecomorphs that differ in canine tooth length, degree of serration, and postcranial features indicative of

dissimilar predatory behavior [6-13]. Despite these differences, it is assumed that they used a similar 'canine-shear' bite to drive their sabers through their prey [14,15]. We investigated the killing behavior of the scimitar-toothed *Homotherium serum* and the dirk-toothed *Smilodon fatalis* using a comparative sample of living carnivores and a new quantitative approach to the analysis of skull function. For the first time, we quantified differences in the relative amount and distribution of cortical (CB) and trabecular bone (TB) in coronal sections of skulls to assess relative skull stiffness and flexibility [16-19]. We also use finite element analysis to simulate various killing scenarios that load skulls in ways that are likely to favor distinct proportions of CB/TB across the skull. Our data reveal that *S. fatalis* had an extremely thick skull and relatively little TB, consistent with a large investment in cranial strength for a stabbing canine-shear-bite. However, *H. serum* had more TB, and likely deployed an unusual predatory behavior that was more similar to the clamp-and-hold technique of the lion than *S. fatalis*. These data broaden the killing repertoire of sabertooths and highlight the degree of ecological specialization among members of the large carnivore guild during the Late Pleistocene of North America.

RESULTS

Profiles of CB and TB

As CB tends to have high stiffness and TB has greater flexibility [16-19], we hypothesize that if dirk-tooths and scimitar-tooths had distinctive killing bites that loaded their skulls differently, they should diverge in the quantity and distribution of CB/TB as well. To test this, we quantified the relative amount of cortical (CB) and trabecular bone (TB) of complete skulls of the two sabertooths and three extant large carnivores, African lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), and African wild dog (*Lycaon pictus*) (Fig. 1A; see methods for justification

of comparative sample). Our results reveal that the skulls of all species show two clear peaks in CB surface area relative to the total area of the skull (RCBT) to varying degrees with the exception of the wild dog (Fig. 1B, left). The first lies at the upper fourth premolar (carnassial), and the second at the temporomandibular joint (TMJ). In the wild dog, the peak at the carnassial is not pronounced, and CB area increases more gradually across the skull than in the feliforms (Fig. 1B, left). Across all five species, there is considerable variation in the distribution of CB surface area across the skull, with *S. fatalis* exceeding all species in the snout (slices #1-5; Fig.1B; Fig. 2) except at the anterior-most point of the upper carnassial, where it is surpassed by the spotted hyena (slice #3; Fig. 1B). The snout of *H. serum* has values of relative CB area that are below those of *S. fatalis* except at slices #1 and #5, the anterior-most point of the canine and the posterior-most point of the upper carnassial, respectively. Between those two positions, the snout of *H. serum* is more similar to that of the extant lion in relative compact bone surface area and much less than observed in the hyena and *S. fatalis*. (Fig. 1B, left). Beyond slice #5, both saber-tooths have similar values of CB that fall below those of the wild dog and hyena posteriorly (slices #5-10; Fig. 1B).

On a per slice basis, the proportion of CB (RCBS) fluctuates across the skull in all five species, with all showing a decline at the TMJ (slice#8, Fig. 1C, left). Within the snout, the proportion of CB per slice is greatest in the spotted hyena and *S. fatalis*, and least in the lion and *H. serum* (Fig. 1C, left). Interestingly, the snout of the wild dog is similar to that of the spotted hyena and *S. fatalis* in the proportion of compact bone at two anterior locations (slices #2-3), but then declines for the remainder of the snout (slices #4-5; Fig. 1C, left).

TB surface area relative to total skull area (RTBT) in *S. fatalis* is most similar to that of the spotted hyena, and to a lesser extent, *H. serum* and the wild dog (Fig. 1B, right). The lion

stands out with an unusually large proportion of TB at the TMJ (slice #8, Fig. 1B; Fig. 2) as well as higher values at both the posterior margin of the upper carnassial/frontal region and behind the TMJ (slices #4-5, 9-10; Fig 1B). The relatively large proportion of TB in the lion is confirmed in the analysis of TB area per slice (RTBS), in which the lion displays an exceptionally large proportion of TB per slice at the TMJ and caudal most position. (slice #8, 10, Fig. 1C). On a per slice basis, the values for *H. serum* are also elevated and similar to those of the lion within the anterior-most part of the snout (slices # 1-3; Fig. 1C). However, posteriorly (slices # 4-10; Fig. 1B), *H. serum* has relative TB area per slice values within the range of *S. fatalis* and all extant species except the lion (slices # 5-10; Fig. 1B).

Finite element analysis

We used 3D biomechanical modelling to simulate a variety of killing scenarios, such as stabbing or pulling back, that load skulls differently and therefore are likely to favor distinct proportions of CB/TB across the skull. Biomechanical function and efficiency were assessed via von Mises stress and displacement magnitudes in the different models/scenarios. Von Mises stress is a scalar function of principal stresses (along orthogonal planes) and is a good predictor of ductile material failure (20), whereas displacement magnitude indicates the deformation of individual elements/regions due to external loading.

A comparison of von Mises stress values for each species under the four different loading scenarios reveals that the skulls of the three felids undergo less stress during stabbing bites than the skulls of either *Crocuta* or *Lycaon* (blue line, Fig. 3A). Of the three felids, *S. fatalis* exhibits the least stress during a stabbing bite, followed closely by *H. serum* and then the lion. However,

92 average values of node displacements under a stabbing load are very similar for both sabertooths
93 (Fig. 3B).
94 Contour plots of von Mises stress distributions reveal notable differences between *S.*
95 *fatalis* and *H. serum* during bilateral canine stabbing and pulling back. During bilateral canine
96 stabbing, both sabertooths are similar in showing relatively high stress across their braincase but
97 differ anteriorly, with *S. fatalis* exhibiting less stress across the rostrum than *H. serum* (Fig. 4).
98 However, the situation is different during the pull-back scenario, in which both show similar
99 stress in the rostrum but *S. fatalis* has greater stress across the braincase and zygomatics than *H.*
100 *serum*. All three of the extant species experience higher stresses during bilateral canine stabbing
101 than either of the saber-tooths (Fig. 4).
102 Mean von Mises stress values in *S. fatalis* (Fig. 3A) under laterally directed extrinsic
103 loads (lateral shake) are greater than in any other simulated scenario, and exceed those observed
104 for either *H. serum* or the lion. In both the lion and *H. serum*, the stresses are similar and the
105 laterally directed extrinsic forces largely concentrate von Mises stress around the zygomatics and
106 the rostral region (Fig. 4). However, average values of node displacement under lateral shake
107 loads indicate that *H. serum* experiences considerably lower displacements than the lion or *S.*
108 *fatalis* (Fig. 3B).
109 All the taxa experience lower average von Mises stress values with a jaw-muscle-driven
110 bite (Fig. 3A), but this is particularly true for the skull of *C. crocuta* and *L. pictus* (Fig. 3A).
111 Stresses are lower in this scenario than the others because the primary forces are distributed
112 across the braincase and posterior half of the skull, and the rostrum is relatively unaffected (Fig.
113 4). In contrast, because the extrinsic scenarios have a higher load focus on the anterior half of the

skull, the skulls are more prone to bending under the simulated loads, especially in elongated skulls.

DISCUSSION

Cortical bone (CB) differs from trabecular bone (TB) in having a higher Young's modulus, and therefore, a high supportable load per unit of surface area. However, it has a lower strain index, which gives it greater stiffness and greater ability to resist torque (16-19). Therefore, the large amount of CB in the rostrum of *S. fatalis* (Fig. 1B; Fig. 2) indicates that, similar to the bone-cracking spotted hyena, it was especially equipped to resist larger and more localized stresses than the rostra of both the living *P. leo* (Fig. 1B; Fig. 2) and the scimitar-toothed *H. serum* (Fig. 1B; Fig. 2). In fact, the three-dimensional simulations of different killing-bite scenarios reveal that the rostrum of *S. fatalis* was better able to withstand loads induced when stabbing prey than that of *H. serum* (Fig. 4). Moreover, within our sample of five large carnivorans, the skull of *S. fatalis* is the only one that exhibits a lesser displacement under a stabbing scenario than under a lateral-shake scenario (Fig. 3B).

Contrary to CB, TB has a lower Young's modulus, and the supportable load per unit of surface area is reduced, but TB has a higher strain index that gives it greater flexibility (16-19). Moreover, TB is better than CB in resisting compression and shear (16-19). Accordingly, TB is 25% as dense, 10% as stiff, and 500% as ductile as CB (16-19). The small proportion of TB in the skull of *S. fatalis* (Fig. 1B, C; Fig. 2), particularly in the posterior region, suggests that its skull was not optimized for resisting sustained, multidirectional and large loads imposed by struggling prey (Fig. 3; Fig. 4). As demonstrated by previous researchers (e.g., 21), *S. fatalis* probably used its powerfully-built forelimbs (10,22) with hypertrophied dew claws (23,24) to

bring down and fully immobilize large prey, and then applied one or two quick, strong killing-bites to the throat (e.g., 1,2, 7, 13, 14, 25, 26).

In contrast, the large amount of TB in the posterior region of the skull of *P. leo* (Fig. 1B,C; Fig. 2) reflects its ability to resist the continuous and repetitive multidirectional loads that might occur during a prolonged 'clamp-and-hold' bite (27,28). Results of the FEA analyses also support the idea that the skulls of lions are better adapted to resist laterally-directed loads than those of the sabertooths. For example, although the skulls of *P. leo* and *H. serum* exhibit a similar level of stress when simulating a lateral-shake scenario (Fig. 3A), the rostrum of *P. leo* is less stressed, above the canines (Fig. 4). Moreover, whereas the skull of *H. serum* experiences slightly lower levels of stress under a stabbing than a lateral-shake scenario (Fig. 3A), the skull of *P. leo* experiences similar levels under both scenarios (Fig. 3A), and the average skull displacement of *P. leo* was much lower under a lateral-shake than a stabbing scenario (Fig. 3B).

The rostrum of *H. serum* exhibits an intermediate amount of CB to those of *S. fatalis* and *P. leo* (Fig. 1B,C; Fig. 2), suggesting that the skull of *H. serum* had an intermediate ability to resist high peaks of locally concentrated and unidirectional forces. This is consistent with the results obtained from biomechanical simulations of bilateral canine stabbing, in which *H. serum* experienced levels of stress in between that observed in *S. fatalis* and the three extant taxa (Fig. 3B; Fig. 4).

On the other hand, as the skull of *H. serum* was also in between both *S. fatalis* and *P. leo* in quantity of TB (Fig. 1B,C), its ability to resist continuous and multidirectional loads also should be intermediate to these two felids. Again, the biomechanical simulations for different prey-killing scenarios support this because the skull of *H. serum* and the lion display similar

overall levels of stress under a lateral-shake scenario, and considerably less than *S. fatalis* (Fig. 3A; Fig. 4).

Our results suggest that *H. serum* deployed a predatory behavior among large felids, not previously supported with quantitative data, that was in between the canine-shear-bite of *S. fatalis* (or dirktooths in general) and the clamp-and-hold technique of lions (or conical tooths). We argue that, like *S. fatalis*, multiple debilitating slashing bites onto the throat of large prey was the most likely predatory behavior for *H. serum*, and probably for all scimitar-tooths, as originally proposed by previous researchers based on qualitative assessments of morphology (e.g., 7). However, unlike *S. fatalis*, our results suggests that the skull of *H. serum* was less stressed by laterally directed loads, which is consistent with a predatory behavior that regularly subjected the skull to such loads as observed in the lion. In support of this, an analysis of upper canine tooth bending strength in carnivorans found that the canines of *H. serum* were more resistant to bending and presumably fracture under mediolaterally directed loads than were the canines of *S. fatalis* (29).

The skull of the scimitar-tooth *H. serum* likely was able to support multidirectional loads incurred by struggling prey more often than was *S. fatalis* because of profound differences in their forelimb morphology. Scimitar-tooths were somewhat cursorial predators in open habitats, whereas dirk-tooths behaved as ambush predators in more closed environments (11). Consequently, the forelimbs of *H. serum* exhibit greater adaptations for speed, while those of *S. fatalis* emphasize adaptations for strength. Relative to *S. fatalis*, *H. serum* had less robust humeri (diameter/length), less broad humeral epicondyles, relatively shorter olecranon processes and a longer radius to humerus ratio, all of which are consistent with a reduced mechanical advantage of the forelimb muscles and less muscle mass (30). In addition, although the claws of *H. serum*

are compressed and curve-shaped, those of digits II-V are reduced and less retractile than those of *S. fatalis*, indicating an adaptive trade-off in the scimitar tooth between having improved traction for pursuing prey and enhanced grappling ability (31). All of these forelimb characteristics suggest less of a reliance on the forelimbs for immobilization of the prey than was the case for *S. fatalis*, and consequently a need for a craniodental skeleton better equipped to support lateral shaking (12). Therefore, our results suggest a gradient of potential functional adaptations in a group of highly specialized predators from the clamp-and-hold technique of the living lion through *H. serum* to the exceedingly specialized canine-shear-bite of *S. fatalis.*

Finally, we note that our analysis of cortical and trabecular bone thickness and distribution in these five carnivorans revealed a previously unrecognized and unique feature of *S. fatalis*. Based on the specimen we scanned, *S. fatalis* had an extremely thick skull as evidenced by the coronal sections as well as our quantitative measures (Fig. 1). The combined thickness of CB and TB, as well as CB alone, in the rostrum far exceeds that of any the other four species. At the temporomandibular joint, *S. fatalis*, *H. serum* and the spotted hyena exhibit greater total bone thickness than the lion, and unlike the lion, much of this thickness is CB rather than TB. Spotted hyenas are capable of cracking large bones with their strong teeth and jaws, and their massive TMJ likely reflects the associated high bite forces (32, 33). Similarly, the extraordinary thickness of the skull of *S. fatalis* in both the rostrum and TMJ suggests an exceptionally large investment in cranial strength in *S. fatalis*, and argues for extremely high bite forces in this cat. Therefore, although both the CB/TB and FE analyses are conducted in a single specimen and might not represent the pattern for the entire species, our results support clear differences in predatory behavior between the scimitar-tooth *H. serum*, and the dirk-tooth *S. fatalis*. In future work, we plan to take advantage of the large sample of *S. fatalis* from the Rancho La Brea tar seeps to

explore intraspecific and ontogenetic variability in skull morphology and strength. In addition, given that previous studies have revealed profound interspecific differences among saber-tooth locomotory and predatory strategies among (34), future studies including more species of living felines and other recognized species of *Smilodon* and *Homotherium*, such as their South American vicars, *Smilodon populator* (35) and *Homotherium venezuelensis* (36), could provide additional insights into the diversity of cranial biomechanics in this group of extinct mammalian predators.

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AUTHOR CONTRIBUTIONS:

B.F., B.V.V. designed research; A. P.-R., B.F., S.L., B.V.V. performed research; B.F., B.V.V., A.P.-R., S.L., wrote the paper.

The authors declare no conflict of interest.

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Figure 1. Amount and distribution of cortical (CB) and trabecular bone (TB). A, *S. fatalis* skull (left); palatal view of thesameskull showing the positions of the ten coronal slices selected for quantifying the area of CB and TB (middle), and representative slice taken at position #8, the temporomandibular joint (right), with CB in yellow and TB in green. B, Bivariate plots of cortical bone area relative to total skull area (RCBT) and trabecular bone area relative to total skull area (RTBT) across the ten coronal slices. C, Bivariate plots of cortical bone area relative to total skull area per slice (RCBS), and trabecular bone area relative to total skull area per slice (RTBS) across the ten coronal slices. The ten slices are: 1, anterior-most point of the canine; 2,

posterior-most point of the canine; 3, anterior-most point of the fourth upper premolar; 4, junction between the metacone and paracone of the upper fourth premolar; 5, posterior-most point of the fourth upper premolar; 6, anterior-most point of the squamosal-jugal suture on the zygomatic arch; 7, posterior-most point of the squamosal-jugal suture on the zygomatic arch; 8, temporomandibular joint (TMJ); 9, anterior-most point of the tympanic bulla; 10, anterior-most point of the occipital condyles. The slices defined at interdental gaps are taken at alveolar margins. All the skulls are scaled isometrically to 200 mm from prosthion to inion.

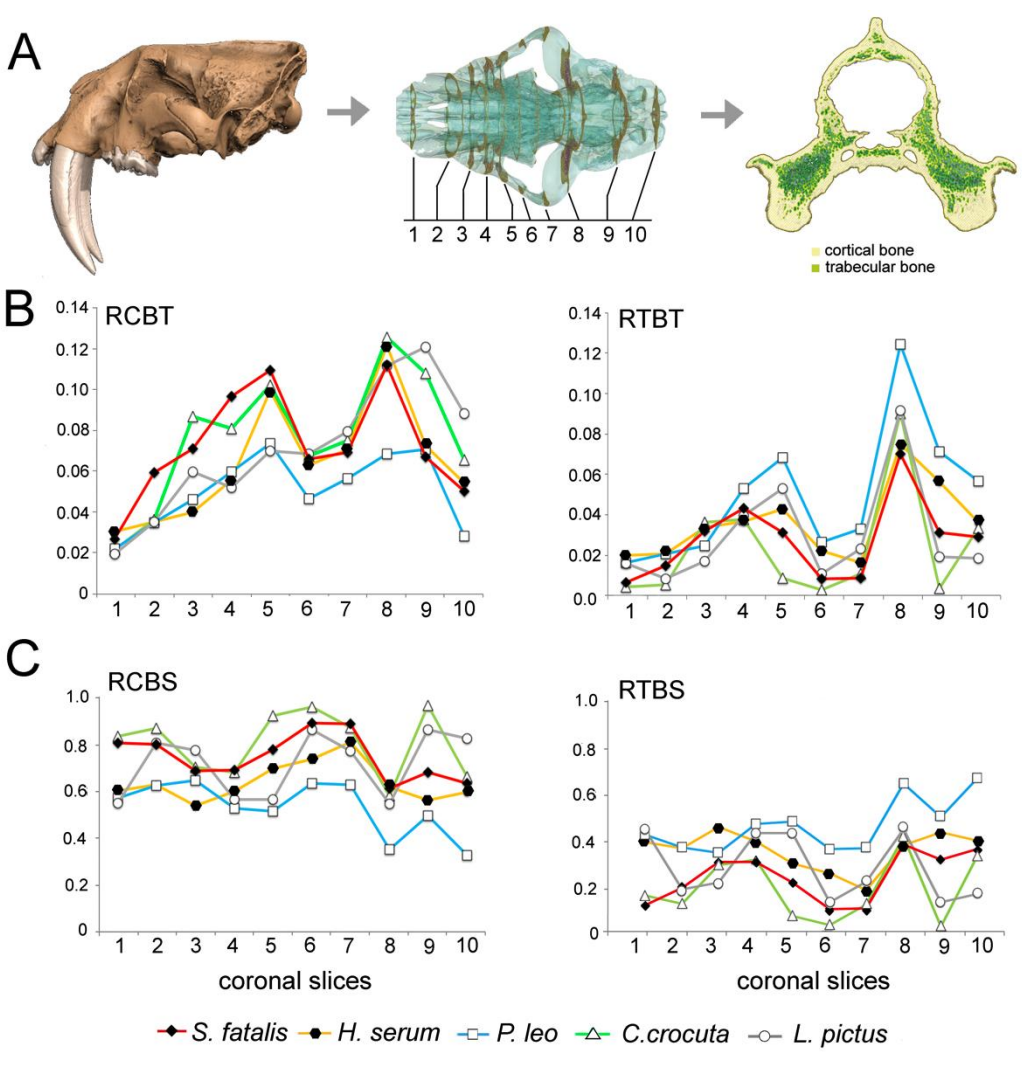


Figure 2. Selected coronal slices in the five large carnivores included in the sample scaled to the same maximum mediolateral width. A, the dirk-toothed *S. fatalis fatalis*; B, the conical-toothed *Panthera leo;* C, the scimitar-toothed, *H. serum serum;* D, the spotted hyaena *Crocuta crocuta*; E, the African wild dog *Lycaon pictus*. Left shows coronal slice # 3, and right shows coronal slice #8. Cortical bone, yellow; trabecular bone, green.

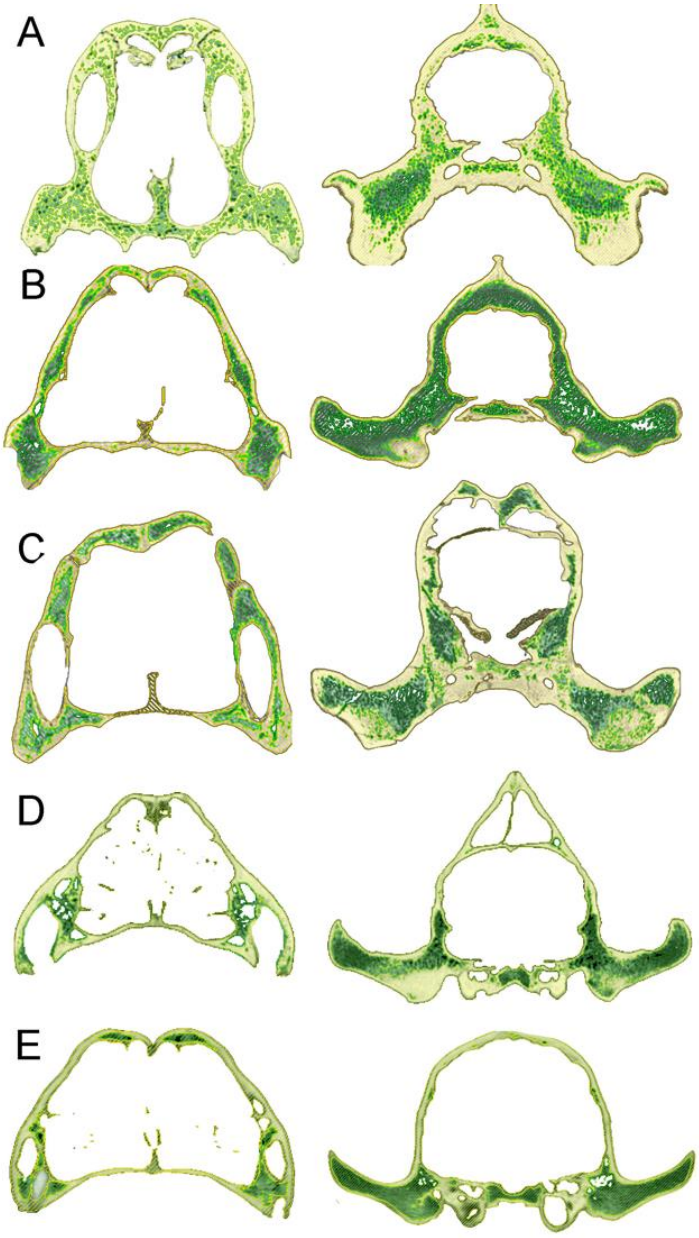


Figure 3. Finite Element Analysis. A, average (per element) von Mises stress (MPa) for each species in a given loading scenario. B, Average nodal displacement (mm) of the models for each species in a given loading scenario as a proxy for model deformation. Data are for models under extrinsic and intrinsic loads during bilateral canine biting.

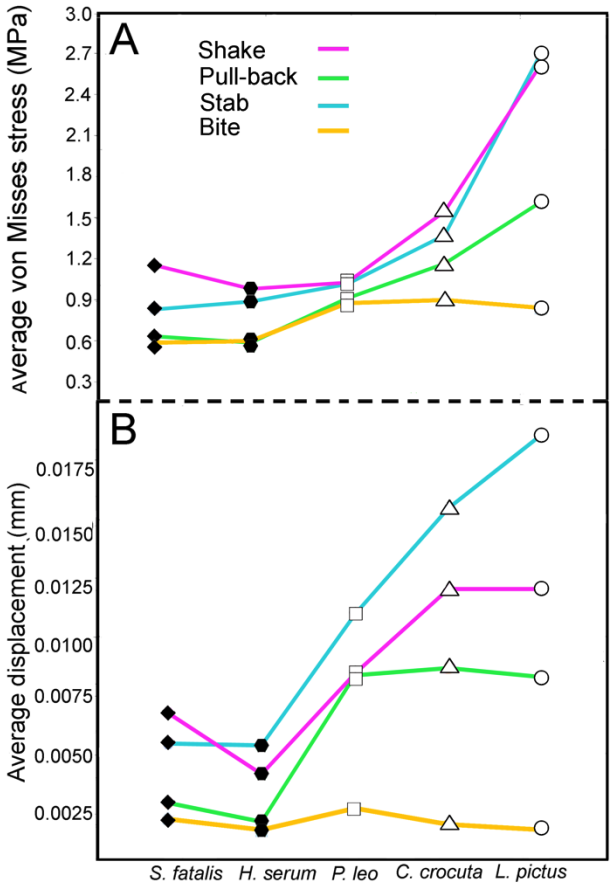
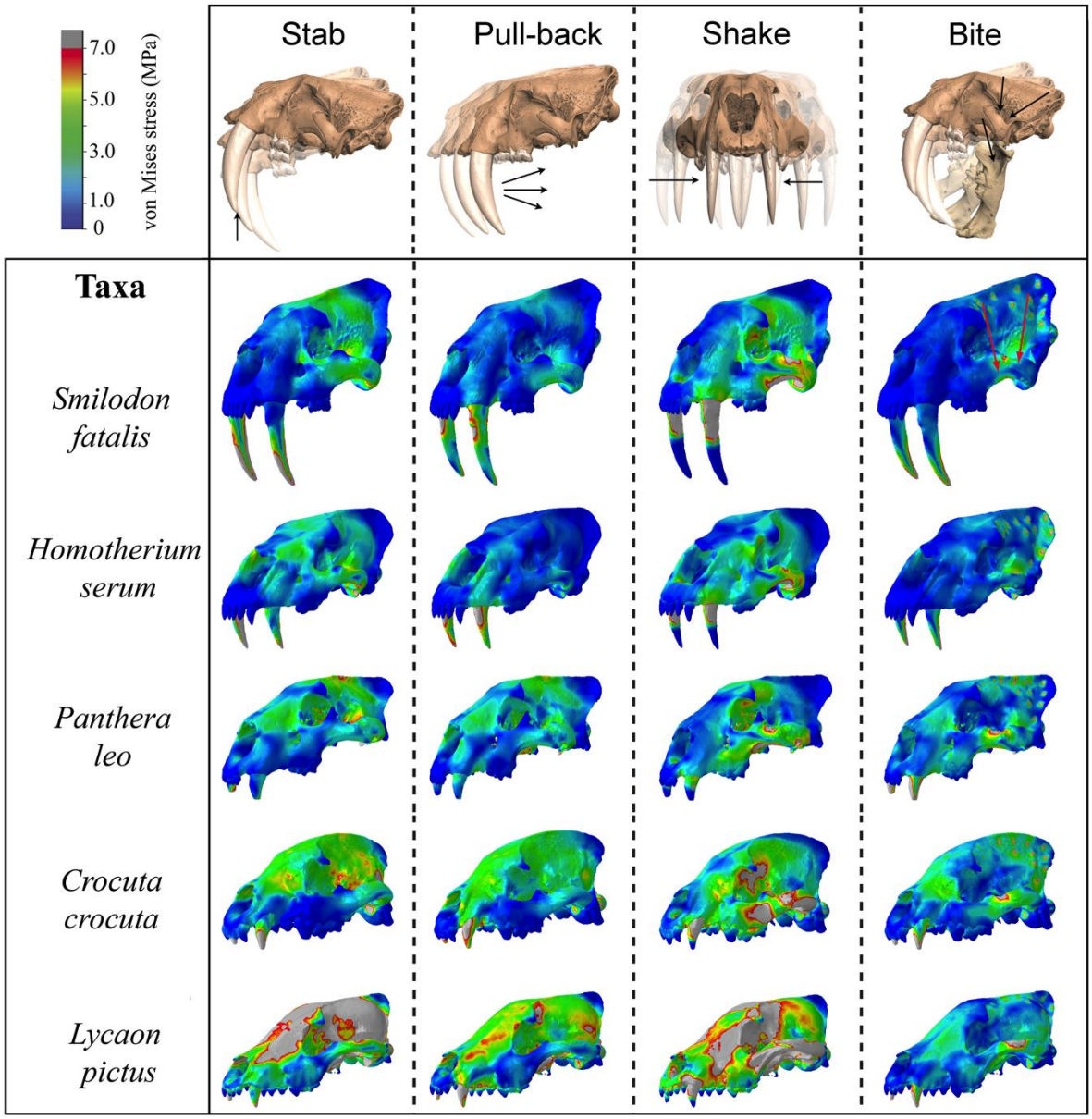


Figure 4. Von Mises stress contour plots obtained from Finite Element Analysis of the crania of both sabertooths and living carnivores under four loading conditions (stabbing, pull-back, lateral shake, and jaw-powered bite) during bilateral canine biting. See also Figure S2 for the simulations of the extrinsic scenarios including the adductor muscles and a fifth intrinsic scenario considering jaw adductors plus neck muscles. In Figure S3 the results under unilateral canine biting are shown.



STAR METHODS

Acquisition of CT scans

The crania of the two extinct felids, *H. serum* and *S. fatalis*, as well as three extant carnivorans, African lion (*Panthera leo*), African wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta*) were CT scanned. All specimens were adults as indicated by fully closed synchondroses and complete tooth eruption. The three extant hypercarnivorous taxa were chosen because researchers have proposed that *H. serum* was more of a carrion-feeder than lion-like active predator (37-39), whereas others have suggested *H. serum* was more similar to pack-hunting canids (12) based on its more gracile limbs and lack of fully retractile claws (31, 40). All specimens were scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility and the scans are available on the UT Digital Morphology website (www.digimorph.org).

Both saber-tooths were scanned at the University of Texas High-Resolution X-ray CT (Facility Archive 1478 for *H. serum* and Facility Archive 0860 for *S. fatalis*). The acquisition properties for *H. serum* were 1024x1024 pixel size for 16-bit TIFF images, 419 kV, 1.8 mA, with voxel size (mm) of 0.1904 (X), 0,1904 (Y), 0.6500(Z) (total slices = 495). The acquisition properties for *S. fatalis* were1024x1024 16-bit TIFF images, 420 kV, 1.8 mA, with voxel size in mm of 0.2143(X), 0.2143 (Y), 0.5000 (Z) (total slices = 629). The specimen of *S. fatalis* (LACMRLP R37376) is from from Rancho La Brea (Los Angeles, California) collected at pit 91, and *H. serum* at (TMM 933-3444) was discovered at Friesenhahn cave (Texas, USA).

We also used extant taxa for comparative purposes, as follows: (i) lion *Panthera leo* (MVZ 117849) of unknown sex as a large pantherine, specimen collected from Skukuza (Kruger

Park, Tranvaal, South Africa), and scanned at the University of Texas High-Resolution X-ray CT (Facility Archive 0320), acquisition properties were 512x512 16-bit TIFF images of the whole skull, 420 kV, 1.8 mA, and the voxel size in mm was 0.5273(X), 0.5273 (Y), 1.0000 (Z) (total slices = 406); (ii) spotted hyena, *Crocuta crocuta* (UCMVZ 184551) as a bone-cracker model, a male collected from Masai Mara National Reserve, Kenya, and scanned at the University of Texas High-Resolution X-ray CT (Facility Archives 0277), acquisition properties were 512x512 16-bits and converted 8 bits TIFF images, 420 kV, 1.8 mA, with a voxel size in mm of 0.3242(X), 0.3242 (Y), 0.5000 (Z) (total slices = 528); (iii) African wild dog, *Lycaon pictus* (USNM 368441), as a pack-hunter hypercarnivore, a male collected in Bechuanaland, Makeleapudi, and scanned at the University of Texas High-Resolution X-ray CT, acquisition properties are 1024x1024 16-bit TIFF images, 419 kV, 1.8 mA, (total slices = 523).

Museum abbreviations are as follows: Museum of Vertebrate Zoology at Berkley (MVZ); University of California Museum of Vertebrate Zoology (UCMVZ); United States National Museum of Natural History at Washington DC (USNM); Los Angeles County Museum, Rancho La Brea (LCMRLP); and Texas Memorial Museum (TMM).

Quantification and distribution of CB vs TB

The dataset for each of the scanned skulls consisted of a stack of 16-bit TIFF images, all of which were adjusted for brightness and contrast to eliminate background noise using ImageJ (41). All images were normalized at 0.5% and the histogram was adjusted to the range of interest (ROI) using the semiautomatic brightness/contrast tool of ImageJ (41). Subsequently, all images were converted to 8 bits and exported to 3D-slicer (42) to generate the 3D models of each skull. To select the total amount of bone, and to avoid possible overestimations due to Compton and

500 photoelectric effects (43), we used a range of gray values of 70-255 and created a slice with all
501 the bone. Subsequently, we manually added to this layer the relevant low density structures
502 (e.g.,TB) using a range of grey values between 40-70. We decided to use this range of gray
503 values in order to reach a compromise between capturing all the visible and very small
504 trabeculae but avoiding: (i) the oversegmentation of this relevant bony structures; and (ii) the
505 selection of other undesirable artifacts that are a result of Compton and Photoelectric effects; and
506 (iii) the selection of non-relevant small particles. This resulted in a layer with all the information
507 selected between 40-255 but excluding the background noise due to Compton and photoelectric
508 effects (40). Using this layer, we then segmented CB and TB, respectively, as those structures
509 with gray values ranging from approximately 185-255 for CB and 40-185 for TB.

510 For each 3D model of a skull, we selected ten 1-mm thick coronal slices at key points that
511 were homologous in all the species (Fig. 1A). CB and TB were segmented in each of these ten
512 slices excluding petrosal bones and teeth, based on the values of thresholding specified above
513 using 3D-slicer (42). Thus, for each slice, we generated three independent layers, first for all
514 bone, second for the cortical bone (yellow), and third for trabecular bone (green). Each layer was
515 saved as a stack of TIFF images to be imported into imageJ (41). All the CTs were processed
516 using a bicubic interpolation (44) in order to convert anisotropic voxels (in Z direction) to
517 isotropic-sized voxels (the same X,Y,Z values). Afterwards, the stacks for each skull were scaled
518 to a total length of 200 mm from prosthion to inion isometrically and oriented to the same plane
519 in imageJ (41). After converting the stacks into binary, we used the plug-in of ImageJ, 'analysing
520 particles' (45) to obtain the total surface area of CB and TB (including intratrabeuclar spaces),
521 respectively, in each slice.

For both fossil specimens, we used semi-automatic thresholding to select the grey values corresponding to the matrix (non-bony) material prior to selecting the ten coronal slices. The values for this thresholding varies across slices and depends upon the nature of matrix infilling. After selecting the slices, we manually segmented them to remove matrix still present inside the trabecular bone of the skull. Damaged trabeculae during the fossilization process in the skulls of both saber-tooths were not observed. Furthermore, the inclusion of the intra-trabecular spaces in the calculation of TB avoids possible (but not visible), very small damaged trabeculae. Therefore, there is not an appreciable potential impact of diagenesis on accuracy of measures of CB and TB in both fossil skulls. Mirroring to compensate for missing structures was done in only a few instances. The exceptions were a few struts of the frontal sinus in *S. fatalis*, and a small portion of the palate of *H. serum*, that were restored by mirroring the preserved counterparts. Restored parts of the skull had a minimum potential impact on the calculation of CB and TB across the skulls.

Both three-dimensional surface models were imported into MeshLab (46) in PLY or STL formats (Polygon File Format or the Stanford Triangle Format) for mesh repair, cleaning and simplification.

Values of CB and TB were scaled by: i) the sum of CB and TB of the ten slices (i.e., total area of bone quantified across the skulls); and (ii) the total area of CB plus TB of each slice. Both approaches are complementary in the following way: the first approach shows not only the distribution of CB and TB across the skull, but also the heterogeneous distribution of bone across slices; with the second approach the contribution of CB or TB in each slice is shown without regard to the heterogeneous distribution of bone across the skull.

The proportion of cortical to trabecular bone tends to decrease with increasing size among felids (47). Therefore, larger species have less cortical bone and more trabecular bone. However, this allometric effect does not affect our results, given that we analyzed the distribution of cortical and trabecular bone across ten functional key points of the skull, rather than just the total amounts of CB and TB. Moreover, both *H. serum* (skull length=326mm) and *S. fatalis* (skull length=322mm) have similar skull sizes to the living lion (skull length=408 mm), and yet they vary greatly in CB/TB across their skulls.

Finite Element Analysis

The 3D models of all skulls were imported into Hypermesh 11 (Altair Engineering) for the generation of solid meshes (consisting of approximately 1,000,000 tetrahedral elements per model) and the setting of boundary conditions. All skull models were scaled to the same surface area to allow comparisons of form and function independent of size (48). Material properties for bone and teeth were assigned in Hypermesh based on published values in comparable studies on mammalian carnivores (bone: E = 13.7 (cortical) & 9.29 (trabecular) GPa, υ = 0.30, teeth: E = 38.6.0 GPa, υ = 0.4) (46-48). All materials were treated as isotropic and homogenous.

Five different functional scenarios were tested. Three extrinsic scenarios: (i) stabbing prey using both canine teeth with a dorsally directed extrinsic force of 500 N applied to the tips of both canines (stab in Figure 4); (ii) pulling the head posteriorly with both canine teeth embedded in the prey and an extrinsic force of 500 N distributed over the posterior edge of the canines (pull-back in Figure 4); and (iii) shaking the head laterally while holding prey with both canine teeth and an extrinsic force of 500 N applied to the left side of both canines (shake in Fig. 4). The extrinsic force (total of 1000 N for each scenario) was selected based on reported

magnitudes for neck-muscle-driven bite force (21). For the extrinsic feeding scenarios, constraints were placed on the articular surface of the squamosal (five nodes on each side), as well as the occipital condyle (ten nodes) to restrain the model from movement in x-, y- and z-directions to simulate the fixed contact of the skull with other skeletal elements (i.e. mandible and vertebral column).

A further intrinsic scenario (iv) was analyzed that simulated a jaw adductor muscle-driven biting assuming a gape angle of 25 degrees following (50). For this purpose, jaw adductor muscle forces were estimated using the attachment area of each muscle (Fig. S1), as a proxy for physiological cross-section area and multiplying it by an isometric muscle stress value of 0.3 N/ mm2 (51). This approach likely underestimates the total muscle force and resulting bite forces due to simplifying a three-dimensional muscle volume to a two-dimensional surface area. However, given the lack of accurate data on muscle volume and architecture for fossil carnivorans, this approach provides a repeatable method for estimating muscle force across taxa and permits functional comparisons. Models in this scenario were constrained at the tip of the canine tooth (one node on each side) to restrain the model from movement in x- and y- direction (i.e. medial/lateral and anterior/posterior), but not in z-direction to simulate some penetration of the canines into the prey during biting.

In addition, a combined functional scenario (v) was tested simulating the simultaneous action of the jaw closing muscles and the neck musculature. For this, an extrinsic force of 500 N on each side was added to the aforementioned intrinsic scenario and distributed over the back of the skull and the mastoid region. The magnitude of the load was selected to be the same as with the extrinsic scenarios, based on reported magnitudes for neck-muscle-driven bite force (21). The directions of the muscle forces were determined by creating vectors between the muscle origin

and insertion sites, using corresponding mandibular models or simplified templates, where this was not possible (i.e. postcranial muscles).

Further to these scenarios and to simulate the combined action of the jaw adductor muscles and external forces (i.e., stab, pull-back, lateral shake) experienced during movement of the prey and/or the head, all extrinsic scenarios were further analyzed with adductor loads active. Cranial (adductor) and postcranial muscles were considered separately in the functional analyses to evaluate their contribution to the stress behavior. However, combined loads of the cranial and postcranial musculature were tested as well (see supplementary Figure S2). Results show that the combined muscle forces have very little effect on the stress distribution. The simulations were performed during bilateral (Figs. 3,4) and unilateral (Fig. S3) canine biting. All models were subsequently imported into Abaqus 6.141 (Simulia) for analysis and post-processing. Biomechanical performance for the FE models was assessed via contour plots of Von Mises stress distribution, reaction forces, and average Von Mises stress and displacement values per element with the top 1% of values removed to avoid the influence of individual stress singularities at constrained or loaded nodes. The jaw-joint reaction forces quantify the internal force generated at node constraints (TMJ), the Von Mises (VM) stress distributions represent a function that measures how stress distorts a material, and the displacement values per element measure how the elements of the mesh are displaced when a given force is applied (52).